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Quantified distribution of diatoms during the stratified period of Boadella reservoir

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Abstract

We collected data and samples, from June to November of 1999 and 2000, to *in situ* quantify the abundance of phytoplankton in Boadella reservoir. Samples were taken at different stations along the reservoir and diatoms were persistent in the epilimnion and were the main phytoplankton component, with a peak of abundance up to $\sim 5\ 10^5$ particles ml^{-1}. The diatom growth during the initiation of the summer bloom was high in the reservoir upstream concurrent with maximum Chlorophyll *a* concentrations. A delay in the onset of the diatom bloom, together with lower values of the volume concentration, was found in 1999 compared to the results in 2000 and was attributed to the different stratification of the reservoir as a result of meteorological conditions. The diatom population sank from the epilimnion by sedimentation and formed aggregates that accumulated at the bottom of the epilimnion. Sedimentation to the hypolimnion occurred at the end of the bloom, where peaks of Chlorophyll *a* were found.

Introduction

Recently, limnologists have begun to study the importance of spatial organization on ecological processes within communities and the environment. Especially in reservoirs, longitudinal changes and hydrodynamics play a major role in determining phytoplankton (and zooplankton) dynamics and changes in water quality (Straškraba et al., 1993; Hamilton & Schladow, 1997; Berman & Shteinman, 1998). Generally, studies of phytoplankton distribution in water bodies reveal complex interactions with the water climate, which in turn depends on variables with a two or three-dimensional signal (Reynolds, 1992).

Several studies (Zohary et al., 1998; Armengol et al., 1999) demonstrate the importance of interannual and short-term variabilities in meteorological conditions on phytoplankton distribution in lakes. Interannual meteorological changes result in different stratification patterns of the water column and eventual delays of this stratification that postpone the timing of bloom initiation, change the growth rate or change the maximum biomass attained by the phytoplankton population (Zohary et al., 1998).

Spatial and temporal changes in phytoplankton distribution are also regulated by physical factors such as light (Garnier et al., 1995; Moline, 1998; Dussenberry et al., 1999), mixing processes and temperature values of the water column (Gervais et al., 1997; Zohary et al., 1998; Berman & Shteinman, 1998; Goericke & Welschmeyer, 1998; Signorini et al., 1999). Further, phytoplankton growth rates may vary at different locations of a lake or a river depending on the level of turbulence in the region (Köhler, 1997).

Biological factors such as grazing (Tittel et al., 1998) or bacterial colonization (Grossart & Ploug, 2000), sinking (Grossart & Simon, 1993; Kiørboe et al., 1994, 1998) or coagulation processes (Jackson, 1990; Logan & Wilkinson, 1990) are crucial for phytoplankton communities. Aggregation of phytoplankton cells result in larger aggregates with higher settling velocities (Alldredge & Gotschalk, 1988; Jackson & Lochmann, 1992) that eventually accumulate at density interfaces of the water column (MacIntyre et al., 1995). Such flocs, observed after phytoplankton blooms and known as lake snow, can explain the frequent mass sedimentation following these blooms (Kiørboe et al., 1994). Further, fast sinking aggregates determined the fate of fine particles suspended in the water column, increasing the vertical flux of carbon from the water surface to the bottom of the lake (Hill & Nowell, 1990). Factors such as nutrient availability are important to determine phytoplankton distribution (Cottingham et al., 1998; Vrede et al., 1999). The size distribution of the phytoplankton and, in particular the classification between picoplankton and larger cells are fundamental aspect of these organisms. Ning et al. (2000) demonstrated that nutrients mainly affect communities of large phytoplankton (especially fast-growing diatoms) while small phytoplankton (picoplankton) are controlled by high temperature values of the water column instead of high nutrient concentrations. Sediment resuspension might also affect the phytoplankton distribution in lakes providing a potential source of phosphorous for phytoplankton (Olgivie & Mitchell, 1998). Vertical fluxes of nutrients in the water column were coincident with intense mixing events initiated by high winds (MacIntyre et al., 1999).

We report here the spatio-temporal particle size distribution of a diatom bloom in Boadella reservoir based on number and volume particle concentration measurements obtained with a particle size analyzer (Lisst-100) and chlorophyll measurements performed with a fluorimeter linked to the Lisst-100 instrument. Microscope observations and counts of the samples harvested at different depths of the water column showed that the major percentage of the phytoplankton population were diatoms. Mainly, we here describe the horizontal and vertical distribution of diatoms and their relationship with the physical climate. Several sampling stations, distributed along the axis of the main tributary river that supplies water to the reservoir, were considered under study (Fig. 1). These stations were sampled in June–November of 1999 and 2000, corresponding to the stratified period of the reservoir. The growth rate of cells for different depths will be also calculated from the particle number concentration.

Materials and methods

Study area

The study site (Boadella reservoir) is located in Northeast Spain (Fig. 1), in the eastern prePyrenees (42° 20′ 15″ N–2° 21′ 07″ E). Boadella reservoir (a reservoir of maximum capacity of 62 10^6 m^3) is a deep-stratified monomictic and eutrophic reservoir. Its primary distinguishing characteristic is its small catchment area, dominated by granite soils that result in low salt concentrations. This feature limits the lake buffering that is further accentuated by the effects of seasonal perturbations. The maximum nutrient concentrations in the lake are relatively low ($NO_3{}^- <$ 16 μM, soluble reactive phosphorous $<$ 1 μM, total $P < 2\ \mu$M). At the end of spring, low P concentration may contribute to the dominance of small diatoms over other classes of algae in the following stratified lake season (June–November), as also described in Vrede et al. (1999).

Sampling and measurement of physical and chemical variables

Campaigns were carried out during the stratified period of the lake, from the 1st of June to mid-November of 1999 and 2000. The sampled transect consisted of six stations located along the main tributary of the reservoir (Muga river), with fixed buoys as a reference situated at the maximum depth in the respective cross sectional area of the lake. Seven campaigns were carried out in 1999 and eight in 2000. During almost the whole period, the lake remained stratified, and mix completely at the end of November due to surface cooling.

Summer and Autumn of both years were characterized by exceptionally low rainfall over the area of study although June and July of 2000 were characterized by cloudy days. In July-2000, the mean month air temperature was 3 °C lower than the mean long-term temperature. The mean annual water inflow to the lake is 64 10^6 m^3. In the summer period usually outflows of $\sim$25 10^6 m^3 are used for irrigation and $\sim$5 10^6 m^3 are used for water supply. Due to the low rainfall, during the 1999 campaign no water was taken out for irrigation and small changes of water level (less than 0.4 m

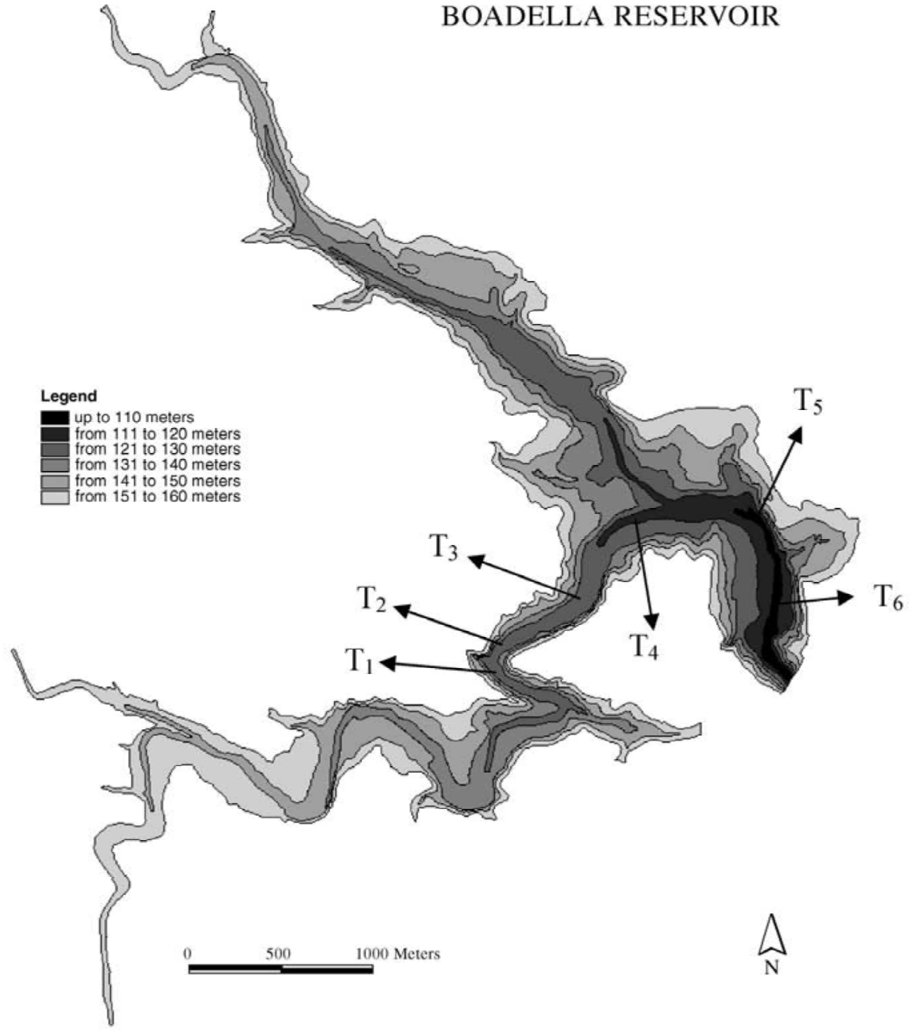

Figure 1. Bathymetric map of Boadella reservoir with sampling stations. Contour intervals (heights above sea level) are in meters.

per month) were measured. At the end of 1999, strong precipitation partially refilled the lake, which allowed a regular management of the lake. Therefore, during the summer of 2000 the outflow for irrigation was reestablished again. This fact made the total volume of the water of the lake to change from the 40% of the total lake capacity at the beginning of June to the 23% (24 m of maximum depth) at the end of November. Muga and Arnera rivers are the tributaries to Boadella reservoir. The Muga river is the most important, supplying the 70–80% of the total incoming water. During summer, water inflows from Arnera and Muga rivers were low. For this reason, the plunge point of the river into the water column of the reservoir was located upstream the reservoir. Because of this fact, the behavior of this reservoir was close to the behavior of a lake, where the stratification pattern basically depended on the surface heat fluxes.

A laser *in situ* scattering and transmissometry probe (Lisst-100, Sequoia Scientific, Inc.) was used to measure the particle size distribution. Particle size distribution profiles were carried out at each station with a vertical spatial resolution of 0.25 m. The laser analyzer consists of a laser beam, an array of 32 ring detectors to analyze the light received, a data storage unity and a battery system, and is controlled by a shipboard computer. The laser analyzer measures the volume concentration of particles for 32 size classes logarithmically spaced in the range d_j = 1.2–200 μm, by using a procedure based on the diffraction theory. It incorporates a pressure sensor from which the depth can be known with an accuracy of 5 cm. The Lisst-100 has been found to successfully measure bacterial concentrations (Vila et al., 2002), phytoplankton concentrations (Serra et al., 2001), concentration of sediments in laboratory experiments (Traykowski, 1999) and in the field (Colomer et al., 2001; Colomer et al., 2002, Serra et al., 2002).

The particle volume distribution of a suspension of particles, V_T, is obtained by integrating over the whole spectra of size classes (n_{vj}). The particle number concentration of the size class j (n_j), that is, particles with diameter d_j, is calculated from the particle volume concentration, n_{Vj}, by using $n_j = n_{Vj}/d_j{}^3$. Therefore the total number concentration, N_T, is determined by integrating over the whole spectra of size classes $N_T = \sum_j n_j$. Finally, the mean diameter of the particle size distribution is calculated according to

$$\mathrm{d} = \sqrt{\sum_j n_{Vj} / \sum_j n_j d_j} \text{ (Allen, 1981).}$$

In situ measurements of Chl *a* concentration were performed with a submersible fluormeter (Mini$^{\mathrm{tracka}}$II, Chelsea Instruments Ltd) linked to the laser analyser. It has an excitation wavelengh of 470/30 nm and an emission one of 685/30 nm. The calibration of the instrument was done by correlating the output voltage of the fluormeter with the Chl *a* concentration. In 125 observations, the relationship between the Chl *a* concentration and the fluorescence signal of the fluormeter was Chl *a* [μg Chl *a* L^{-1}] = 0.0088 $F - 0.01$, where F is the output of the fluormeter in relative units. A fairly good correlation was found between Chl *a* contents and the fluorescence (F) values ($R^2 = 0.93$). Measurements of Photosynthetically Active Radiation (PAR) were performed with an underwater spherical quantum sensor (LI-193SA, LI-COR Environmental Division, Nebraska U.S.) linked with a datalogger LI-250. Fifteen seconds averaged of the light received (in μmol) at each depth were considered.

Water samples were taken at 5-m intervals from the surface to the bottom with a double cone-shaped end device, ensuring low shear rates on the samples (Jørgensen et al., 1979). Additional water samples were also taken at depths where the laser analyzer detected maximum local volume concentrations. Samples, stored in dark bottles until processed, were filtered through 47 mm, 0.45 μm-pore diameter of cellulate nitrate filters (Millipore) to determine the concentration of photosynthetic pigments by spectrophotometric analysis. Also, counts and identification of phytoplankton were done under microscope on polycarbonate filters (0.22 μm-pores size; 25 mm; MSI). At least 20 fields containing > 400 cells were counted for each sample with a Zeiss Axioskop microscope.

Finally a multiparametric probe (Hydrolab, Hydrolab Corporation) provided the conductivity (accuracy =1%) and temperature (accuracy = 0.1 °C and resolution = 0.01 °C) at different depths (accuracy = 5 cm).

Results and discussion

The study was designed to follow the spatio-temporal changes during summer-fall when water inflows were low and the reservoir was stratified. Diatoms (with diameters in the range 2–10 μm) were the dominant epilimnetic phytoplankton species encountered, representing 92% of the total population at 2 m and 7 m in June-1999 as could be observed under the microscope. The rest was composed of green algae. In September-1999, the epilimnetic samples were composed mostly of diatoms with ~97% of total population and the rest were green algae. The samples harvested from the hypolimnion during this month contained a large number of inorganic particles that did not allow a correct characterization of the phytoplankton species under the microscope. In June and July-2000, diatoms represented 98% of total phytoplankton and, in September-2000, 62% of the total consisted of diatoms and 19% consisted of green algae. The phytoplankton population also contained some clorophyceae cells. The particle size distributions in the number representation obtained with the Lisst-100 shows that there is a peak of particles with diameters from 2.5 μm to 10 μm (Fig. 2A,B) for the campaign carried out in 1999 and 2000. The number concentration was found to decrease with depth. Therefore, the range of sizes measured with the Lisst-100 was in accordance with the range of particle sizes observed under the microscope.

The maximum particle concentration at the lake downstream, T6 ($5\ 10^5$ ml^{-1} in 1999 and $3\ 10^5$ ml^{-1} in 2000), were measured in July at the surface of the lake (Figs. 3A,C, where contours represent the number concentration in the log-scale), decreasing down to the bottom of the epilimnion (with typical concentrations

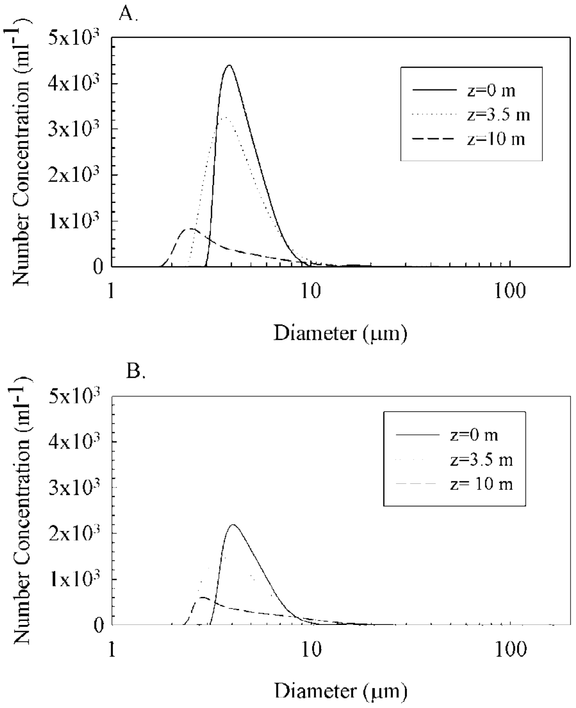

Figure 2. Particle size distributions in the number representation measured *in situ* with the Lisst-100 and corresponding to different depths of the water column for (A) June 1999 and (B) June 2000.

between 2.5 10^4 ml^{-1} and 10^4 ml^{-1}). In Figures 3A and C, the base of the epilimnion (defined as the depth where the vertical gradient of temperature was larger than 0.3 °C m^{-1}) is plotted as a dashed line. In mid September, the base of the epilimnion deepened (as the thermocline deepened, coincident with the end of the stratified period of the lake) meanwhile the width of the subsurface bloom shrank remaining next to the surface. The high particle concentration values at the bottom of the reservoir in September–October (Figs 3A, C), which were found mostly within and below the thermocline may be attributed to the dispersion of particles produced by physical processes, such as internal waves shoaling at the sediment–water interface or boundary mixing in the lake upstream due to the impingement of the thermocline at the bottom of the reservoir or at the body walls, as were observed in Monolake (MacIntyre et al., 1999). Concurrent with these measurements, the time evolution of the vertical distribution of Chl *a* concentration at T6 can be seen in Figures 3B (corresponding to the 1999 study) and D (for the 2000 study). In mid-June and mid-September of 1999, Chl *a* presented the maximum values (Fig. 3B), related to changes in relative abundance of phytoplankton. In 2000, the maximum value of Chl *a* was found at the beginning of July (Fig. 3D). Figures 3B and D show that the subsurface Chl *a* concentration presents a non-homogeneous distribution in the epilimnion in the early stages of the phytoplankton bloom (June–July) with a peak of Chl *a* at the thermocline level, decreasing from the base of the epilimnion to the lake bottom. Here, it is clearly seen that the bottom of the seasonal epilimnion crosses the contours of maximum Chl *a* concentration, during the diatom bloom development. Also, from August to October, the epilimnetic Chl *a* concentrations were homogeneously distributed with depth compared to the early stages of the bloom development. During the particle bloom increase phase, the subsurface Chl *a* maximum at T6 was located between 6 and 8 m (Fig. 3B) and was 2 times the value at the lake surface. In October-1999, while the epilimnion deepened, relatively high values of Chl *a* were found near the surface. At the end of the bloom development phase, relatively high concentrations of Chl *a* (up to 2.6 μg L^{-1}) were found in the lake hypolimnion, especially in 1999 (Fig. 3B). At the end of the studied period (November), T6 presented a constant value of Chl *a* with depth (Figures 3B, D) as a result of the overall mixing of the lake. The fact that the peak of Chl *a* was situated at the base of the epilimnion in contrast to the peak of the number of diatoms, situated at the surface, indicates that cells have different clorophyll contents as a result of different light conditions at different depths.

The difference between the maximum value of the Chl *a* concentration attained and the Chl *a* concentration at the surface was largest in station T2 with a ratio of 2.7 in June-1999, corresponding to the early stages of bloom development (Fig. 4A). On the contrary, when the particle bloom was in its decaying phase (see Figs 4B, D), the ratio between the maximum value of Chl *a* and that at the surface was lower, being 1.3 in T6 and 1.1 in T2 (Fig. 4B). Horizontal differences in Chl *a* distribution were also detected for the stations situated along the reservoir. As shown in Figure 4 the highest Chl *a* values were always found at station T2, with a value of Chl *a* concentration, 9.6 μgl $^{-1}$ (mid-June 1999, Fig. 4A) and a value of 6.8 μg l^{-1} (mid-June 2000, Fig. 4C) located at the base of the epilimnion. In addition, the subsurface maximum of Chl *a* in the early bloom phase was wider at upstream stations than at stations situated at the station situated close to the dam of the reservoir. The preferential initiation of the bloom at upstream stations can be explained by taking into account that the supply of nu-

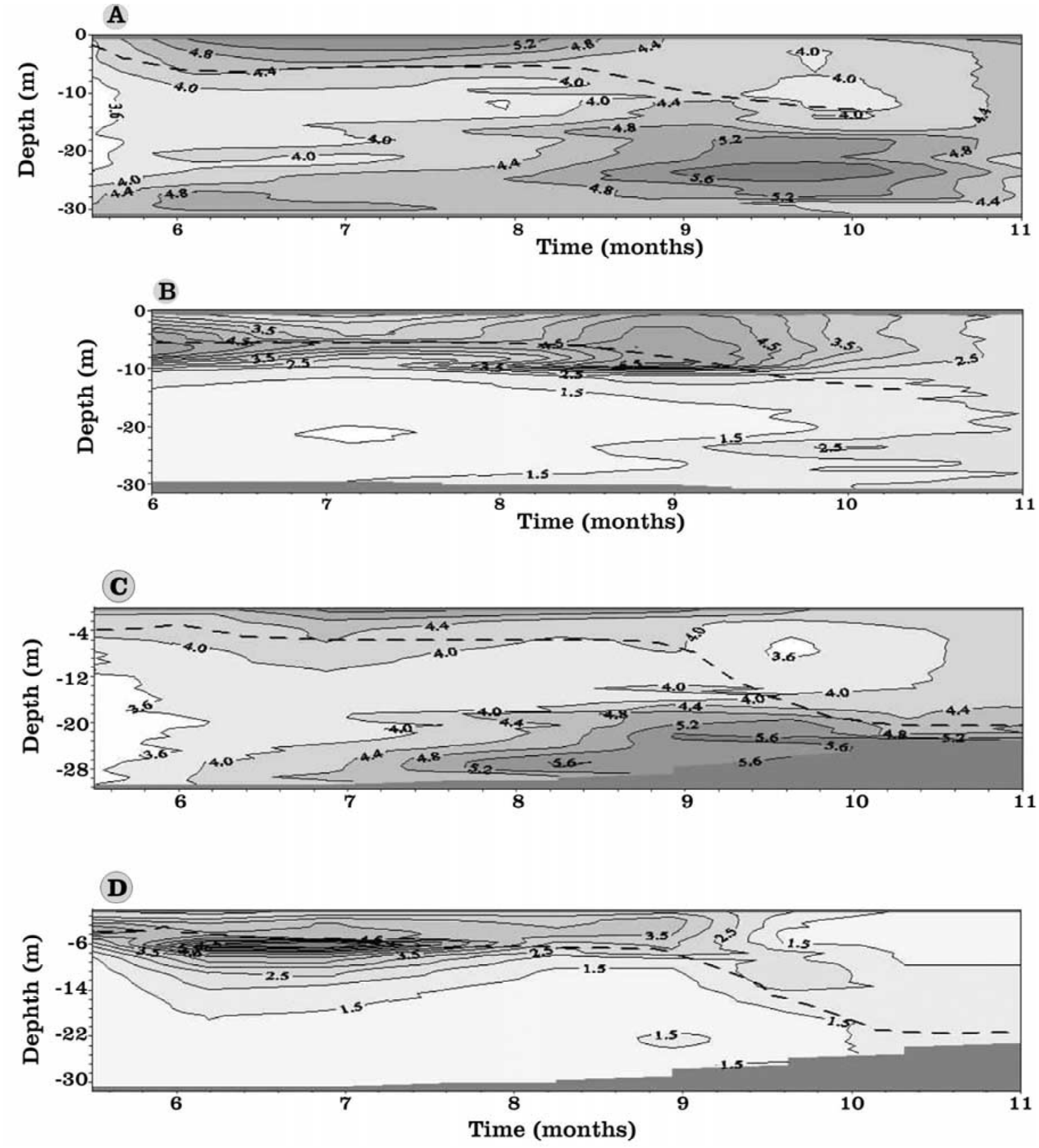

Figure 3. Contours of temporal evolution (June–November) of (A) particle number concentration (log of particles ml^{-1}) and (B) Chl *a* concentration (μg l^{-1}) measured at the lake downstream, station T6, in 1999. (C) particle number concentration (log of particles ml^{-1}) and (D) Chl *a* concentration (μg l^{-1}) measured at the lake downstream, station T6, in 2000. Contours are based on linear triangular interpolation between different adjacent points. The broken line delineates the thermocline layer.

trients due to mixing is higher at stations where mixing is highest, i.e. upstream. This fact is corroborated by other studies performed in rivers, (Köhler, 1997), shallow lakes (Gervais et al., 1997; Ogilvie & Mitchell, 1998), moderately sized lakes (MacIntyre et al., 1999), and estuaries (Ning et al., 2000). These studies show

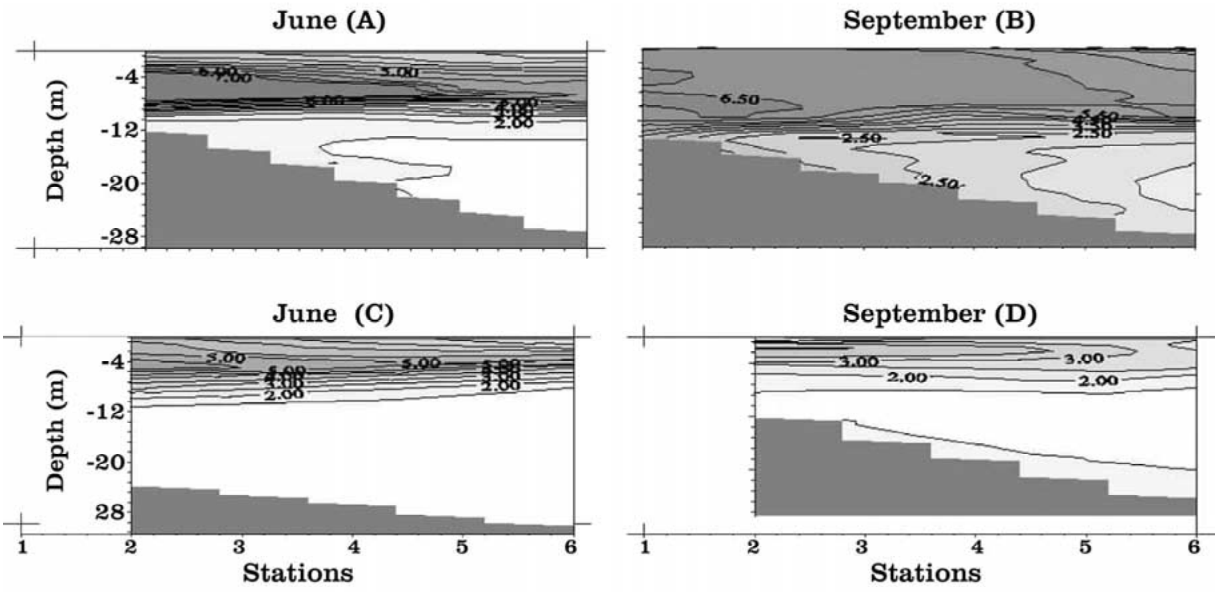

Figure 4. Two dimensional contour plot of Chl *a* concentration (μg l^{-1}) measured from T1 to T6 during 1999 (A and B) and 2000 (C and D).

that the growth rate of phytoplankton located at zones with high levels of mixing is higher than that of phytoplankton in calm zones. In Figure 5, the growth rate of the green algal bloom (defined as the ratio between the increment of particle number with time), calculated between the first of June to mid-July was larger (~2 times) in station T2, in the upstream part of the lake, than in T6, downstream the lake. The growth rate was maximum at the surface of the reservoir, decaying approximately exponentially with depth in the epilimnion, according to the available light for the phytoplankton development. Therefore, the low light intensity level that reached the deepest layers of the epilimnion limited the phytoplankton growth rate as in microcosm experiments (Huovinen et al. 1999) and in the sea (Goericke & Welschmeyer, 1998). Contrary to the studies reported by Huovinen et al., (1999), no photoinhibition was found at the surface where light intensity was high.

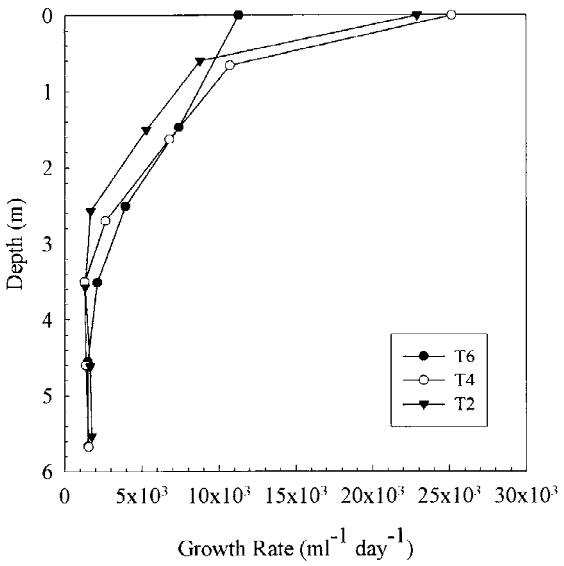

Figure 5. Growth rate of the diatom population in Boadella reservoir at stations T2, T4 and T6 during the bloom development.

The phytoplankton bloom in the epilimnion was found to present approximately constant particle volume concentrations with depth; (see Figs 6A, B). The maximum particle volume concentration in the epilimnion fell at mid-August in 1999, while this maximum appeared earlier (mid-July) in 2000. This delay of the time initiation of the bloom can be related to different meteorological conditions, as found by other authors (Zohary et al., 1998). Further, the maximum value of the particle volume concentration in the bloom was higher in 2000 (~23 μl/l) than the value reached in 1999 (~15 μl/l).

At the end of the bloom (September 1999), when the thermocline started to deepen, a maximum of particle volume concentration was found at the base of the epilimnion (Fig. 6A). In the 2000 study, the maximum in the particle volume concentration at the base of the epilimnion was found earlier (~mid-July,

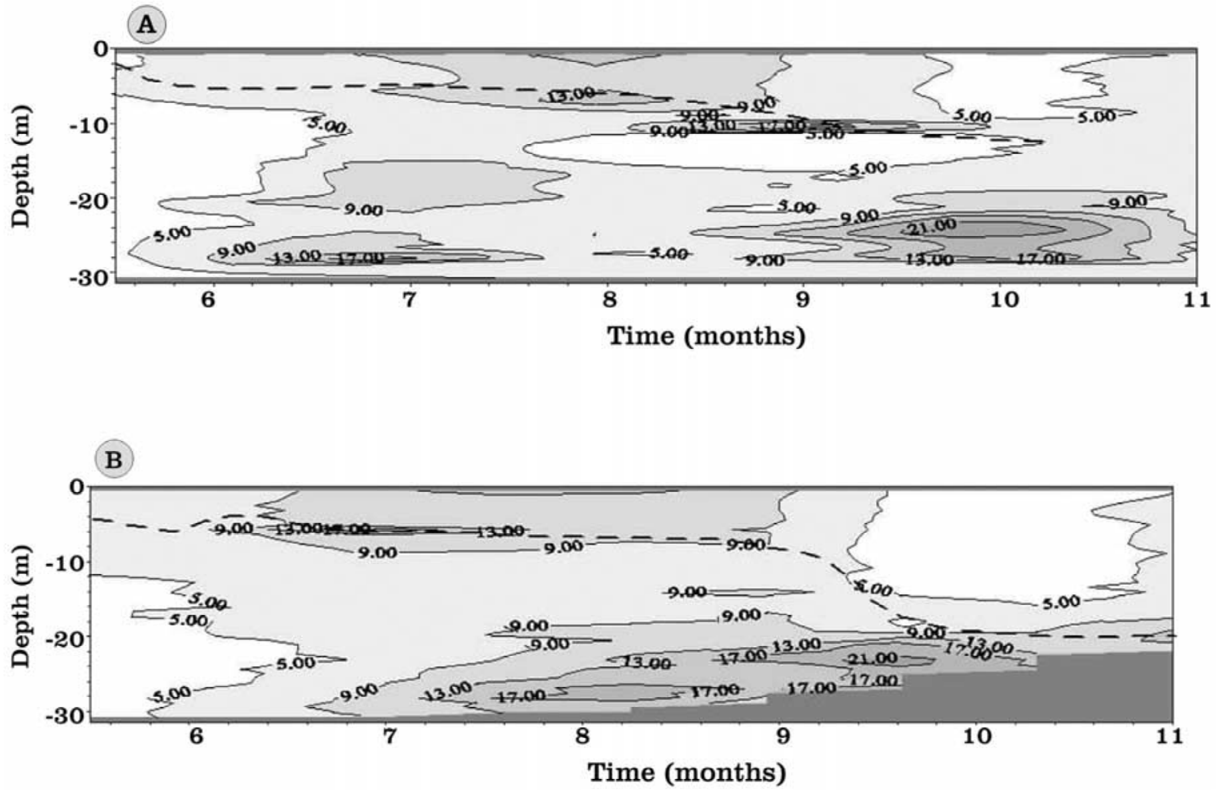

Figure 6. Contours of temporal evolution of particle volume concentration ($\mu l\, l^{-1}$) measured at station T6 during 1999 (A) and 2000 (B).

Fig. 6B). The fact that the maximum particle volume concentration corresponded to a maximum mean diameter of the phytoplankton population, (Fig. 7) and that the maximum of the particle volume concentration did not correspond to a maximum in particle numbers (Figures 6A and 3B for 1999 and Figures 6B and 3D for 2000) suggest that diatom cells aggregated when they settled through the water column, accumulating afterwards at the base of the epilimnion. Such aggregation of particles due to settling processes was described previously in laboratory experiments (Li & Logan, 1997). Accumulation of phytoplankton aggregates at the thermocline level at the end of a bloom phase has been also found in Lake Constance (Grossart & Simon, 1993) or at density discontinuities (MacIntyre et al., 1995). The formation of aggregates can be explained by taking into account that as particles settle through the epilimnion they aggregate by single particle interactions or through scavenging of small particles by large sinking aggregates (Li & Logan, 1996). Similar conditions have been found in the sea (Kiørboe et al., 1994; MacIntyre, 1995) where phytoplankton blooms may terminate by aggregation of the cells into large flocs, known as marine snow.

Conclusions

A diatom bloom dominated the phytoplankton population of Boadella reservoir during the stratified period of 1999 and 2000. The concentration of diatoms, measured *in situ* with a laser analyzer, was in the size range of 2.5–10 μm in accordance with the range of sizes observed with microscope.

Results reveal that different stratification patterns corresponding to different meteorological conditions prevaling each year determined the vertical dynamics of the diatom bloom, such as the onset of the bloom and its concentration evolution throughout the year. Differences in horizontal distribution of the diatom population were also found between stations situated upstream the river compared to those situated close of the reservoir, which could reflect different nutrient concentrations as a result of mixing characteristics of each station.

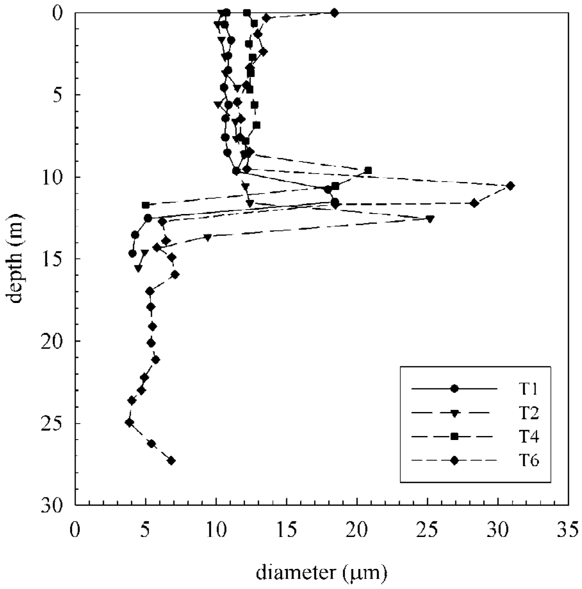

Figure 7. Vertical profile of mean particle diameter at stations T1, T2, T4 and T6 in September of 1999.

Different chlorophyll contents were found for cells situated at the bottom and cells situated at the top of the epilimnion. This fact might be caused by different light intensities attaining each depth. Cell growth rate was calculated and found to be maximum at the top of the mixed layer. Therefore, light intensity was not enough to inhibit their growth. Laboratory experiments should be done in order to determine if higher light intensities than those in the field could inhibit the growth rate of diatoms.

Finally, the maximum volume concentration of diatoms at the base of the epilimnion at the end of the bloom together with an increase of the mean particle size distribution were attributed to the presence of aggregates produced by single particle interaction due to sedimentation or by the scavenging of particles by large fast sinking aggregates.

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