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Planktonic Bloom-Forming *Nodularia* in the Saline Lake Alchichica, Mexico

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ABSTRACT

Lake Alchichica displays a characteristic cyanobacterial bloom associated with the onset of the stratification period (April-June). It mostly consists of the nitrogen-fixing cyanobacterium *Nodularia spumigena*. Filaments of *Nodularia* were straight, usually with an evident colorless, transparent sheath, with gas vesicles and without akinetes. The bloom developed in waters with a conductivity (K_{25}) of 13.47 to 14.14 mS cm^{-1} (total dissolved solids around 8.7-9.2 g l^{-1}). Water column temperature was between 14.1 and 21.2ºC, the pH fluctuated between 8.8 and 10.0, and dissolved oxygen between 0 and 9.3 mg l^{-1}. The annual mean concentration of N-NO_3 was highest in 2001 (1.0 μM) and lowest in 2000 (0.4 μM). For P-PO_4 the highest mean value was measured in 2002 (0.8 μM) with the lowest value in 1999 (0.4 μM). We monitored the bloom throughout four annual cycles (1999–2002). The intensity of growth and extent of the presence of *N. spumigena* in Lake Alchichica differed among the years. The highest mean density was observed in 2001 (1.36×10^{11} cells m^{-2}), while the lowest values were found in 2000 (1.54×10^{10} cells m^{-2}). Mean values for 1999 and 2002 were 2.08×10^{10} cells m^{-2} and 2.29×10^{10} cells m^{-2}, respectively. *N. spumigena* is found regularly during a three-month period, but peak concentrations are reached only for a few weeks. In calm weather and following solar heating, the *Nodularia* filaments floated to the lake surface, causing the bloom to become apparent. The intensity of growth was correlated with the annual concentration of N-NO_3, indicating the role of the cyanobacteria as a source of new nitrogen to the lake.

INTRODUCTION

Blooms of the nitrogen fixing cyanobacteria *Nodularia spumigena* Mertens have been reported around the world. They are common in the Baltic Sea (Komárek et al. 1993; Musial & Pliński 2003), in the North Sea and in brackish Elesmere (Nehring 1993), and in numerous estuaries and bays along the southern and western coast of Australia and New Zealand (Musial & Pliński 2003). Blooms have also been reported for North and South America: in Great Salt Lake (Felix & Rushforth 1979), in brackish coastal waters and inland lakes and ponds in British Columbia, Canada (Nordin & Stein 1980), in Pyramid and Walker lakes in Nevada, USA (Cooper & Koch 1984; Galat et al. 1990), in Brazil (Werner & Rosa 1992), and in a shallow coastal lagoon in Uruguay (Pérez et al. 1999). Cyanobacterial blooms cannot be explained simply by the biological features of the species. The phenomenon is induced by many environmental factors which play an important limiting and controlling role. Among these factors Musial & Pliński (2003) and Mazur Marzec et al. (2006) mention phosphorus and nitrogen supply, as well as the N:P ratio, surface water temperature, light availability, calm weather, thermal stratification, and salinity.

The occurrence of *Nodularia* blooms in the hyposaline Lake Alchichica, Mexico, has previously been observed for several years, associated to the onset of the stratification period (April-June). Arredondo Figueroa et al. (1983) and Alcocer et al. (2000) reported *Nodularia* blooms in Lake Alchichica in the 1980s and 1990s (Oliva et al. 2001). Similar *Nodularia* blooms also develop in Lake Atexcac (Macek et al. 1994; Tavera & Komárek 1996), a nearby lake that shares ecological and morphological features with Lake Alchichica. According to personal observations and recorded data, the intensity and extent of the presence of *Nodularia* appeared to differ among the years. In the present paper we discuss the spatial and temporal dynamics of *Nodularia* during four annual cycles (1999–2002) in Lake Alchichica. The main physical and chemical variables are also presented.

AREA OF STUDY

Lake Alchichica is a deep crater lake located in the state of Puebla (19° 24’ N and 97° 24’ W), Central Mexico (Figure 1). The annual air temperature in the area fluctuates between 5.5 and 30°C with a mean value of 14.4°C. Having an arid climate, with annual precipitation of less than 500 mm and an annual evaporation rate of 1590 mm (Adame et al. 2008), this high altitude plateau (≥ 2300 m above sea level) named Los Llanos de San Juan can be described as a ‘‘cool desert’’.

Figure 1–Lake Alchichica, Puebla, Mexico.

The surface area of Lake Alchichica is 2.3 km^2 (diameter 1733 m). It has a volume of 9.42 x 10^7 m^3, a maximum depth of 62 m and a mean depth of 40.9 m (Filonov et al. 2006). The lake is warm monomictic (Alcocer et al. 2000). Mixing takes place from the end of December or the beginning of January until the onset of the stratification period by the end of April or beginning of May. A well-developed thermocline is present from June-July until October-November. After November, the thermocline deepens and becomes weaker until its breakup in late December or early January. Besides the spring bloom of *Nodularia*, Lake Alchichica displays a winter diatom bloom coinciding with the mixing period.

Lake Alchichica is a unique hyposaline (8.5 ± 0.2 g l^{-1}; Na-Mg and Cl-HCO_3 dominated) and alkaline (pH = 9.0 ± 0.1) aquatic system (Vilaclara et al. 1993), characterized by several endemic species and unique features such as tufa towers. The endemic biota described include the atherinid fish *Poblana alchichica* (De Buen 1945), the ambystomatid salamander *Ambystoma taylori* (Brandon et al. 1981), the isopod *Caecidotea williamsi* (Escobar Briones & Alcocer 2002), and more recently the centric diatom *Cyclotella alchichicana* (Oliva et al. 2006).

MATERIALS AND METHODS

Sampling took place monthly at the central and deepest part of the lake during 1999–2002. Mid-day *in situ* profiles of temperature, dissolved oxygen, pH and conductivity (K_{25}) were obtained with a calibrated Hydrolab® DS3/SVR3 multiparameter water-quality data logger and logging system (discrete readings every meter). Ten water samples (depth 2, 5, 10, 15, 20, 25, 30, 40, 50 and 60 m) for phytoplankton analysis were obtained with a 5 l Niskin-type water sampler. Two 500 ml sub-samples from each sampling depth were fixed, one with 4% formaldehyde and the other with Lugol´s solution (1%). Cyanobacteria were counted in a 50 ml settling chamber with a Zeiss inverted microscope following the Utermöhl method (APHA 1985; Wetzel & Likens 2000). The length and width of *Nodularia* filaments, vegetative cells and heterocytes were measured with an eyepiece micrometer. A hundred independent measurements were made for each cell type. The length of the filament measured was then divided by the length of the cells. This procedure was repeated several times with different filaments and an arithmetic mean was established (APHA et al. 1985). Integrated values for the water column were obtained using linear interpolation, and the total abundance of *Nodularia* was expressed per unit area (cells m^{-2}) rather than per volume units since the phytoplankton rarely homogeneously distributed (Payne 1986).

Another set of samples was collected from the same depths for nutrient analyses. These samples were maintained in the cold (4ºC) and in darkness until analysis. Nitrate and phosphate (soluble reactive phosphorus) analysis followed standard methods (Strickland & Parsons 1972), adapted by Kirkwood (1994) for a Skalar Sanplus segmented flow autoanalyzer system.

Figure 2–*Nodularia spumigena* straight filaments showing heterocytes. Scale bar = 10 µm.

RESULTS

Nodularia in Lake Alchichica showed the following morphological traits: filaments were straight and composed of discoid vegetative cells 7-12 µm wide (mean 8.1 µm) and 2.7-3.6 µm long (mean 3.4 µm), with gas vesicles. Filaments usually had an evident colorless, transparent sheath. Heterocytes were 6.1-10.9 µm wide (mean 10 µm) and 4.5-6.4 µm long (mean 5.6 µm). They were present after every 12 to 16 vegetative cells (mean 13 cells) (Figure 2). Akinetes were never observed. According to its morphological features and comparison with other descriptions (Nordin & Stein 1980; Pérez et al. 1999), our species corresponds to *Nodularia spumigena*. It is important to point out the existence of several morphotypes associated with local environmental conditions (Musial & Plinski 2003; Mazur Marzec et al. 2006). A definitive identification of *N. spumigena* requires studies that include ultrastructural and molecular biology considerations (Albertano et al. 1996; Hayes & Barker 1997). Such studies are still pending on the *Nodularia* of Lake Alchichica.

The K_{25} of Lake Alchichica varied from 13.47 to 14.14 mS cm^{-1} (around 8.7-9.2 g l^{-1}) during the study period, confirming its hyposaline nature. The water column temperature ranged between 14.1 and 21.2ºC, the pH fluctuated between 8.8 and 10.0, and dissolved oxygen between 0 and 9.3 mg l^{-1} during the four years. Anoxic conditions were present in the deeper layers during the stratification period. Table 1 presents the $N\text{-}NO_3$ annual mean concentration, being highest in 2001 (1.0 µM) and lowest in 2000 (0.4 µM). For $P\text{-}PO_4$ the highest mean value was measured in 2002 (0.8 µM) and the lowest value in 1999 (0.4 µM). *N. spumigena* blooms in Lake Alchichica became apparent when calm weather and solar heating were present and filaments floated to the lake surface (Figure 3).

Table 1–Annual range and mean concentration values of $N\text{-}NO_3^-$ and $P\text{-}PO_4^{3-}$ in Lake Alchichica, 1999–2002.

Year	1999	2000	2001	2002
$N\text{-}NO_3$ (µM) Range Annual mean value	0.04-4.2 0.7	0.01-1.9 0.4	0.06-5.2 1.0	0.01-4.8 0.5
$P\text{-}PO_4$ (µM) Range Annual mean value	0.01-3.2 0.4	0.05-3.6 0.6	0.2-4.0 0.7	0.12-4.2 0.8

N. spumigena was the dominant species of the phytoplankton assemblage within the cyanobacteria bloom in all four years. The intensity of growth and extent of the presence of *N. spumigena* in Lake Alchichica differed among years (Figure 4). In 2001 the highest mean integrated column density was found (1.36 x 10^{11} cells m^{-2}), while 2000 had the lowest values (1.54 x 10^{10} cells m^{-2}). Mean values for 1999 and 2002 were 2.02 x 10^{10} and 2.29 x 10^{10} cells m^{-2}, respectively. The maximum single-depth density was 1.05 x 10^5 cells ml^{-1} (surface water, May 30th 2001). The species was found along a four-month period (April to July) with peak concentrations lasting a few weeks only. In 1999 *Nodularia* was present for longer (7 months), including the mixing phase of the lake, when a diatom bloom is usually present. In 2002 the presence of *Nodularia* began in May and lasted until September.

We tried to establish a criterion to assess the presence of a bloom. The average value (4.64 x 10^{10} cells m^{-2}), using all data when *Nodularia* was present, was used as a criterion for bloom conditions. Values above this average were considered as bloom. According to this criterion, blooms were present in June 1999, in May and June 2001 and in June 2002, but not in 2000 (Figure 4).

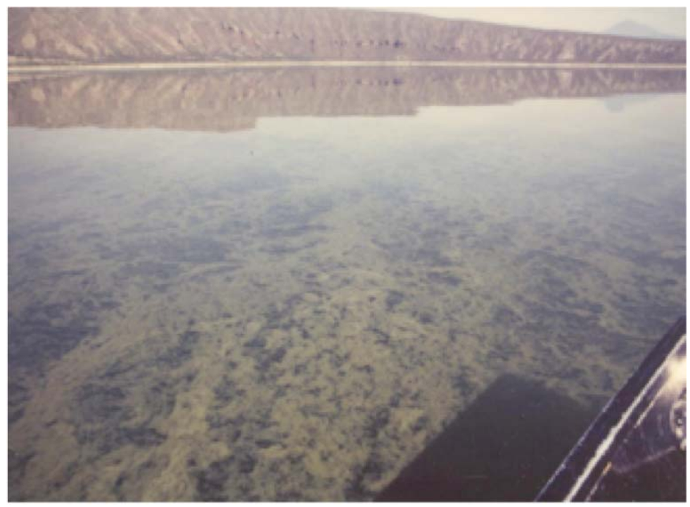

Figure 3–Accumulation of filaments during the *N. spumigena* bloom.

DISCUSSION

N. spumigena trichomes exist in different forms. In the Baltic Sea, *N. spumigena* displays three different forms: straight, coiled and spirally coiled (Komárek et al. 1993). In contrast, the population from Lake Alchichica is always straight, similar to other North and South American *N. spumigena* populations such as those in brackish coastal waters and inland lakes of British Columbia, Canada (Nordin & Stein 1980), in Walker and Pyramid Lakes, Nevada (Cooper & Koch 1984; Galat et al. 1990), in Great Salt Lake, Utah (Stephens 1990), in Rio Grande do Sul, Brasil (Werner & Rosa 1992), and in Castillos Lagoon, Uruguay (Pérez et al. 1999).

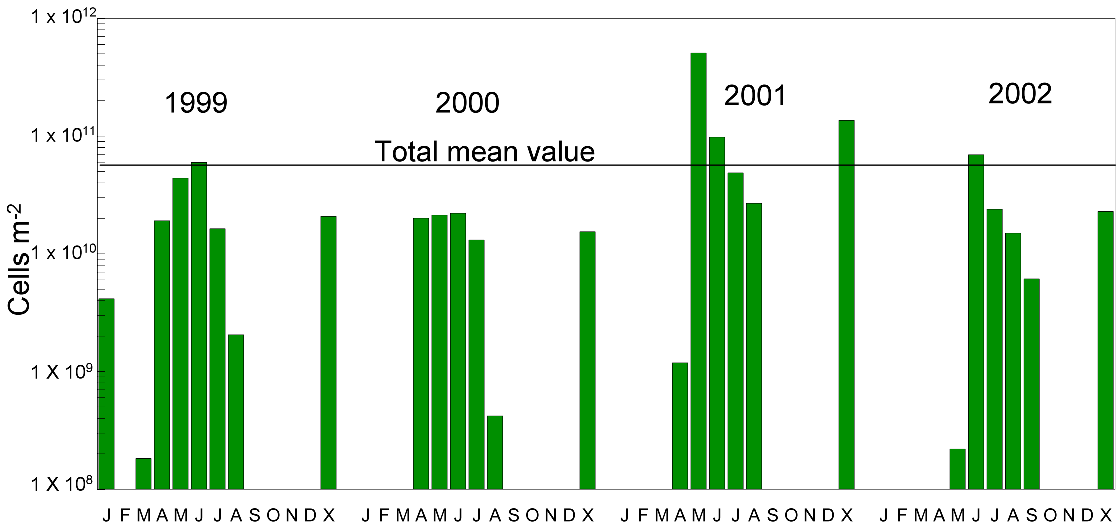

Figure 4–Interannual variation of densities of *N. spumigena* integrated over the water column in Lake Alchichica, 1999–2002. X = annual mean value.

Analyses of the 16S rRNA nucleotide sequence by Lehtimäki et al. (2000) indicated a great similarity between genotypes of the genus *Nodularia*. Although this gene is conserved and cannot therefore be used as a tool in the taxonomic identification of *Nodularia* species, there was a notable difference in the gene sequence between toxic and non-toxic *Nodularia* species. Laamanen et al. (2001) and Lyra et al. (2005) concluded that in the Baltic Sea there are only three species of *Nodularia*: one planktonic and toxin producing, with gas vesicles, which fits the description of *N. spumigena*, and two benthic, non-nodularin-producing species, without gas vesicles, namely *N. sphaerocarpa* and *N. harveyana*. The Lake Alchichica population is planktonic and contains gas vesicles; however, there is currently no evidence that this species produces toxins like *N. spumigena* from the Baltic Sea. Levels of nodularin will be tested in the future.

Some blooms of *N. spumigena* have been related to eutrophication processes (Hallegraeff 1993), although Pérez et al. (1999) mentioned that cyanobacterial blooms may be natural events and are not necessarily a consequence of eutrophication. The presence of *Nodularia* blooms in Lake Alchichica agrees with the last point of view, since this is an oligotrophic lake.

There are several factors that influence the growth and the extent of development of *N. spumigena* blooms in water bodies, the most important being salinity, temperature and light availability (Hamel & Huber 1985). *N. spumigena* requires salt concentrations between 5 and 20 g l^{-1} to be present. Maximum growth is achieved at salt concentrations from 5 to 10 g l^{-1}, especially when sulfate and sodium are dominant (Nordin & Stein 1980). Salinity in Lake Alchichica is in the range between 8.5 and 9 g l^{-1}, and its water contains high concentrations of sulfate and sodium (Vilaclara et al. 1993); both characteristics appear adequate for *Nodularia* growth requirements. High water temperatures promote *Nodularia* blooms in saline and brackish waters (Lehtimäki 2000). According to Nordin & Stein (1980), best growth is achieved between 25 and 30ºC. The highest temperatures in Lake Alchichica surface waters range between 18 and 21ºC, below the optimum range. Nordin & Stein (1980) indicate pH values above 10.0 to be the best for *Nodularia* growth; Lake Alchichica's pH is close to this optimum value. Light availability is also an important factor for *Nodularia* to develop. From April to June, while *Nodularia* usually reaches its maximum densities, solar radiation showed the highest values (up to 1200 W m^{-2}). In addition, Lake Alchichica is a transparent lake with a photic zone depth between 13 and 38 m (Adame et al. 2008). A short period that combines high solar radiation and calm weather appears to favor accumulation of the cyanobacteria at the lake surface, making presence of *Nodularia* clearly visible. Cloudy and windy weather prevents the cyanobacteria from accumulating at the water surface (Lehtimäki 2000).

Nitrogen and phosphorus concentrations and the N/P ratio are also important factors. Scarcity of nitrogen promotes development of nitrogen fixing cyanobacteria such as *Nodularia* (Paerl 1996). Due to its nitrogen-fixation capacity, *Nodularia* has a competitive advantage when N is the limiting nutrient for phytoplankton growth. The low dissolved inorganic nitrogen: soluble reactive phosphorus ratios (1.2-12.9, mean 6.71) found in Lake Alchichica by Adame et al. (2008) clearly suggests nitrogen to be the nutrient that most likely limits phytoplankton growth.

Several investigations have shown that low inorganic N concentrations precede blooms of nitrogen fixing cyanobacteria, while a decrease in phosphate levels has been observed in conjunction with blooms of *N. spumigena* (Cooper & Koch 1984). High concentrations of ammonium, nitrate, and organic nutrients are released into the water during cyanobacterial decay (Engström-Öst et al. 2002). In Lake Alchichica, the highest N-NO_3 concentrations were coupled with the highest *N. spumigena* growth (2001), and the lowest NO_{3-} concentrations with the lowest densities (2000).

It is difficult to compare *N. spumigena* densities from different lakes, since values are given in different units (filaments ml^{-1} or cells ml^{-1}) and are not calculated on an area basis (i.e., cells m^{-2}). Maximum densities are commonly found at or close to the surface (around a depth of one meter) but in our case *N. spumigena* was usually found in the upper 10 m and some times throughout the entire water column (60 m). Lake Alchichica peak concentrations (1.05 x 10^5 cells ml^{-1}) are much higher than those reported from Walker Lake (3.4 x 10^4 cells ml^{-1}) by Cooper & Koch (1984) and from Pyramid Lake (3200 cells ml^{-1}) by Galat et al. (1981). Felix & Rushforth (1979) mentioned maximum densities of one thousand filaments per milliliter in Great Salt Lake. According to Paerl (1988), densities above 10^4 to 10^6 cells per milliliter of a single species could indicate the presence of a bloom. Following this criterion, *N. spumigena* bloomed in Lake Alchichica only in May 2001 with values between 4.1 x 10^4 and 1.1 x 10^5 cells ml^{-1} were observed in the top five meters. The rest of the time, densities were always below 10^4 cells per milliliter.

N. spumigena appears to be an important source of nitrogen for Lake Alchichica. Falcón et al. (2002) measured acetylene reduction rates of up to 78.9 ± 12.1 µmol m^{-2} h^{-1} during the 2001 bloom. As mentioned previously, N-NO_3 concentrations after the 2001 bloom were the highest of the whole period, while the minimum N-NO_3 concentrations coincided with the lowest *N. spumigena* densities in 2000. This observation provides indirect support for the relevance of this species as a source of new nitrogen to the lake, as has been observed in other saline lakes (Hamilton Galat & Galat 1983). Nitrogen appears to be incorporated in the lake throughout the *Nodularia* bloom, and the nitrogen is released as ammonia during its mineralization by heterotrophic bacteria. Other modes of incorporation such as foraging are considered to be of low importance due to the fact that this species is poorly used as food for zooplankton (Hamilton Galat & Galat 1983).

In conclusion, while the water temperature is below its optimum range, the salinity, pH and light conditions explain the presence of *N. spumigena* in Lake Alchichica. The concentrations of nitrogen and phosphorus and their ratio determine the peak growth of *N. spumigena* during the onset of the early stratification. The intensity of *N. spumigena* growth appears to be related with the post-peak N-NO_3 concentration, indicating the role of the cyanobacteria as a source of new nitrogen to the lake through N_2 fixation and subsequent mineralization.

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