Limnological investigations in Lake San Pablo, a high mountain lake in Ecuador

Vorgelegt von
Dipl.-Biol. Jorge Enrique Casallas Guzmán
aus Bogotá, Kolumbien

Von der Fakultät III – Prozesswissenschaften der
Technischen Universität Berlin
zur Erlangung des akademischen Grades
Doktor der Naturwissenschaften
- Dr. rer. nat. -

genehmigte Dissertation

Promotionsausschuss:

Vorsitzender: Prof. Dr. rer. nat. Ulrich Szewzyk
Berichter: Prof. Dr. Ing. Martin Jekel
Berichter: PD Dr. rer. nat. Günter Gunkel
Berichterin: Prof. Dr. Brigitte Nixdorf

Tag der wissenschaftlichen Aussprache: 02.11.2004

Berlin 2005

D 83

CONTENTS

FIGURES

TABLES

Summary

"Limnological investigations in Lake San Pablo, a high mountain lake in Ecuador"

Equatorial high mountain lakes are singular lakes that lie between 2,500 and 4,000 m above the sea level (a.s.l) mainly in the Andes of Ecuador, Peru, and Colombia. They are typically cold-water lakes with water temperatures below 20 °C. Their limnological characteristics are determined by some environmental parameters typical for tropical regions, such as high radiation input, low seasonal variation of temperature and light input, and high daily temperature variation.

Lake San Pablo, with a surface of 583 hectares and a maximal depth of 35 m, is located at 2,660 m a.s.l. in the Andes of Ecuador. Intensive agricultural activities, land erosion in the catchment area as well as the inflow of untreated waste water directly into the lake have contributed to eutrophication and to the present deteriorated state of the lake. In the present study, limnological investigations were carried out at Lake San Pablo between 1998 and 2001. On the basis of this middle-term monitoring program, enclosure experiments, (which were carried out to evaluate the role of physical and chemical parameters as limiting factors of plankton productivity), and 24-hours samping series the composition of the biological communities, the thermal behavior of the lake, its trophic state, as well as the relationship between biotic and abiotic factors should be determined.

During this study a temperature stratification of low stability occurring from late September to late May was observed. This leads to a temperature difference between epi- and hypolimnion of nearly 2 °C, with a monomictic circulation phase during the summer moths between June and August. Furthermore, a nightly convective mixing due to afternoon winds and nightly cooling processes was observed. This induces the destratification and mixing of the trophogenic zone, which can reach into the tropholytic zone up to 20 m depth. This sort of thermal behavior depends on local daily weather conditions and is known as "atelomixis".

Based on the results, it can be said that Lake San Pablo is a meso- to eutrophic lake with a high level of total phosphorus (mean TP concentration in the lake is 0.23 mg/l) and a soluble reactive phosphorus (SRP) concentration between 0.05 and 0.12 mg/l in the epilimnion during the stratification period. Total nitrogen (N) concentration is moderately high, being usually near 1 mg/l. The N:P atomic ratio lies between 5 to 25, indicating a limitation by nitrogen, mainly during stratification periods, and sometimes by phosphorus, generally after overturn. The complex water mixing processes in the lake also seem to play an important role as limiting factor in biological productivity.

The analysis of phytoplankton indicates low species richness and relatively high abundance of existing organisms and high biomass (maximal Chl. a: 32.8 µg/l). The phytoplankton is represented principally by the filamentous diatom *Aulacoseira granula*, and also by some Chlorococcales as *Scenedesmus linearis* and *Pediastrum boryanum*, and the Euglenophyceae *Trachelomonas volvocina.* The zooplankton community is very poor and is represented by the Crustacea *Daphnia pulicaria*, *Metacyclops mendocinus* and the Rotatoria *Keratella tropica*, *Trichocerca similis*, *Anuraeopsis fissa* and *Asplanchna sp*. The organisms in the lake seem to be well adapted to the natural high UV-radiation.

These results could be used as the basis for planning future programs for the mitigation and control of eutrophication in the lake.

"Limnologische Untersuchungen im San Pablo See, ein Hochgebirgssee in Ecuador "

Äquatoriale Hochgebirgsseen sind eine besondere Art von Seen, die zwischen 2.500 und 4.000 m über dem Meeresspiegel liegen und hauptsächlich in den Anden von Ecuador, Peru und Kolumbien vorkommen. Im allgemein sind sie Kaltwasserseen mit Wassertemperaturen unter 20 °C. Ihre limnologischen Merkmale werden durch einige typische tropische Umweltparameter bestimmt, wie z.B. hohe Strahlungseingabe, niedrige saisonbedingte Variationen von Temperatur und Lichteingabe, sowie hohe tägliche Temperaturschwankung.

Der San Pablo See, mit einer Oberfläche von 583 Hektar und einer maximalen Tiefe von 35 m, liegt 2.660 m über den Meeresspiegel in den Anden von Ecuador. Intensive landwirtschaftliche Nutzung des Einzugsgebietes, Bodenerosion und die direkte Einleitung von Abwasser in den See haben zum aktuellen Eutrophiezierungsgrad und dem gegenwärtigen schlechten Zustand des Sees beigetragen. Im Rahmen der hier vorgelegten Studie wurden zwischen 1998 und 2001 limnologische Untersuchungen am San Pablo See durchgeführt. Anhand von diesem mittelfristigen Monitoring-Programm, von Enclosure-Experimente (die durchgeführt wurden, um den Einfluss von physischen und chemischen Umweltfaktoren auf die Limitierung der Planktonproduktivität im See zu untersuchen) und von 24-Stunden Untersuchungen, sollten die Zusammensetzungen der biologischen Gemeinschaften, die thermischen Verhältnisse, der trophischen Zustand des Sees sowie die Beziehungen zwischen vorhandenen biologischen Gemeinschaften festgestellt werden.

Während dieser Studie konnte festgestellt werden, dass eine thermische Schichtung von niedriger Stabilität von Ende September bis Ende Mai auftritt. Diese führt zu einem Temperaturunterschied zwischen Epi- und Hypolimnion von ca. 2 °C, mit einer monomiktischen Zirkulationsphase während der Sommermonaten zwischen Juni und August. Weiterhin wurde ein nächtlicher konvektiver Mischungsprozess festgestellt, der durch starke Nachmittagswinde und nächtliche Abkühlungsprozesse verursacht wird. Dieser Prozess führt zu einer Destratifizierung und Durchmischung der trophogenischen Zone, die bis tief in die tropholytischen Zone eine Wassertiefe von bis zu 20 m erreichen kann. Solch ein thermisches Ereignis hängt von lokalen Wetterbedingungen ab, kann mehrere Tage und sogar Wochen dauern und ist als "Atelomixis" bekannt.

Nach den Ergebnissen der Untersuchungen kann festgestellt werden, dass der San Pablo See ein meso- bis zu eutrophischer See ist, der einen hohen Gesamtphosphor-Gehalt (mittlere P-Konzentration im See 0.23 mg/l) und eine Konzentration von löslichem reaktiven Phosphor (SRP) zwischen 0.05 und 0.12 mg/l im Epilimnion während der Stratifikationsphase aufweist. Die Stickstoffkonzentrationen (N) sind mäßig und betragen meist ca. 1 mg/l. Das atomare N:P-Verhältnis liegt zwischen 5 und 25 und zeigt eine Limitierung durch Stickstoff während den Stratifikationsphasen und manchmal auch durch Phosphor während den Zirkulationsperioden. Die im See herrschenden Zirkulationsprozesse scheinen wichtige limitierende Faktoren zu sein.

Die Phytoplanktonanalyse zeigt eine geringe Artenvielfalt mit einer relativen hohen Abundanz der vorhandenen Organismen und hoher Biomasse (maximum Chl. a: 32.8 µg/l). Das Phytoplankton wird hauptsächlich durch die fädige Diatomeae *Aulacoseira granulata* sowie durch einige Chlorococcales, u. a. *Scenedesmus linearis* und *Pediastrum boryanum*, und der Euglenophyceae *Trachelomonas volvocina* dominiert. Das Zooplankton im See ist extrem artenarm und es wird durch den Crustaceen *Daphnia pulicaria*, und *Metacyclops mendocinus* sowie durch die Rotatorien *Keratella tropica*, *Trichocerca similis*, *Anuraeopsis fissa* und *Asplanchna sp.* repräsentiert. Es scheint, dass die im See lebenden Organismen an die hohe natürliche UV-Strahlung gut angepasst sind.

Diese Ergebnisse können als Basis für die Planung von Programmen für die Kontrolle der Eutrophikation im See verwendet werden.

1 Introduction

The first studies on freshwater bodies were carried out as early as the 17th century in Europe. Investigations made on this topic in the course of the following centuries provided the foundations for the origin of limnology as science at the beginning of the 19th century. Since then, the development of this science has taken place principally in Europe and North America, where the majority of investigations in this subject has been carried out. Consequently, the knowledge of temperate aquatic ecosystems and their dynamics is large and well understood. Despite the economic, social and cultural importance of aquatic systems for the development of tropical regions, investigations carried out in such regions are rare and consequently information on tropical limnology is scarce. Current knowledge has been obtained principally during the last decades of the 20th century, when several investigations, predominantly in low tropical regions, were performed (Lewis, 1973; Melack, 1996; Nilssen, 1984; Payne, 1986).

1.1 Lakes and water reservoirs at high altitude in tropical regions

Two of the most remarkable characteristics of tropical regions are that only slight atmospheric temperature variations occur throughout the year, and the seasonal climatic changes experienced in middle and high latitudes do not occur there. However, marked differences occur within daily temperatures. The altitude above sea level (a.s.l.) also influences this phenomenon. In fact, at high altitudes in the tropics, nocturnal frosts may appear almost every night throughout the year, while diurnal temperatures may be quite warm. Another hallmark of tropical regions is that the “seasons” are characterized by precipitation patterns (Osborne, 2000). These specific characteristics originate atmospheric thermal layers with ranges of stable temperature (Holdridge, 1978).

Tropical high mountain lakes lie between 2,000 and 4,000 m above sea level (a.s.l.), the Lake Titicaca being one of the best known. Some features of these lakes are geographical isolation; water temperatures lower that 20° C and low oxygen saturation values (< 7 mg/l). Because of their tectonic, glacial or volcanic origin, they are generally deeper that lowland lakes.

Due to altitude and the consequent climatic conditions, the dynamics of lakes and reservoirs at high altitudes are different to those of aquatic systems at lower altitudes.

All these circumstances determine that circulation and overturn patterns in tropical lakes and reservoirs that do not necessarily follow an annual rhythm, as in temperate regions, but instead occur according to regional climatic conditions. In other words, thermal stratification in tropical aquatic systems depends on temperature variations between day and night (Gunkel & Casallas, 2001; Löffler, 1964; Powell et al., 1984; Roldán & Ruiz, 2001).

Some investigations have contributed to the understanding of thermal patterns of tropical high mountain lakes (Hutchinson & Löffler, 1956; Löffler, 1964). These aquatic systems are classified in general as oligothermic with frequent circulations and no formation of stratification. For this reason, they have been called cold polymictic (Hutchinson & Löffler, 1956; Roldán, 1992). Since thermal stratification of water bodies at high altitude, if it occurs at all, is rather unstable, of short duration and without thermocline formation, the use of the terms epilimnion, metalimnion and hypolimnion is not completely correct from the productive point of view when applied to these lakes. In other words, in some tropical lakes the epilimnic zone does not correspond to the trophogenic zone, as is more typical in temperate lakes. Consequently, for mountain lakes, it is more convenient to define two water regions: a euphotic or trophogenic zone in superficial layers, and an aphotic or tropholytic zone in deeper ones (Roldán, 1992).

1.2 Limnological investigations in Ecuador

Limnological investigations performed in Ecuador are few, and consequently, knowledge on its aquatic systems is scarce. Steinitz-Kannan et al. (1983) refer to the first investigations carried out in that country, and present results of their investigations in Ecuadorian lakes since 1966. Miller et al. (1984) present the first productivity data from some Ecuadorian lakes, included Lake San Pablo, and annotate environmental problems caused by human activities in some of them. In addition, some taxonomic investigations have been carried out on phytoplankton (Rott, 1981a), rotifers (Koste & Böttger, 1992; Koste & Böttger, 1989), ostracods and copepods (Löffler, 1963) and the value of macrophytes as bioindicators in high mountain lakes (Kiersch et al., 2002). Gunkel (2000) gives a review of available data from Lake San Pablo and Gunkel & Casallas (2002a) make remarks about its trophic state and present the first evaluation of limitations on productivity caused by deep diurnal mixing (Gunkel & Casallas, 2002b). The same authors describe and discuss chemical, physical, and biological aspects of the lake (Casallas & Gunkel, 2002). In studies about socio-economic and environmental problems that affect lakes and catchments areas of the province of Imbabura carried out on behalf of the national government, causes of environmental deterioration in these areas were evaluated and options and programs for their recovery were proposed (Dumont, 1994; Paredes Castillo, 1994).

1.3 Lake San Pablo

Lake San Pablo (Figure 1-1) is located 100 km north of Quito, the capital of Ecuador, at 0°13' N latitude and 78°14' W longitude, and lies at 2,660 m a.s.l. near the town Otavalo in the province of Imbabura. With a surface of 6.7 km^2, maximum depth of 35.2 m, and mean depth of 24.5 m, the lake is the second biggest of the country (Galárraga et al., 1992). The main characteristics of Lake San Pablo and its catchment area are presented in Table 1.

The lake has a circular form, occupying apparently an old pale on the floor of an inter-Andes plateau (Steinitz-Kannan et al., 1983). Regarding the geomorphology of the lake's catchment area, four physiographic units can be determined. The lake itself is located in the low area of River Itambi valley, which corresponds to a physiographic unit of lacustrine deposits. Soils of the catchment area and lake's surroundings (Appendix C) are fundamentally of volcanic origin, and are predominantly oozy, sandy or sandy-oozy (Orstom-Pronareg, 1983a; Orstom-Pronareg, 1983b).

Lake waters are generally still during the night and the morning, developing strong currents in the afternoon hours, especially during the dry season between July and August (Casallas & Gunkel, 2002; Gunkel & Casallas, 2002b; Steinitz-Kannan et al., 1983).

The main water source of the lake is the River Itambi, a small mountain stream located at the southeast side of the lake, which contributes approximately 90% of the total water input. There are other temporal water inputs of minor importance, which supply water to the lake only during rainy seasons. The main water outlet is a “Totora” (*Schoenoplectus totora*) swampy zone at the northwest side of the lake, the River Jutunyacu, also called Peguche. (Figure 1-2). Water renovation time has been estimated at 3.2 years (Galárraga et al., 1992). The mean annual precipitation can reach 1,000 mm and is little higher than evaporation, which reaches up to 858 mm (Figure 1-3). The rainy season takes place between October and May and the dry between June and September (INAMHI, 1999).

Mean temperatures are 8.3 °C at night and 22.7 °C during the day, and the lowest and highest temperatures can reach 0.5 °C and 29.5 °C respectively (data from meteorological station installed at the shoreline of Lake San Pablo in 1998).

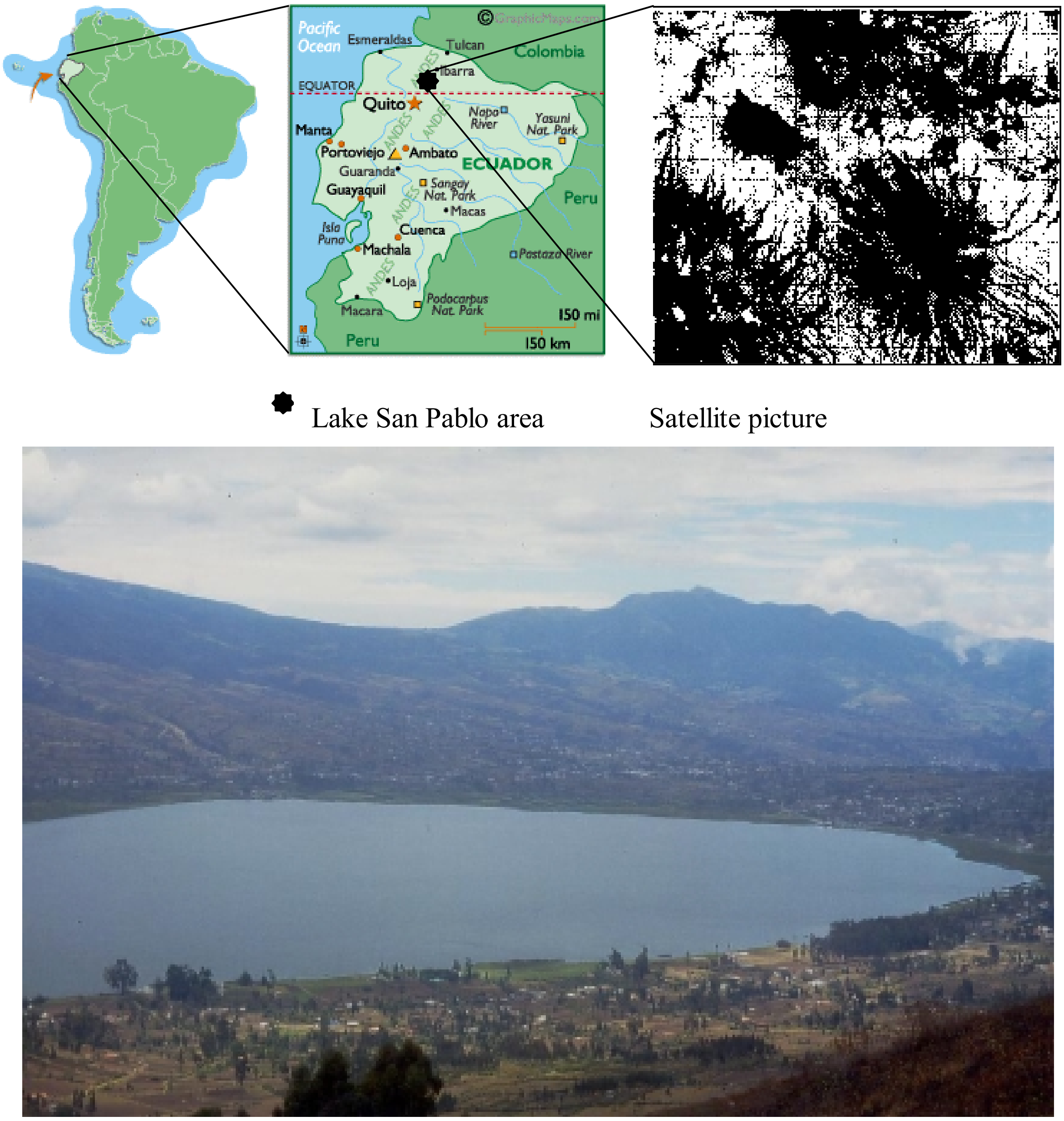


Figure 1-1. Top: Geographic localization of Lake San Pablo and satellite picture of the region (LANDSAT 14 July 1998. scale 1:50.000). Bottom: Aerial picture of the lake.

Table 1. Morphometric parameters and water balance of Lake San Pablo. Morphometric data from EPN (1995); water balance data from Galárraga (1992).

Altitude (a.s.l.)	2,660 m
Maximum length	3,560 m
Maximum width	1,400 m
Shoreline	10.4 km
Shoreline development	1.21
Lake surface	668 ha
Volume	163.9 x 10^6 m³
Maximum depth	35.2 m
Mean depth	24.5 m
Watershed area	147.9 km²
Form of the watershed area	nearly cirular
Factor watershed/lake surface	22
Mean altitude of watershed area	3,100 m
Main fluvial tributary of the lake (aprox. 90%)	River Itambi
Drainage area of River Itambi	60.3 km²
Main fluvial outflow	River Jutunyacu
Water Balance	
Inflow:	
Water flow generated in the watershed area	43.8 x 10^6 m³/y
Precipitation on the lake surface	5.0 x 10^6 m³/y
Total inflow	48.8 x 10^6 m³/y
Outflow:	
Irrigation in the watershed area	6.9 x 10^6 m³/y
River Jutunyacu	26.2 x 10^6 m³/y
Channel	10.4 x 10^6 m³/y
Evaporation from the lake surface	6.9 x 10^6 m³/y
Total outflow	43.5 x 10^6 m³/y
Water renovation time	3.2 years

The catchment area of the River Itambi includes a 60.3 km² mountainous area, with cultivated zones that reach up 3,400 m a.s.l. (Galárraga et al., 1992; Carrera, 2002; Carrera & Gunkel, 2003). Natural vegetation in this area and around the lake has almost completely disappeared, and has been replaced by agricultural fields and a secondary forest, which intensifies the risk of erosion. Additionally, a 40 hectares cut-flower agroindustry has been established on this area, and a human population of approximately

20,000 habitants is settled there. All these factors create a strong pressure on soil and water resources.

Nowadays, Lake San Pablo exhibits eutrophication problems due to the direct and indirect input of waters and solid residues with a high content of nutrients and other substances. They originate from domestic wastewaters, intensive agriculture, agroindustry (pesticides, fungicides, etc.) and cattle breeding (Appendix K). This represents a serious source not only of nutrients but also of germs, since this activities are developed directly on the shore of the lake (Carrera, 2002; Carrera & Gunkel, 2003).

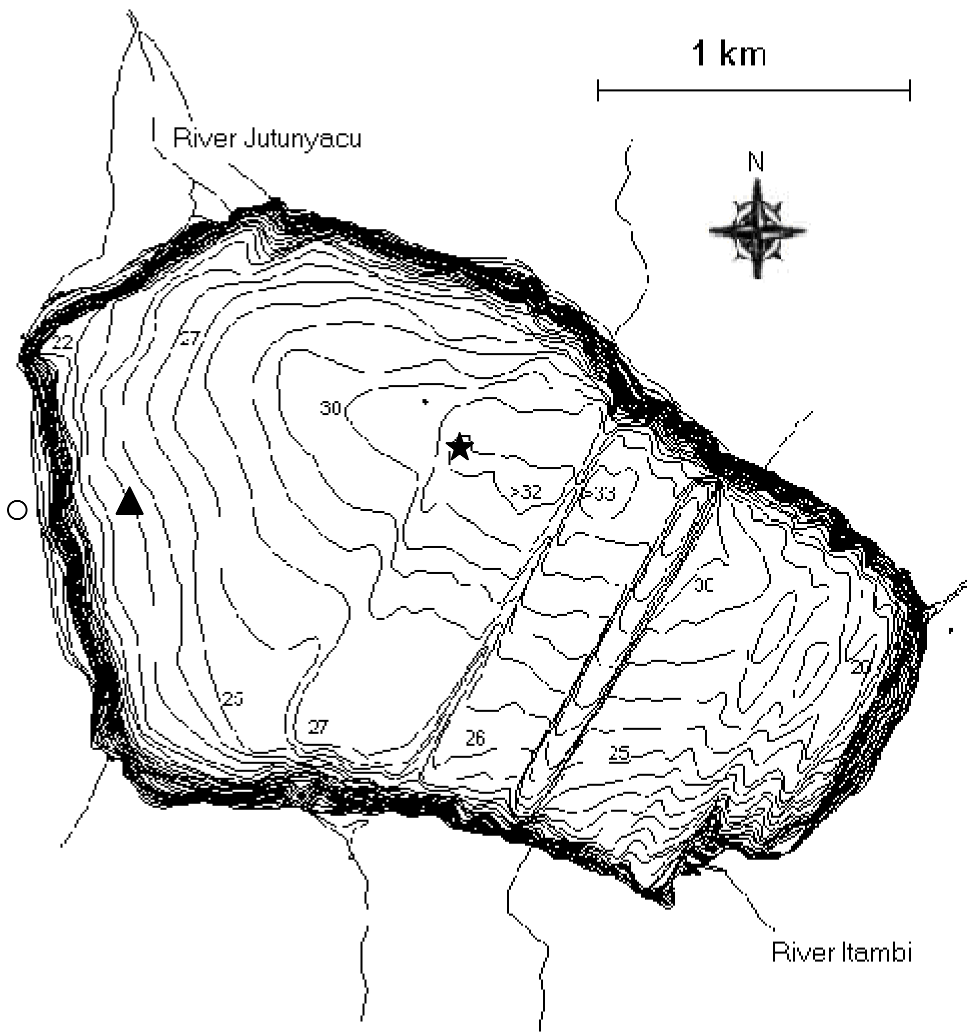


Figure 1-2. Bathymetric map of Lake San Pablo. The numbers indicate the depth in meters. ★ Monitoring sampling spot; ▲ platform (Enclosure and automatic temperature sensors); ○ meteorological station.

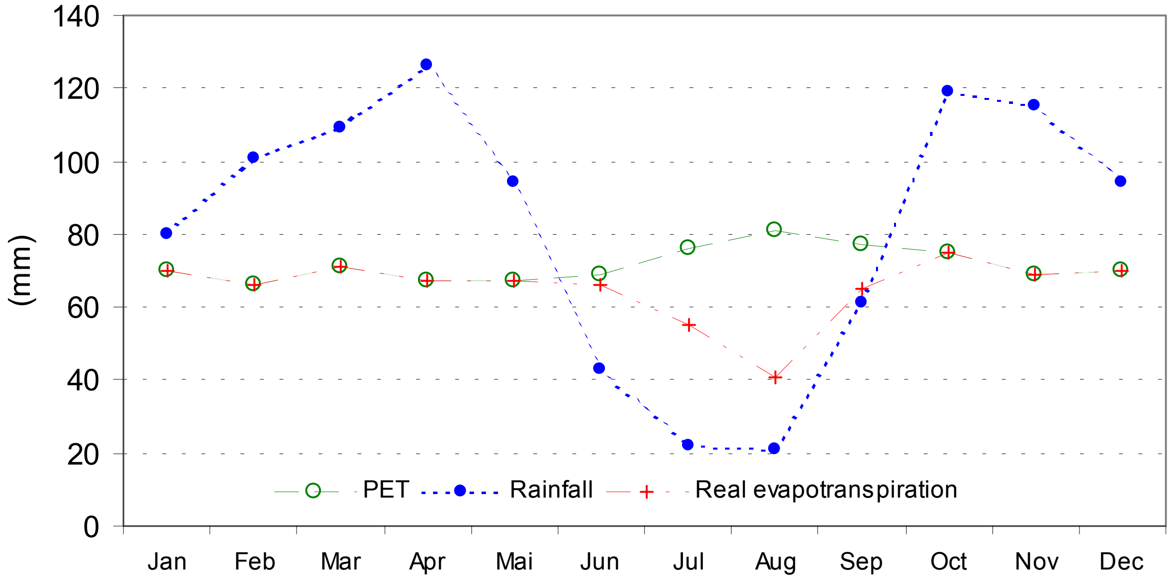


Figure 1-3. Annual distribution of precipitation in the region of Lake San Pablo. PET: Potential evapotranspiration.

2 Objectives of the present study

The main objective of the research work presented here was to perform a medium-term monitoring program at the Lake San Pablo, in order to determine its trophic state and to elucidate which environmental factors play an important role on the control of biomass development. Through the analysis of physical, chemical and biological data from water samples collected from the lake during three years of study, following aspects should be covered:

- Description of the thermal behavior pattern of the lake and the relationships between it and the biotic and abiotic factors.
- Biological species composition and description of the biological communities present in the lake.
- Nutrient and gas contents, their temporal and vertical distribution and their influence upon the dynamics of biological communities.
- Clarification of environmental aspects that could act as limiting factors in productivity.
- Analysis of spatial and temporal relationships between physical and chemical variables that determine the hydrodynamic behavior and the supply and distribution of nutrients in the lake.

This study was carried out as part of the research project "Limnological investigations of equatorial high mountain lakes in Ecuador", performed by the Department for Water Quality Control at the Institute of Environmental Technology of the Technical University of Berlin and in cooperation with the National Polytechnic University of Ecuador (Escuela Politécnica Nacional, EPN, Quito, Ecuador). The project was financed by the German Research Council (Deutsche Forschungsgemeinschaft, DFG) and the Ministry of Economic Cooperation and Development (Bundesministerium für wirtschaftliche Zusammenarbeit und Entwicklung, BMZ). Other studies on the lake and its catchment area have also been carried out as part of the same project (Carrera, 2002; Gunkel, 2002; Kiersch et al., 2002; Carrera & Gunkel, 2003).

3 Material and Methods

In order to achieve the objectives proposed in section 2 of the present work the investigation was divided in two phases:

1. A monitoring program carried out during the years 1998 and 1999, in which water samples were taken every two weeks during 1998 and every four weeks during 1999. From these samplings, the data necessary for the establishment of annual behavior patterns of physical, chemical and biological variables were obtained.

2. An experimental program realized between 1998 and 2001 in which 14 enclosure-tests were designed and performed in order to determine the effect of specific environmental variables on the biological communities and on the trophic state of the lake. Additionally, a 24-hours sampling program was carried out to evaluate the daily mixing patterns and its effects on physical, chemical and biological variables, and to verify whether daily vertical migrations of zooplankton take place in the lake, as has been suggested by Steinitz-Kannan et al. (1983).

Climatic data, e.g. air temperature, precipitation, wind velocity and direction were registered by a meteorological station from ecoTech® installed on the shoreline of the lake.

Additionally, already available data on the lake basin, like bathymetry and morphometry, were used in this work for calculation of heat content and thermal stability of the lake. Further information on the catchment area such as aerial photography, cartographic maps, slope maps, soil maps and vegetation maps were also used (Appendices B-D).

As part of the Lake San Pablo investigation program, additional studies were carried out by other co-workers. Identification of macrophytes and the characterization of its distribution pattern in the littoral zone of the lake were achieved in 1996 (Kiersch et al., 2003). Sediment samples were taken between July and August 1998 at different spots of the lake with a sediment corer sampler. Physical and chemical characterization of sediment cores was made with standard methodology and dating was performed using ^{210}Pb (Gunkel, 2003). The macroinvertebrates of the littoral area were also collected and identified. The structure and dynamic of the main water inflow, the River Itambi was studied by Carrera (2002; Carrera & Gunkel, 2003). Some of these results have been used in the context of this work and will be considered in the results and in the discussion.

Although no specific studies on fish populations were done, some exemplars were captured for their taxonomic identification. Direct observations and information from the local inhabitants were also useful for an evaluation of the fish.

3.1.1 Physical and chemical parameters

A sampling station was established at the deepest point of Lake San Pablo (Figure 1-2). This point was determined with a sonar device from the company UWITEC®. Temperature, conductivity, oxygen, pH and Secchi disk transparency of the water body were measured *in situ*. Temperature and conductivity were measured each 0.5 m with the conductivity-temperature probe LF 196 from WTW®, and transparency with a standard Secchi-disk. Water samples from 3, 6, 9, 14, 20, 25, and 29.5 m for chemical analysis and determination of dissolved oxygen and pH were obtained using a water sampler type 443590 from Hydro Bios®. Oxygen and pH were measured with an oxi-probe type 530 and a pH-probe type 320, both from WTW®.

For chemical analysis, a fraction of each water sample was filtered through filters of cellulose acetate type GF/F with 0.45-µm pore size from Whatman, and together with the non-filtered remainder of the sample were refrigerated at 4 °C until analyses. Chemical analyses were carried out at the "Subsecretaría de Saneamiento Ambiental" in Quito, Ecuador, following the methods described by the American Public Health Association (1989). The following parameters were determined: soluble reactive phosphorus (SRP) from filtered samples using the ascorbic acid method; total phosphorus (TP) from unfiltered samples by the ascorbic acid method with previous sulfuric acid/nitric acid digestion; dissolved inorganic nitrogen (DIN) from filtered samples. The different inorganic nitrogen fractions were determined as follows: a) nitrite-nitrogen with the diazotizing method; b) nitrate-nitrogen with the cadmium reduction method with posterior diazotizing; c) ammonium-nitrogen with the Nesslerization method. Organic nitrogen was determined from unfiltered samples, with the micro-Kjeldahl technique. Total nitrogen (TN) values were obtained as the sum of the values of dissolved inorganic nitrogen and organic nitrogen. Total organic carbon, total inorganic carbon and dissolved organic carbon were determined with a TOC analyzer from SHIMADZU (TOC-5000). Biochemical oxygen demand (BOD_5) was calculated through differential oxygen content. This last was determined with the Winkler method. Silica was analyzed with the molybdosilicate method. The last two mentioned parameters were only analyzed during 1998.

By the middle of 1998, an automatic temperature registration system type multi*Logger* mL with 8 channels with sensors type Pt100 from ecoTech® was installed on a buoyant platform near the western shoreline, at the downwind end of the lake, where the maximal depth is 28 m. With this equipment, air temperature as well as water temperatures at six different depths (0.5, 1.0, 3.0, 9.0, 15.0 and 20 m) were registered every five minutes.

Stability of the stratification and heat content of the lake were calculated using the temperature values registered during the years 1998 and 1999 and the bathymetric map of the lake, according to Scott (1964) and Idso (1973). The stability indicates the quantity of work required to mix the whole water of a lake to a uniform temperature without addition or subtraction of heat, and can be calculated from equation (1). The stability is useful because it quantifies the stratification's resistance to disturbance produced by the wind.

$$S = \frac{1}{A_0} \int_{z_o}^{z_m} A_z (z - z_g)(\rho_z - \rho_m)\, dz \qquad (1)$$

where:

S = Stability (g cm/cm2)
A_o = surface area of the lake (cm2)
z = depth under consideration (cm)
z_o = surface or depth cero
z_m = maximum depth (cm)
A_z = area at depth z (cm2)
z_g = depth of the center of gravity of the unstratified lake (depth of ρm) (cm)
ρ_z = density at depth z (g/cm3)
ρ_m = density at complete mixing (mean density) (g/cm3)

In the present work, the stability values were calculated with equation (2):

$$S = \sum_{z_o}^{z_m} (z - z_g)(\rho_z - \rho_m) \frac{A_z}{A_0} \Delta_z \qquad (2)$$

where ρ_m is calculated as:

$$\rho_m = \frac{1}{V} \sum_{z_o}^{z_m} \rho_z A_z \Delta_z \qquad (3)$$

The heat content of a lake represents the amount of heat in calories that would be released on cooling from its maximum temperature to 0 °C, or the amount of heat that has been transferred to the lake to heat it from 0° C to its maximum temperatures at various depths (Wetzel, 1983). Since the lowest temperature of many lakes is not 0° C, the minimum and maximum temperatures of strata are used to calculate the heat content. Equation (4) was used to calculate the total heat content for each sampling date at the Lake San Pablo:

$$\theta_w = \sum_{z_o}^{z_m} t_z A_z h_z \tag{4}$$

where:

θ_w = heat content of the water in calories
t_z = mean temperature in °C of a layer of water of thickness hz (in cm)
Other parameters as described before.

In order to allow comparisons between different lakes, the heat content is usually expressed as calories per units of surface. Hence, the value of θ is divided by the surface area of the lake, A_o, in cm^2. With these values, it is possible to estimate the heat budget[1] of a lake, which is the difference in heat content over a time interval (e.g. a year). In other words, the annual heat budget is the total amount of heat won during a year expressed in cal/cm^2.

3.1.2 Biological parameters

3.1.2.1 Phytoplankton

For the determination of abundance and biovolume of phytoplankton and for the measurement of the content of chlorophyll *a* (Chl. a), water samples were collected at the depths mentioned under physical and chemical parameters in section 3.1.1, and from additional samples collected at 0.5, 11 and 16 m.

For qualitative and quantitative analysis of phytoplankton species, about 100 ml from each water sample were refilled in polyethylene bottles and preserved with Lugol's solution, according to Schwoerbel (1986). These aliquots were protected from light and transported

[1] The use of the term "budget", as usually defined, is inaccurate but the word is firmly entrenched in the limnological literature. Actually, it makes reference to the heat storage capacity of a lake (Wetzel & Linkens, 1991).

to the limnology laboratory of the Department for Water Quality Control at the Technical University of Berlin, Germany, for later analysis.

In Berlin, the abundance of the most representative species at each sampled depth was determined in all collected samples. Furthermore, for each sampling date, the water samples were separated in three groups according to the depth from which they were taken: upper strata (0.5 to 9 m), middle strata (11 to 16 m) and deeper strata (20 to 29.5 m). Then, integrated samples for each stratum were made taking aliquots of 30 ml from each sample of the corresponding stratum.

All samples were prepared for observation under an inverted microscope type IM 35 from Zeiss by the sedimentation techniques described by Wetzel & Likens (1991) and Utermöhl (1958). Size determination and counting of phytoplankton cells were made according to the methodology proposed by Lund et al. (1958). The estimation of biovolume was made according to Rott (1981b) and Wetzel & Likens (1991). Detailed description of the used methods is presented in appendix E.

Taxonomic identification of phytoplankton and comments on their geographical distribution and ecological features were made using available specialized bibliography (Carney et al., 1987; Donato, 1991a; Donato, 1991b; Fernandez, 1982; Huber-Pestalozzi, 1938; Makarewicz, 1993; Margalef, 1978; Melack, 1979; Molina, 1983; Munawar & Talling, 1986; Rott, 1981a; Whitton, 1968).

For the measurement of Chl. a content, water samples were filtered with a manual pump through glass fiber filters type GF-52 from Schleicher & Schuell within 12 hours after sampling. The exact quantity of filtered water was always registered, which was in every case between 1 and 2 l. The filters were placed into labeled plastic Petri dishes that were protected from light, and then immediately frozen and kept at –20 °C until the extraction and quantification of Chl. a. The extraction and quantification of Chl. a was done according to Nusch (1980). In this method, the extraction of pigments is made with 90% ethanol at 80 °C, and then the quantity of pigments is determined spectrophotometrically. For the present work, a SHIMADZU spectrophotometer, ref. UV-1601, was used.

Since phaeophytins, the degradation products of chlorophylls, absorb light at the same wavelengths but less strongly and both pigments occur in fresh waters, the concentrations of both of them must be estimated for the evaluation of chlorophyll. To do that, the total quantity of pigments is measured spectrophotometrically by determining absorbance at 665 and 750 nm in the filtered extracts. Afterwards, the same extract is acidified, degrading the chlorophyll to phaephytin, and another double determination of the absorbance is carried out at the same wavelength. The chlorophyll concentration can then be determined calculating the difference in absorbance through equation (5), according to Lorenzen (1967):

$$Chl.a\ \left(mg \cdot m^{-3}\right) = \frac{k\, f\left(E_{665\,o} - E_{665\,a}\right) v}{V\, L} \qquad (5)$$

where:

E_{665o}= turbidity-corrected absorption at 665 nm before acidification
= A_{665o} - A_{750o}, where A = absorption value
E_{665a}= turbidity-corrected absorption at 665 nm after acidification
= $A_{665a} – A_{750a}$,
k = absorption coefficient of chlorophyll *a* = 11.0
f = factor to equate the reduction on absorbance to initial chlorophyll concentration, =2.43
v = volume of extract in ml
V= volume of water filtered in liters
L= length of light path through cuvette in cm

3.1.2.2 Zooplankton

Since zooplankters play an important role as major herbivores as well as predators in aquatic ecosystems, it is necessary to evaluate their biomass to understand the metabolism of a lake. Quantitative collection of zooplankton within their natural habitats is in general difficult, because only relatively small sub-samples can be taken from a population, that habitually is very mobile, varying in size and distributed in patches (Wetzel & Likens, 1991).

In addition to the water samples collected for the determination of physical and chemical parameters and of phytoplankton, on each sampling date additional samples for the determination of zooplankton were taken at the same sampling spot. These samples were collected covering three different depth strata: 0 to 10 m, 10 to 20 m and 20 to 28 m. They were taken using a 1.5 m long, 55 µm mesh plankton net from Hydrobios® (ref. 438040), with a 17 cm diameter mouth opening provided with a mouth-closing mechanism.

Each zooplankton sample was transferred to plastic bottles and immediately preserved with 4% sugar-formaline solution with an addition of detergent (Haney & Hall, 1973). These samples were also transported to Berlin for analysis.

Quantitative determination of zooplankton was done according to the methodology proposed by McCauley (1984) with some modifications. Here, specially prepared counting chambers are observed under microscope. A detailed description of the preparation of the counting chambers is presented in appendix F.

The taxonomic identification of zooplankton organisms, whenever possible up to species level, as well as some notes about their geographical distribution and ecological characteristics were made using keys, diagrams and descriptions taken from various scientific publications (Collado et al., 1984; Dos Santos & De Andrade, 1997; Gaviria, 1994; Koste & Böttger, 1989; Reid, 1985; Reid et al., 1990; Rey, 1992; Valdivia Villar, 1988; Villalobos, 1994; Whitton, 1968).

The density D_i in individuals per liter (ind./l) of each zooplankton species or developmental stages were calculated as follows:

$$D_i = N_s \times V_L \qquad (6)$$

where:

N_s = quantity of organisms of species *i* in the original water sample.
- $N_s = n \times V_b / v$, with:
- n = number of organisms or developmental stages of species *i* in sub-sample,
- V_b = volume of sample flask,
- v = volume of observed subsample

V_L = volume of filtered lake water
- $V_L = \pi r^2 d$, where
- r = radius of the mouth of the zooplankton net
- d = vertical distance between the limits of the corresponding stratum.

The zooplankton biomass was determined following the methodology proposed by Masundire (1994a) and McCauley (1984). Here, the biomass is calculated as the product of the abundance of organisms (ind./l) of each species or developmental stages (cohort) multiplied by the corresponding mean dry weight of individuals of the same category. To do this, the organisms were first separated in groups according to their state of development on pre-weighed micro-trays (Sartorius® analytical balance A200s). Then, the length of approximately $n \approx 100$ organisms from a total *m* was measured at 100 magnifications using an inverted microscope with an eyepiece micrometer. After that, each sample with *m* organisms was weighed again and subsequently dried in an oven at 60 °C for 24 hours. Finally, the dry weight was calculated from the difference of both measures. With these dry weight values, a relationship between the body size of an organism and its biomass can also be determined through regression analysis (appendix G).

3.2 Experimental program

3.2.1 Enclosure experiments

In the present work, enclosure experiments were carried out in order to evaluate which environmental factors could play a role in the limitation of plankton production in Lake San Pablo. In these experiments, physical and chemical factors were taken into account. Within the physical ones, the focus was on the question whether algal losses by sedimentation, due to convection currents play a major role as control mechanism by determining the community structure and phytoplankton biomass. Such a factor has been suggested by some authors as a significant controller of phytoplankton dynamic (Knoechel & Kalff, 1975; Margalef, 1978; O'Brien, 1974; Reynolds, 1982).

The effect of ultraviolet radiation was also investigated because of high sun radiation in the Lake San Pablo area, and because it has been demonstrated that it may have deleterious effects on aquatic organisms (Gieskes & Buma, 1997; Häder, 1995; Häder, 1997; Häder, 1999; Hessen et al., 1997; Kinzie III et al., 1998; Lütz et al., 1997; Olesen & Maberly, 2001; Veen et al., 1997).

Spectral irradiance was measured with an optical power meter device from Newport Corporation, Model 1815-C with an 818-series photo-detector, and wavelength-specific filters from SCHOTT®, which were used to cutoff the radiation range of interest, e.g. UV-A, UV-B, infrared, and photosynthetic active radiation, PAR. Within chemical factors that determine the development and composition of plankton, the content and relationship of available nutrients plays a critical role. Especially, phosphorus or nitrogen content can act as a limiting factor in productivity (Roldán, 1992; Wetzel, 1983). For this reason, the effect of an increase in the concentration of these nutrients was also evaluated. In these experiments, phosphorus in the form of $CaPO_4$ and nitrogen in the form of $CaNO_3$ were added in enclosures as nutrient supplements on the first day of the respective experiments.

Conceptual and technical design and construction of the enclosure experiments, also simply called "enclosures", were based on the works of Ravera (1989), Lundgren (1985), Halac et al.(1997), Reynolds et al. (1983) and Carpenter (1993).

Basically, the enclosure technique involves the isolation of a representative part of the entire ecosystem under study, generally by transparent and flexible sheets of synthetic material. According to the objectives of the investigations, the enclosure can be open at both ends and stretch to the bottom of the water body for the isolation of two phases, like water column and sediment, or closed at its deepest end to isolate one phase, e.g. the water column without sediment. Initially, enclosure approaches were used to test ecological hypotheses and to study ecological processes. Later, they have been widely used in fresh water, brackish water and marine environments, not only to study pollution problems and their effects on aquatic organisms, but also in research studies about eutrophication, and the production and degradation of organic matter (Ravera, 1989).

Enclosure experiments are then very useful to test environmental conditions because they are sufficiently large to sustain biological communities under almost “natural” conditions, and at the same time allow a suitable manipulation of experimental factors that can interact with the organisms. Other advantages of the enclosure technique are: a) Initial conditions (e.g. physical, chemical and biological) inside the enclosures are the same as in the natural ecosystem in which the experiment is carried out. b) Initially, the ratios between the different species in the enclosure represent the actual situation in the lake, and the inter-species relationships are not altered. c) Such an isolated system is, at least for a period of time, self-sustaining and contains always several trophic levels. d) Environmental conditions before and after an experimental manipulation (e.g. addition of nutrients, pollutants, etc) are known. e) The possibility of monitoring the experimental manipulations by comparison with a non-manipulated enclosure.

However, some disadvantages should be mentioned: a) Occurrence of a “wall effect”, which induces colonization of the external and internal surfaces of the enclosure with fouling organisms (“Aufwuchs”), that produces changes of biocoenosis composition and reduction of light inputs. b) The form of the enclosure would always be different from that of a natural water body and could cause mechanical reduction of mixing and therefore more sedimentation. c) Limited stability of the system in time.

Finally, the installation and operation of enclosures are costly and time consuming, which makes it sometimes difficult to install enough of them to assure statistical replication of experimental treatments. In such cases, the interpretation of results is reduced to two fundamental aspects, as Carpenter (1993) pointed out: Does the system change? If so, does the manipulation cause it? In experiments done without replications only the first question can be answered statistically. In order to answer the second one affirmatively, it must be demonstrated that the manipulation is the most plausible reason for the change.

Enclosure experiments were carried out at different times between March 2000 and March 2001. All of them were installed at the buoyant platform mentioned in section 3.1.1 and shown in Figure 3-1. The enclosures were constructed with a transparent tubular polyamide-polyethylene film (Trikuron-S with 1.0 m of diameter, from BP-Chemicals) with an external metal ring for stabilisation, as can be seen in Figure 3-2. All enclosures were made to isolate only part of the water column, and were therefore closed at the deepest end. For all experiments, each enclosure was first filled with lake water and then fixed to the platform. For the experiments where the effect of ultraviolet radiation should be tested, the corresponding enclosures were additionally wrapped with a synthetic film with ultraviolet filter (GUVS-11 from Securfol$_{®}$), which excludes ultraviolet radiation A (UV-A) and B (UV-B), and a cover with the same film was put over the open end of enclosure.

A compilation of the different enclosure experiments with the corresponding dates, length of each enclosure and the designation of the treatments are presented in Table 2.

<u>First enclosure experiment</u>

The first enclosure experiment was carried out between March 28th and April 14th 2000 during the rainy season and the stagnation phase in the lake. In this experiment, one 7 m deep enclosures was installed at the buoyant platform. It was exposed to natural light conditions and designated as “Enclosure”. Since closed enclosures could reduce the effect of phytoplankton loss toward deeper layers caused by diurnal mixing processes, the effect of convection currents on the development of plankton could be studied here. This first experiment was made also to test the reliability of enclosure experiments.

Figure 3-1. Set of enclosures at the buoyant platform.

Figure 3-2. View of a self-constructed enclosure coated with UV-filter film and its corresponding cover.

Table 2. Enclosure experiments carried out during stratification and overturn periods. Lake San Pablo was sampled as reference system.

Experiment number and date	Enclosure 1 - Designation - Length (m)	Enclosure 2 - Designation - Length (m)	Enclosure 3 - Designation - Length (m)	Enclosure 4 - Designation - Length (m)
1st experiment March-April 2000	- Enclosure - 7 m			
2nd experiment August 2000	- Without UV - 2.5 m	- Control - 2.5 m	- Without UV - 7 m	- Control - 7 m
3rd experiment August-September 2000	- N-supplemented (0.8 mg/l N) - 7 m	- P-supplemented (0.15 mg/l P) - 7 m	- Without UV - 7 m	- Control - 7 m
4th experiment March-April 2001	- N-supplemented (N1) (1.5 mg/l N) - N-supplemented (N2) (0.2 mg/l N)	- P-supplemented (2.0 mg/l P) - 7 m	- Without UV - 7 m	- Control - 7 m

Second enclosure experiment

The second enclosure experiment was performed during the dry- and strong winds season, between 5th and 17th August 2000, corresponding to the overturn period. This time, four enclosures with two different lengths, 2.5 and 7 m, were installed at the buoyant platform. Here again, the convection currents but also the effect of elimination of ultraviolet radiation were analyzed in enclosures with UV-filter, referred in Table 2 as “Without UV”, against control enclosures without UV-filter, referred as "Control". Since there were enclosures of two different lengths, and organisms in the shorter enclosures are confined to the superficial stratum, it became possible to analyze whether there were differences caused by longer and/or stronger exposure to UV radiation.

Third enclosure experiment

In the third experiment, carried out also during the dry season and the overturn period between August 25th and September 13th 2000, four 7 m long enclosures were installed at the buoyant platform. In addition to the analysis of the effect of ultraviolet radiation on the development of plankton, also the effect produced by an increase in the concentration of phosphorus, added in form of $CaPO_4$ and referred as "P-supplemented", and nitrogen, added in form of $CaNO_3$ and referred as "N-supplemented", was studied against a control enclosure.

Fourth enclosure experiment

For the fourth experiment performed during the rainy and stagnation season between March 26th and April 11th 2001 four 7 m long enclosures were used. This time, similar aspects analyzed in the third enclosure were evaluated again in order to determine the differences caused by the prevailing climatic conditions in the different seasons and to verify the obtained data. The experimental approaches for the enclosures nominated "P-supplemented", "Without UV" and "Control" were as described above. In contrast, the addition of nitrogen was carried out in two phases using different nitrogen concentrations and two different enclosures. First, a nitrogen amount to obtain a concentration of 1.5 mg/l was added to the enclosure designated in Table 2 as “N1-supplemented”, which was observed during 7 days. Then, a second enclosure, referred as “N2-supplemented” was built up and a nitrogen amount to obtain a concentration of 0.2 mg/l was added. This enclosure was monitored from the 7th to the 16th day.

For all enclosure experiments, enclosure water as well as lake water samples were taken each second day for analysis. The sampling methods and the preparation of the samples for the subsequent determination of physical, chemical, and biological parameters were done with the same methodology explained in section 3.1.1 and 3.1.2 with the following variations:

- Water samples for dissolved oxygen, pH, and conductivity measurements as well as for nutrients analysis, phytoplankton and Chl. a determination were taken at 3 m in the 7 m enclosures and at 1 m in the 2.5 m enclosures;
- Zooplankton samples were collected with a 0.5 m long, 55 µm mesh opening zooplankton net from Hydrobios, ref. 438000, with mouth diameter opening of 25 cm, and haul samples were taken from the bottom of the enclosures to the surface;
- Chemical analyses of the samples from the first to the third experiments were done at the laboratory of the Subsecretaria de Saneamiento Ambiental in Quito. The samples for chemical analysis from the fourth experiment were adequately preserved following the recommendations of Mackereth et al. (1989) and then transported to Berlin. These samples were analyzed for nitrate and nitrite by flow injection analysis, FIA (Michel, 2000), and for total phosphorus and SRP by the

acid digestion and ascorbic acid method at the laboratory of the Water Quality Control Department of the Technical University of Berlin.

3.2.2 24 hours monitoring for an analysis of short-term mixing processes and zooplankton vertical migration

With the purpose of analyzing the effects of daily variations of environmental parameters such as temperature and wind patterns on physical, chemical and biological variables, three sampling series were performed, each one covering a period of 24 hours at a specific date within the hydrological cycle.

The first of these sampling series was carried out during the stratification phase, between 18^{th} and 19^{th} March 1998 at 8:55, 13:00, 21:20 and 2:55 hours.

The second set of samplings was carried out after the beginning of the stratification process, between 27^{th} and 28^{th} October 1998 at 16:00, 22:00, 3:30 and 10:00 hours.

The third and last sampling series took place when the beginning of the overturn in 1999 was detected, between 19^{th} and 20^{th} April at 17:00, 1:45 and 6:30 hours. Here, some of the variables analyzed in the routine program were also investigated. Methods used for sampling and for physical, chemical and biological parameter determinations were as described in the corresponding section.

The sampling dates are marked on Figure 4-5 showing also the corresponding thermal phase. Additionally, in Table 3 the parameters analyzed in each sampling series are shown

Table 3. Parameters analyzed during 24-sampling series.

Date of sampling	**Analyzed parameters**			
	Physical	**Chemical**	**Zooplankton**	**Chl. a**
18-19 March 1998	✓		✓	
27-28 October 1998	✓		✓	✓
19-20 April 1999	✓	✓	✓	

4 Results

4.1 Morphological characteristics of the basin

The hypsographic curve and depth-volume curve of the lake are shown in Figure 4-1. They were elaborated with data available from EPN (Escuela Politécnica Nacional, 1995). The depth-area curve represents also a slope curve diagram, which also shows the strong inclination of the shores. It shows that at a short distance from the shoreline depths up to 20 m are already reached. From this depth, the slope then decreases sharply to a depth of 30 m, with abrupt inclinations that can go as low as 35 m in some sectors of the lake.

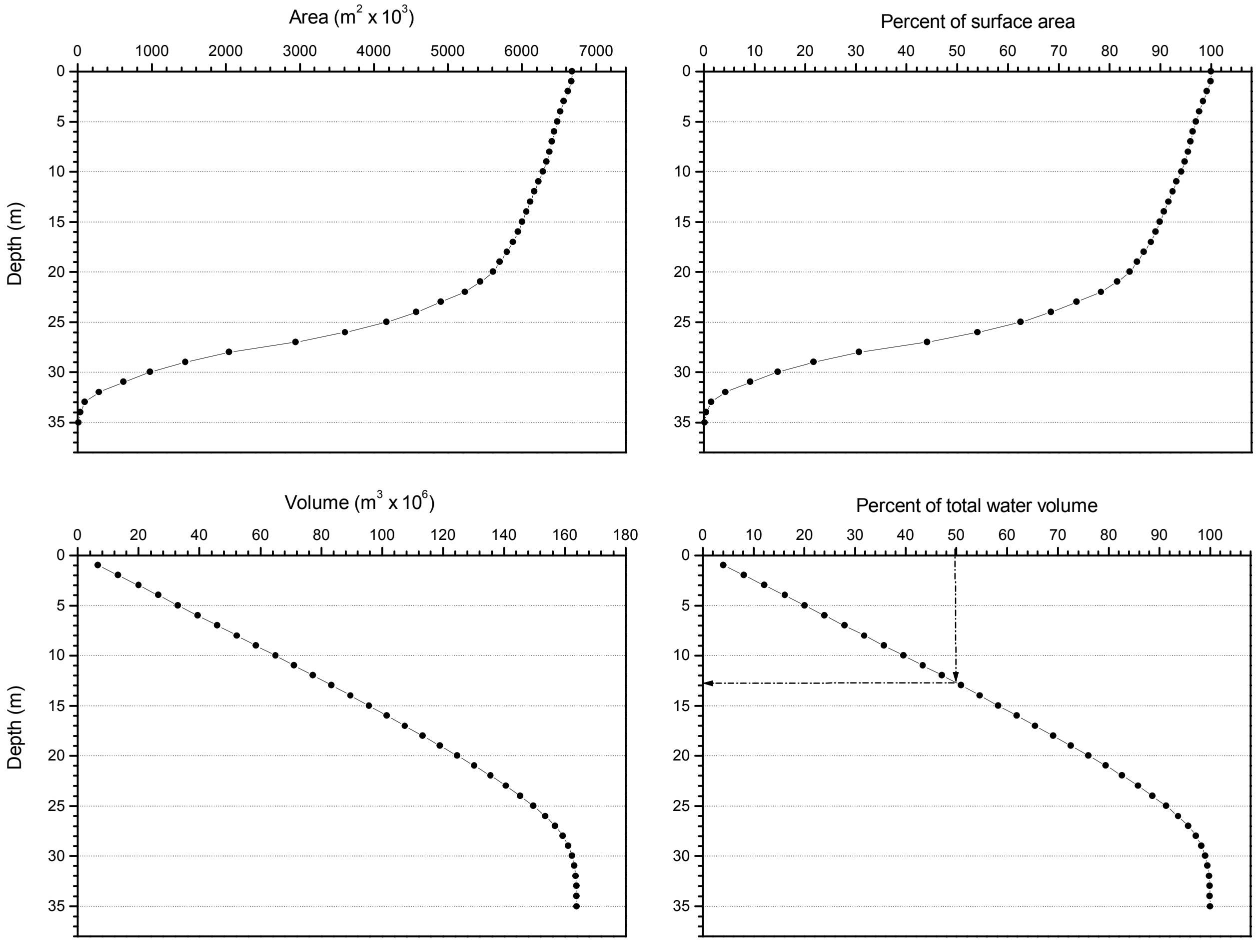


Figure 4-1. Hypsographic curve and depth-volume curve of Lake San Pablo.

In this Figure is also shown that 50% of water volume is reached at a depth of 13 m . Considering that the compensation depth (Z_{eu}) lies between 6.4 and 8.1 m, with a mean value of 7.3 m (Gunkel & Casallas, 2002b), the water volume in the euphotic zone would be 47.2 x 10^6 m^3 according to extrapolation on the volume curve. This value corresponds approximately to 29% of the total water volume. Furthermore, the ratio between tropholytic and trophogenic water volume is 2.43. This ratio has important implications for the production-decomposition relationship, as well as for the content of oxygen and its distribution in the deepest layers.

4.2 Monitoring program

4.2.1 Climatic characteristics of Lake San Pablo area

Air temperatures and wind velocities registered during the years of the investigation are shown in Figures 4-2 and 4-3 respectively.

Mean multi-annual air temperature was 8.3 °C during the night and 22.7° C during the day. The Figures show that weather conditions in general are calm in the morning and the night, with strong winds in the afternoon, principally during dry season. The highest temperatures are registered around noon, leading to heating up of the lake’s surface. Notwithstanding sunny conditions in the afternoon, air temperature falls as consequence of the winds and continues to decrease during the night reaching its lowest level around 5:00 a.m.. With sunrise around 5:30 a.m., air temperature begins to rise again.

In general, regional wind patterns show a lower velocity during the first months of the year coinciding with the rainy season. In the dry season, during the second semester of the year, the winds become stronger. However, the winds clearly vary from year to year. Winds were weaker at the end of 1998 and stronger and more prolonged during 1999 and 2000.

4.2.2 Transparency

Transparency values registered with Secchi disk during 1998 and 1999 varied between 2.1 and 4.2 m, with a mean value of 3.0 m, as shown in Figure 4-4. In 1998, a maximum value of 4.2 m was registered on 18th March during the rainy and stratification season. The lowest values were found during stratification periods on 23rd April and 11th November. In 1999, the highest values of transparency were registered already on 19th February, again during the rainy season. The lowest values lay between 2.1 and 2.4 m and they were measured towards the middle of the year.

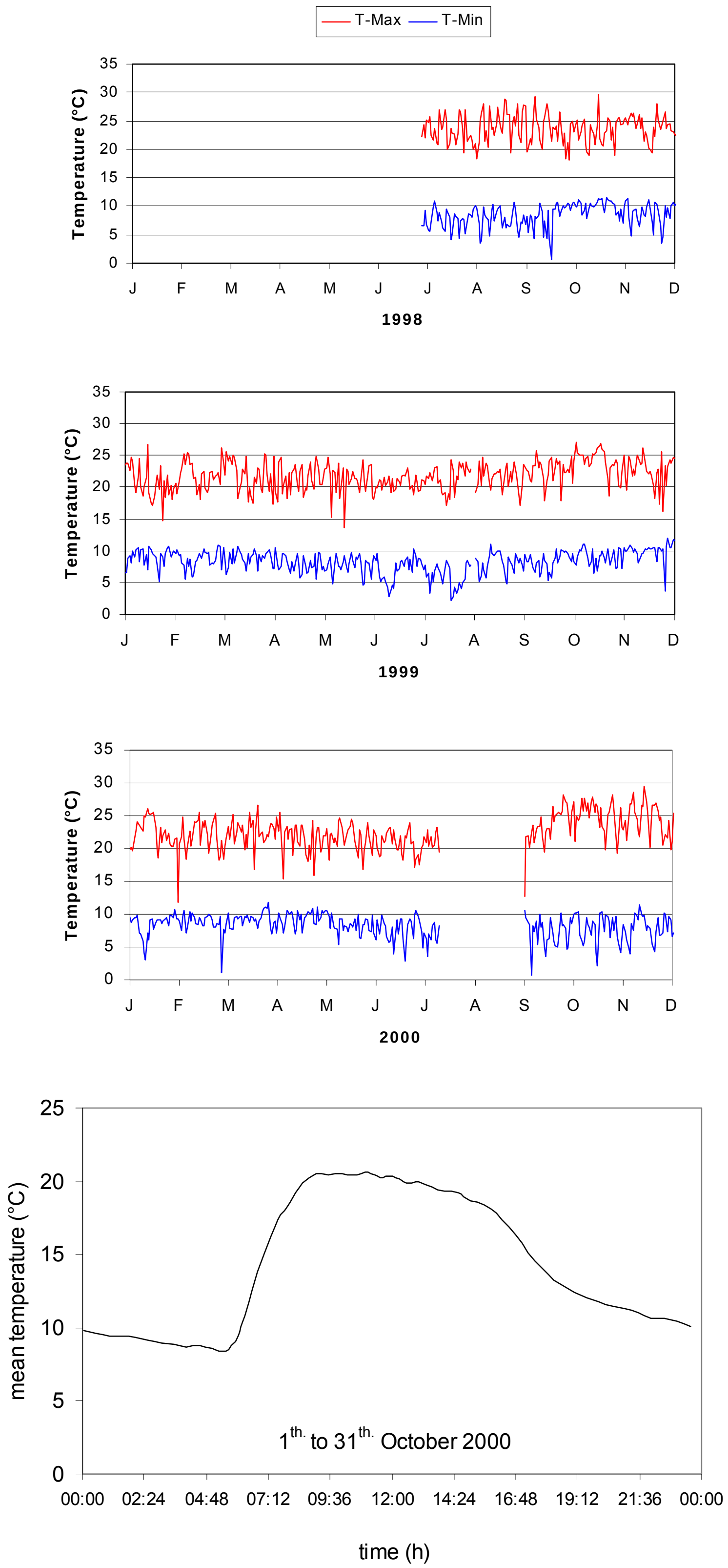


Figure 4-2. Maximal and minimal air temperatures (above) and daily temperature variation (below) in the region of Lake San Pablo during the experimental time.

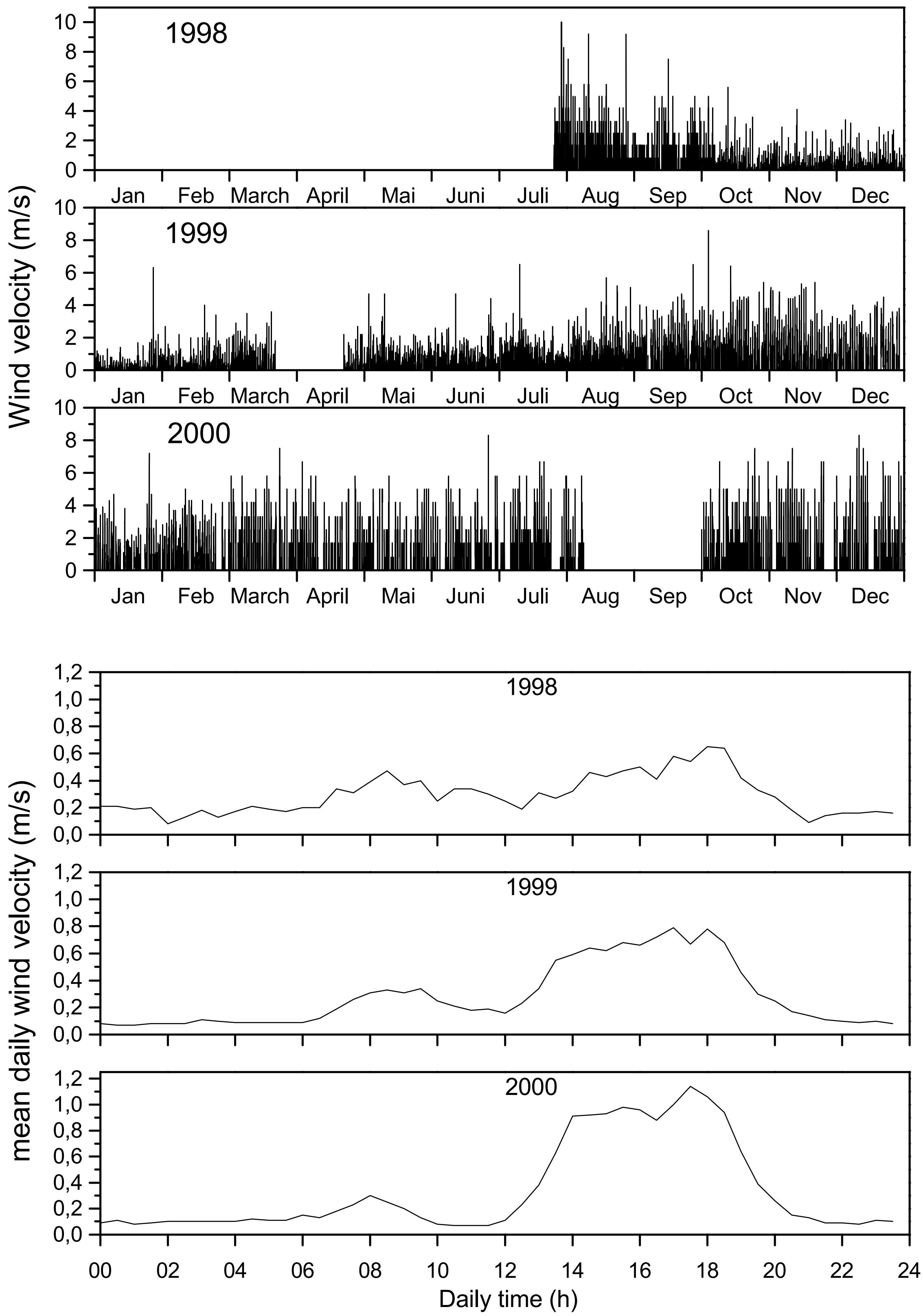


Figure 4-3. Wind velocity in Lake San Pablo area. Top: daily values from each year. Bottom: mean daily wind velocity of wind events > 0.1 m/s. No registration were made during March-April 1999 and August-September 2000 due to a equipment damage.

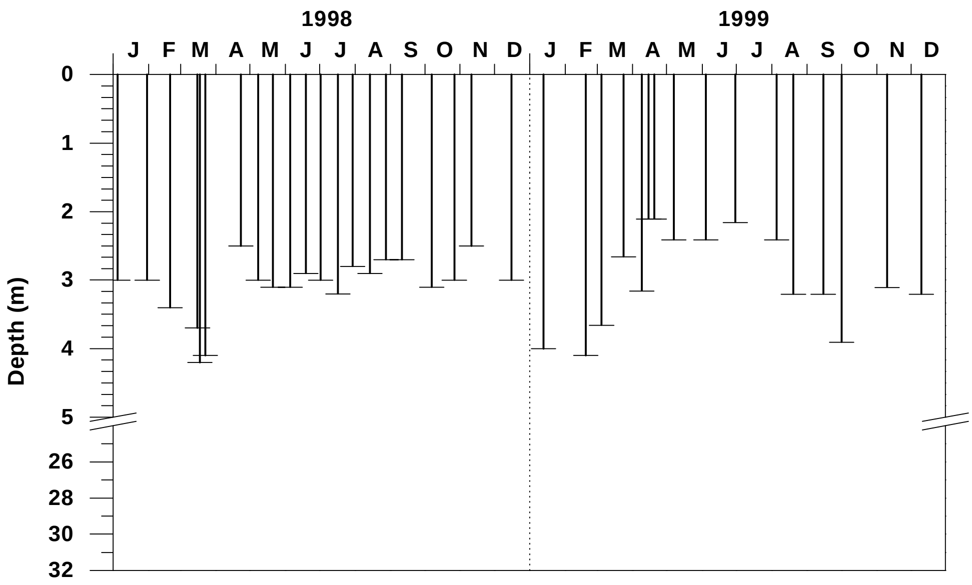


Figure 4-4. Values of Secchi-disc transparency (m) during 1998 and 1999.

4.2.3 Thermal behavior of the water body

Water temperatures registered each 0.5 m depth during 1998 and 1999 are shown in Figure 4-5. Each line represents the temperature at a specific depth (e.g. 0.5, 1 m etc.), with the upper lines corresponding to temperatures in the superior strata, where they were higher and showed stronger variations, and the inferior lines correspond to temperatures in deeper layers.

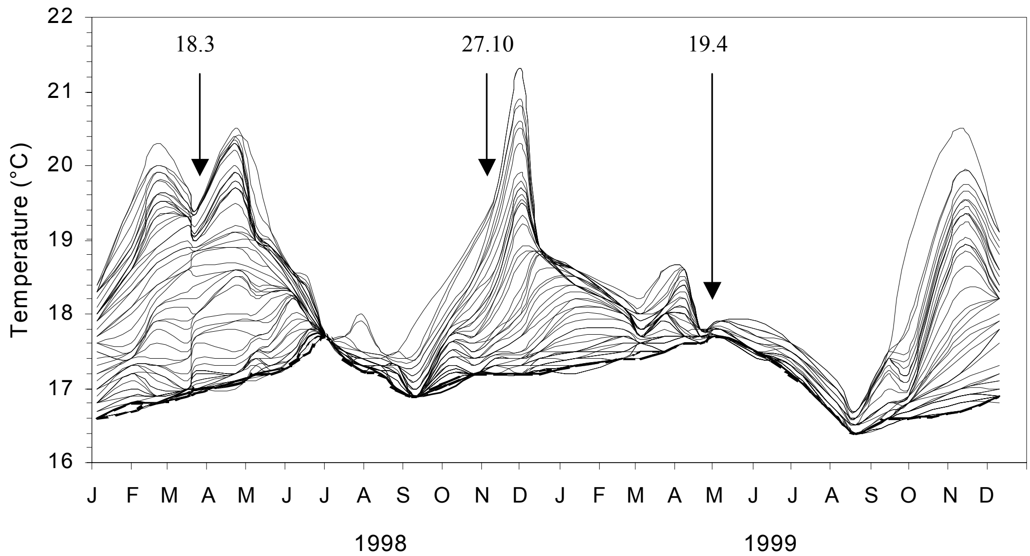


Figure 4-5. Water temperature registered every 0.5 m. Each line corresponds to the temperature at one specific depth. The dates marked above correspond to the 24-hours sampling series.

During the two years of sampling, the minimum temperature registered at 0.5 m was 16.7 °C in August 1999 and the maximum temperature was 21.3 °C in December 1998. This implies a temperature difference of 4.6 °C between the highest and lowest registered temperatures at this depth. At 29.5 m, the difference between the maximum temperature of 17.6 °C in July 1998 and the minimum of 16.4 °C in August 1999 during the same period was only 0.8 °C. The highest temperature difference found on one sampling date throughout the whole water column was 4.1 °C, measured in November 1998.

Thermal data are represented as isopleths diagrams in Figure 4-6. Due to the performed calculations, rare and extreme values are not represented. Nevertheless, this did not interfere with the data analysis. In general, a period of overturn occurs around the middle of the year, from June to August, with a period of thermal stratification between September and May. Stratification and circulation phases showed differences in the exact time when they started and in their duration, varying according to the prevailing climatic conditions of each year.

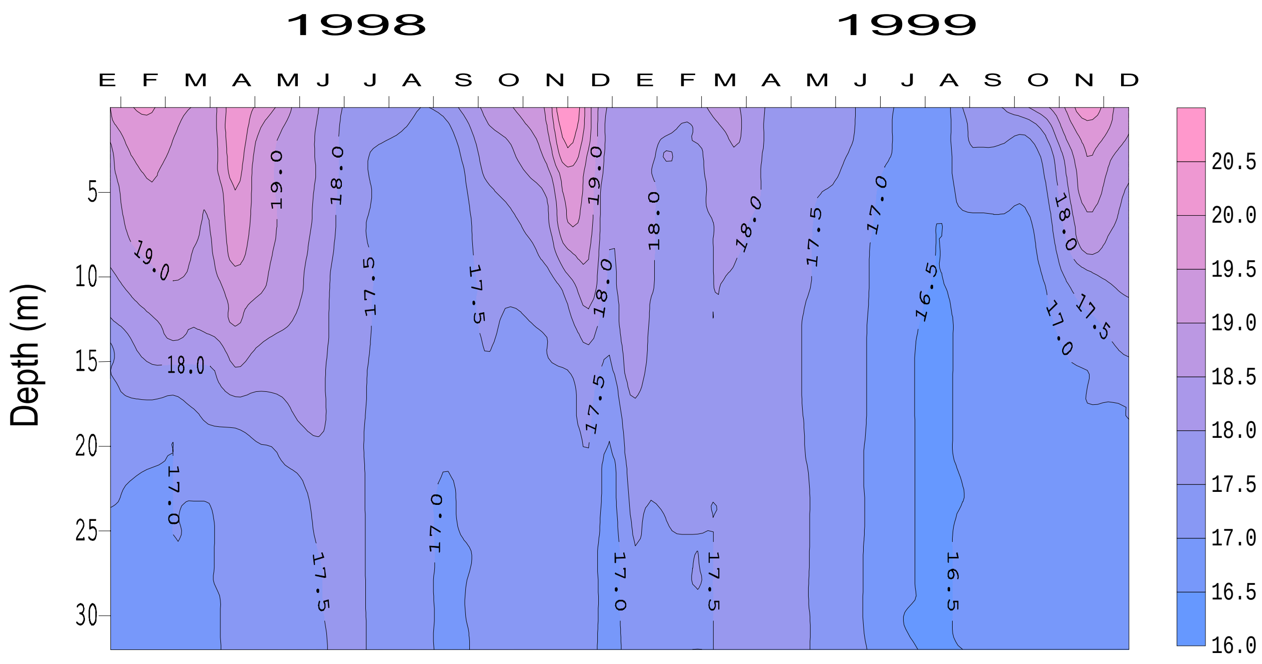


Figure 4-6. Isopleths of water temperature (°C) in Lake San Pablo.

Thus, the year 1998 begun with a thermal stratification that lasted until the end of June, with an overturn period from early July until the end of August. Early in September, the stratification process began again, continuing until April 1999. At the end of April, a new mixing period began and continued until the end of August when the winds became weaker supporting the formation of a new stratification.

In 1999 the stagnation phase during the rainy season was shorter that in 1998, and the period of circulation lasted longer with lower temperatures. A decrease in the temperature of the water column from 17.7° C to 16.7° C was registered at the end of August (Figure 4-5)

4.2.3.1 Stability of the stratification and heat content of the lake

In 1998 the greatest stability was reached during the period of maximum stratification in April, when heat content reached its highest level (Figure 4-7). With the arrival of the dry season and the strong afternoon winds in the months of June and July, the overturn period began, which was directly linked to a decrease in stability. The temperature profile on 2nd July coincided with a moment of absolute isothermy, with a temperature of 17.7 °C along the water column (Figure 4-5). At this moment the stability was annulled and some weeks later the heat content reached the lowest level for this year.

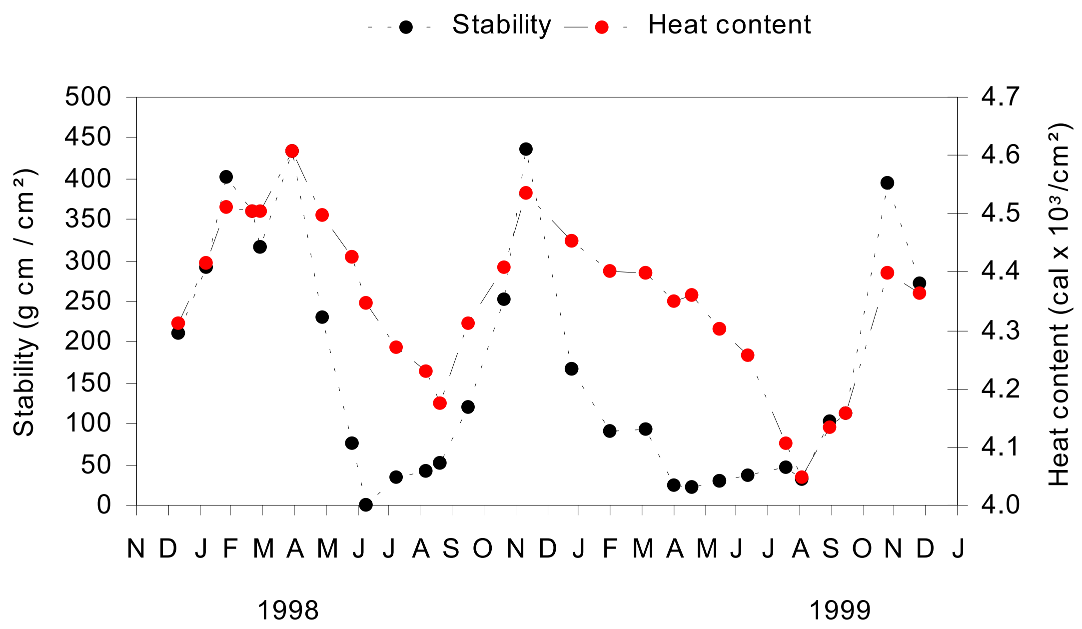


Figure 4-7. Stability of the stratification and heat content in the lake.

Although stability and heat content patterns in 1999 were similar to those of 1998, there was a change in their magnitudes. In 1999 there was no isothermy during the overturn between April and August as it can be seen in Figure 4-5, and the maximum difference of temperature in the column of water during this overturn period was 0.5° C. Although the stability was low, it was not completely annulled. Nevertheless, the minimum value of heat content was lower than the year before. The circulation period in 1999 was longer than in 1998, because the wind season was longer and the wind velocity faster, as shown in Figure 4-3. The wind effect influenced the heat content of the lake, causing more loss of energy and lower temperature than during 1998. The annual heat budget of the lake reached 350 cal/cm² in both years, 1998 and 1999. These values are comparatively low and are related directly to the annual thermal variation.

The water temperatures registered every two hours with the automatic registration device at 0.5, 1, 3, 9, 15 and 20 m between the 24th and 29th of March, the 17th and 22nd April and the 15th and 19th of June of 1999 are shown in Figure 4-8. These three periods were within the stratification phase between March and April and the overturn phase in June. Diurnal stratifications and nocturnal thermal inversion patterns were observed during the stratification as well as during the overturn period: thermal inversions occurred as low as 15 m depth in March and April (stratification) and as low as 20 m in June 1999 (overturn). Therefore, both the stratification as well as the thermal inversion showed variations in intensity and duration, depending on solar radiation, velocity and duration of winds, cloudiness and night temperature. To get a better appreciation of these phenomena, temperature differences between an upper layer (0.5 m) and a lower layer (20 m) during 1st to 14th April 1999 were calculated (Figures 4-9 A). Differences of temperature between these two layers can change drastically reaching almost 2° C during the day, falling to 0.05° C in the night. The estimated mixing depths, as a result of these thermal changes, can reach a depth of 20 m (Figure 4-9 B). In short, day-night overturns depend on the daily climatic conditions and occur independently of the annual thermal pattern.

4.2.4 Chemical parameters

Results from the analysis of chemical parameters of the water samples taken from Lake San Pablo and the mouth of the River Itambi during 1998 and 1999 are shown in Table 4.

4.2.4.1 Values of pH

During 1998 and 1999 pH values lay between 7.3 and 9.0, showing a clear tendency to alkalinity. The highest pH values were registered toward the top layers. During overturn periods a tendency toward homogeneity could also be observed, as Figure 4-10 shows. The waters of River Itambi showed most uniform values varying between 7.4 and 7.9

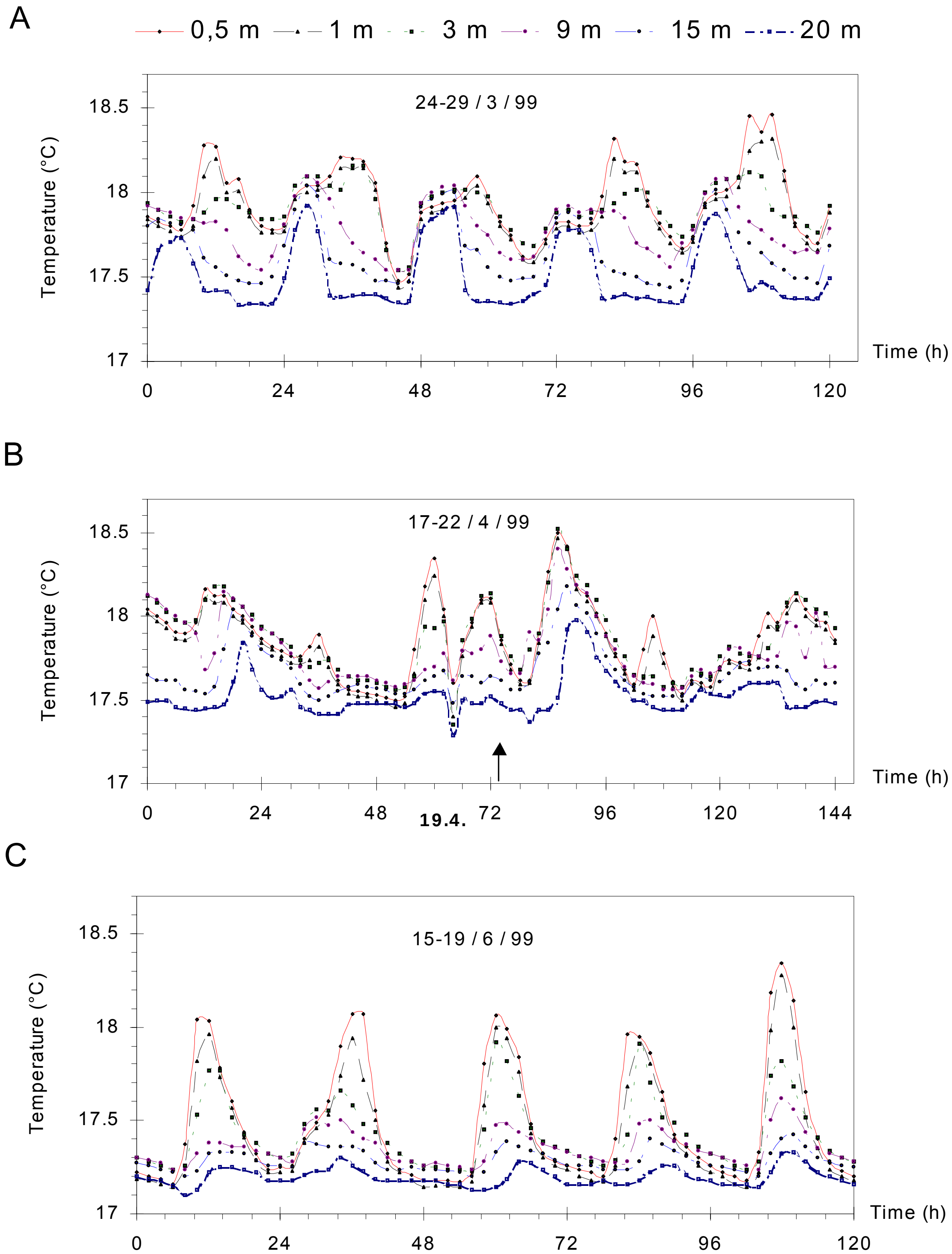


Figure 4-8. Diagrams of daily thermal variations of lake waters during stratification (A and B) and overturn (C). All cases show diurnal stratification and nocturnal cooling. Midnight temperatures during the third 24-hours sampling series (April 19) are shown by an arrow in figure B, indicating an unusually weak stratification.

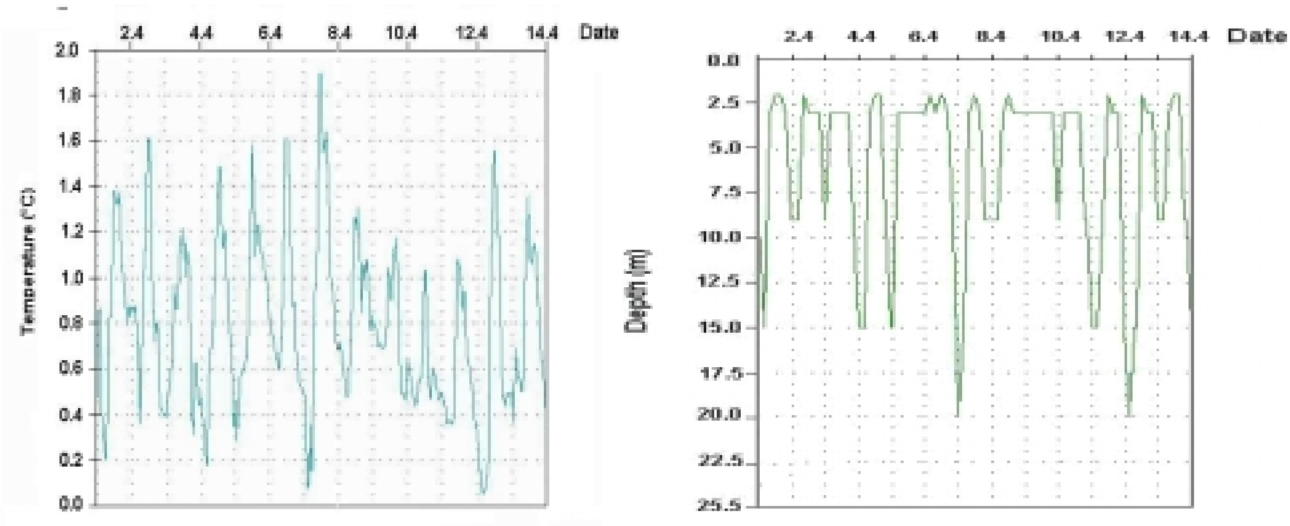


Figure 4-9. A) Temperature difference between an upper (0.5 m) and a lower layer (20 m) at the end of stratification period between 1st and 14th April 1999. B) Resulting daily mixing depth due to nocturnal cooling caused by strong weather changes in the same period.

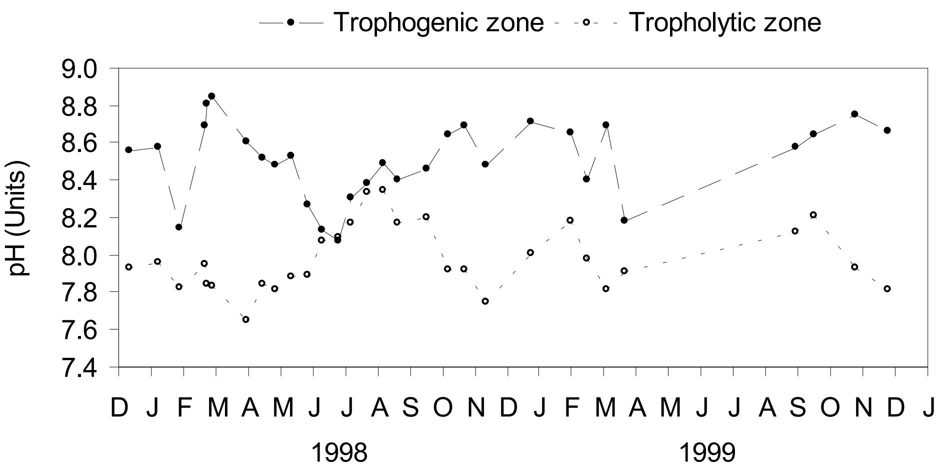


Figure 4-10. Values of pH in the lake during 1998 and 1999.

4.2.4.2 Conductivity

During the time of investigation, the conductivity values varied between 267 and 318 µS/cm, something typical for equatorial and mountain lakes, where mineralisation processes are deficient (Wright, 1927). Mean values for the two years of sampling, as well as the averages for the trophogenic and tropholytic zones are shown in Figure 4-11. Conductivity values were higher during 1998 than during 1999. In both cases, they showed a similar pattern as observed for the temperature: a sort of "stratification" during the rainy season and a tendency to homogeneity during overturn.

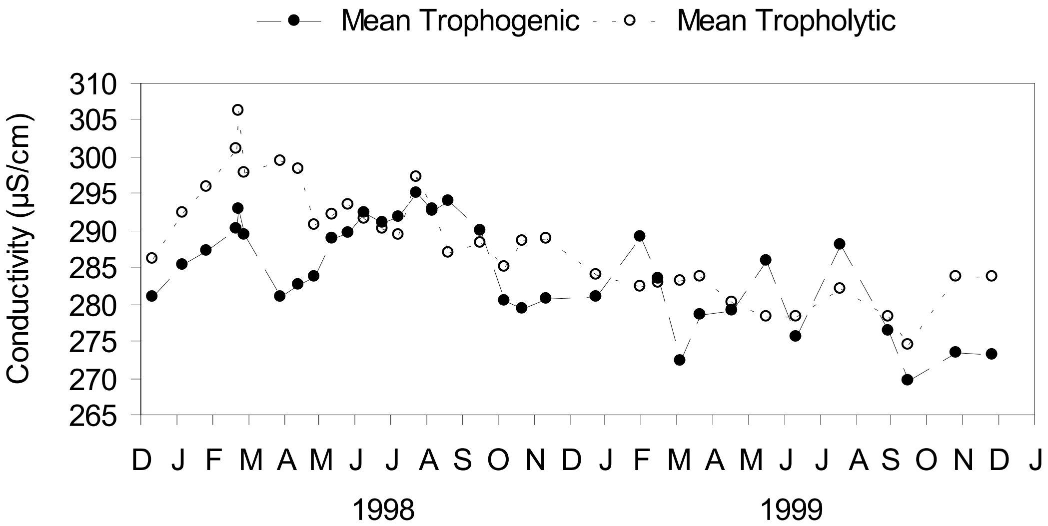


Figure 4-11. Temporal distribution of conductivity values. During 1998, conductivity values were clearly higher in the tropholytic zone than during 1999. During this last year conductivity levels became lower than in the previous year indicating lower salts content.

Table 4. Chemical features of the water in Lake San Pablo and in River Itambi determined during 1998 and 1999.

	Trophogenic zone			**Tropholytic zone**			**River Itambi**		
	Mean	**Min**	**Max**	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**
O_2 (mg/l)	**6.6**	2.6	10.6	**4.2**	0.9	7.4	**6.4**	5.1	8.5
O_2 saturation (%)	**97.8**	38	157	**61.6**	12	107	**87**	68.6	110
pH (units)		7.9	9.0		7.4	8.8		7.4	7.9
Conductivity (µS/cm)	**284**	269	299	**288**	274	306	**249**	169	384
BDO_5 (mg/l)	**3.7**	1.0	7.0	**4.1**	0.3	10.0	**6.1**	3	8
TP (mg/l)	**0.19**	0.06	0.63	**0.24**	0.06	0.59	**0.30**	0.15	0.51
SRP (mg/l)	**0.09**	0.04	0.25	**0.14**	0.01	0.29	**0.16**	0.09	0.27
TN (mg/l)	**0.92**	0.31	1.74	**1.15**	0.27	3.25	**1.7**	0.82	2.72
NO_3-N (mg/l)	**0.044**	0.002	0.237	**0.066**	0.002	0.312	**0.33**	0.002	1.03
NO_2-N (mg/l)	**0.009**	0.003	0.055	**0.037**	0.003	0.155	**0.03**	0.01	0.08
NH_4-N (mg/l)	**0.14**	0.008	1.0	**0.38**	0.008	1.19	**0.68**	0.06	1.78
TC (mg/l)	**32.1**	12.9	47.6	**33.2**	6.1	44.5	**27.5**	8.3	37.9
TOC (mg/l)	**4.3**	0.03	35.2	**3.4**	0.14	34.1	**4.0**	0.35	9.5
TIC (mg/l)	**28.2**	10.4	43.6	**29.9**	0.25	39.7	**23.5**	0.52	33.1

4.2.4.3 Oxygen

The thermal stratification and the overturn in the water column are also linked to the patterns of some chemical parameters, affecting the distribution and re-circulation of nutrients and the content and distribution of oxygen and other gases. Levels of dissolved oxygen registered during 1998 and 1999 are shown in Figure 4-12 as isopleths of percentage of saturation. Water oxygen saturation at 20 °C, calculated according to Mortimer (1981), reached a concentration of 6.4 mg/l. Notably, the oxygen distribution followed the same pattern observed for the temperature. The lowest values of dissolved oxygen concentration in the trophogenic zone were observed during the months of overturn, when the oxygenation of deeper layers took place. Values up to 70 % of saturation were observed along the water column during the overturn, and oversaturation was reached in the superior layers during the stratification period, when an effective oxygen deficit existed in the lower layers. This phenomenon plays a major role in the increment of concentration of soluble reactive phosphorus (SRP) at the sediment-water interface, as will be explained later.

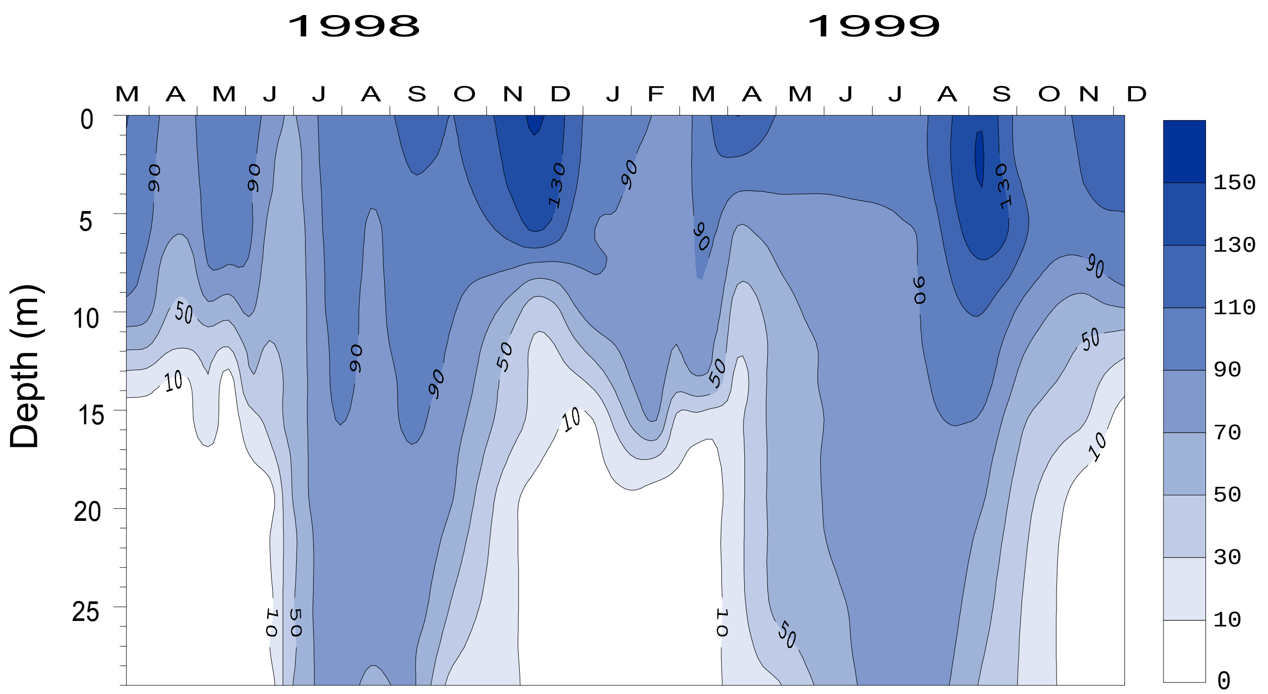


Figure 4-12. Isopleths of dissolved oxygen in Lake San Pablo during 1998 and 1999. Values are given as percent of oxygen saturation. Saturation is reached at a concentration of 6.4 mg/l at 20 °C.

4.2.4.4 BOD_5 values

BOD_5 content was analysed between March 1998 and March 1999, and the vertical distribution of its values is shown in Figure 4-13. During this time, BOD_5 varied between 0.3 and 10 mg/l, with an average of 3.9 mg/l. Between April and May 1998, the highest values were found at the deeper layers (mean = 3.7), while in the superficial zone low values were prevalent (mean = 4.1). Towards the middle of the year, BOD_5 levels tended to homogenize through the whole water column due to the "summer" overturn, reaching 3 mg/l in September. Towards November, when the strongest stratification degree was reached for that year, the levels increased again. Between January and February 1999, BOD_5 levels decreased, being homogenized again in most of the water column. The BOD_5 content followed the pattern of the thermal stratification, and as might be expected, its values influenced the observed levels of oxygen concentration.

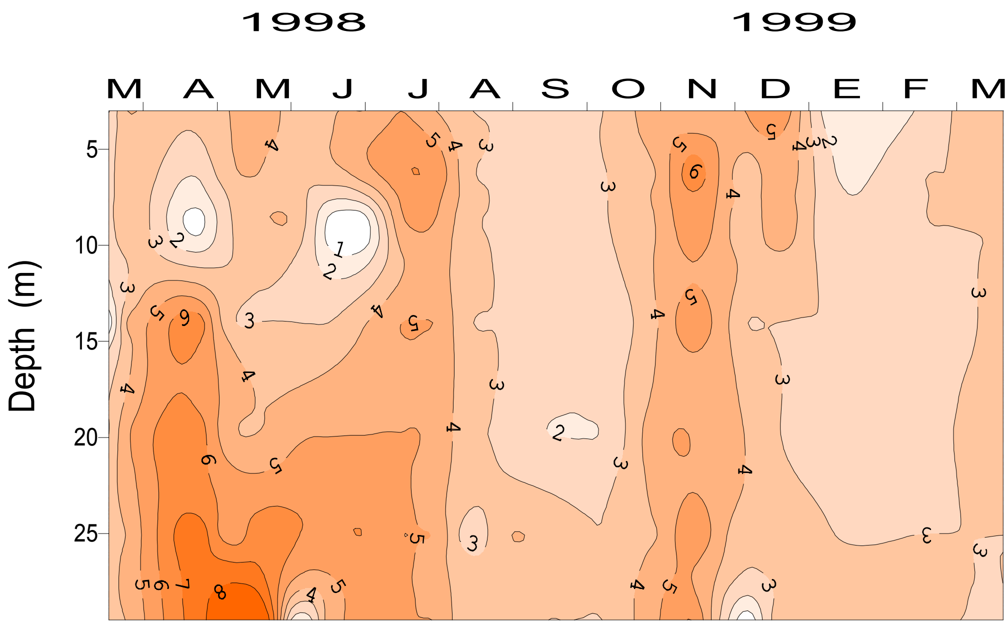


Figure 4-13. Vertical distribution of BOD_5 values in the lake.

4.2.4.5 Nutrients

<u>Total phosphorus (TP)</u>

The concentration of total phosphorus, TP, is shown in Figure 4-14. In the trophogenic zone it usually rose above 0.2 mg/l, with a mean value of 0.19 mg/l and occasionally reached values higher than 0.6 mg/l. In the tropholytic zone, TP values were slightly higher, with a mean value of 0.22 mg/l for the two years. The distribution pattern of TP during those two years was similar to the one observed for the other parameters: homogeneous vertical distribution throughout the water column during overturn and accumulation patches during stratification.

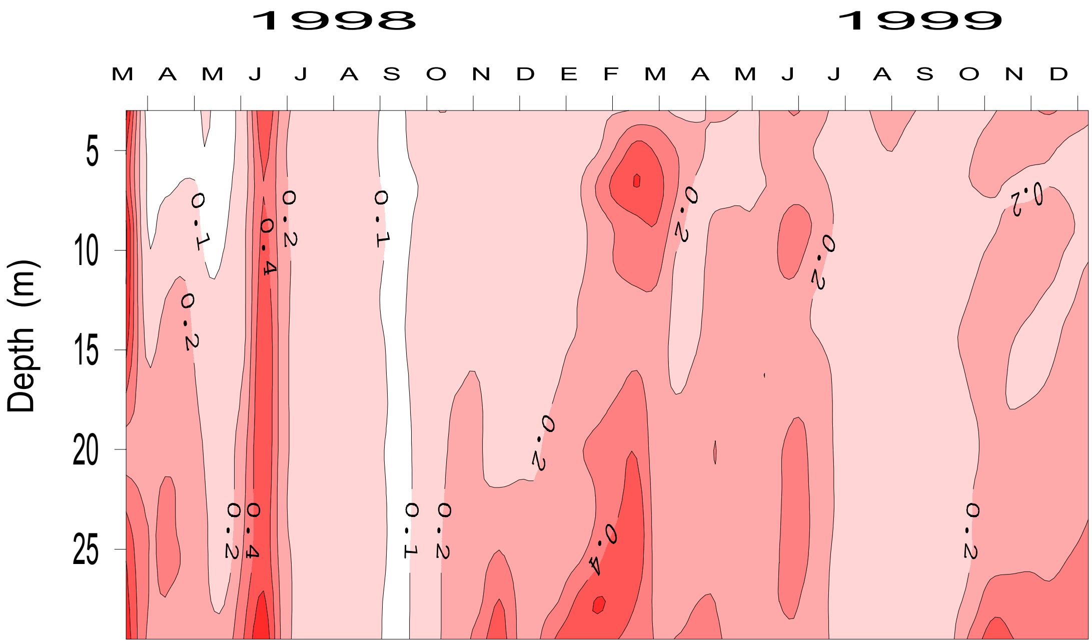


Figure 4-14. Isopleths of total phosphorus (TP) concentration. Values are given in mg/l.

Inputs of nutrients through the River Itambi are considerable. Levels of TP in the inflow waters of the river reached an annual mean value of 0.3 mg/l and the estimated annual load was 2.52 t/a P.

Soluble Reactive Phosphorus (SRP)

Values of soluble reactive phosphorus, SRP, are drawn as isopleths in Figure 4-15, where the vertical distribution of SRP through the water column during the whole sampling period can be seen. A similar distribution pattern, as the one found for the temperature, was registered for SRP. A relatively high concentration of SRP was found throughout the entire hydrological cycle, with a mean value of 0.12 mg/l for the whole lake during the two years of studies and a mean of 0.09 mg/l in the trophogenic zone and of 0.14 mg/l in the tropholytic zone.

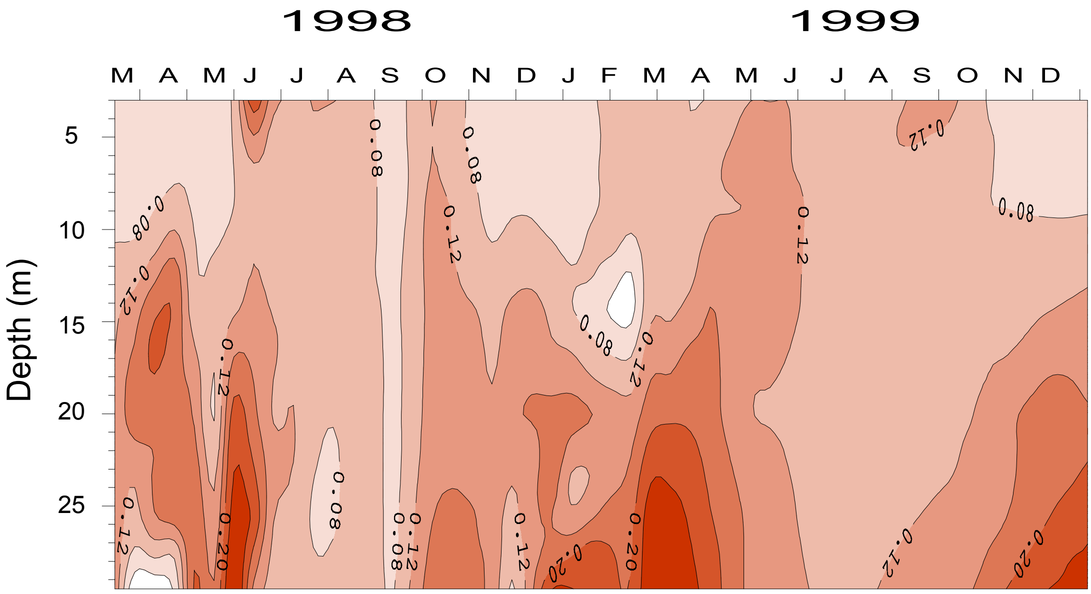


Figure 4-15. Vertical distribution of soluble reactive phosphorus (SRP, mg/l) during the monitoring period.

Low SRP concentrations were observed within the top layers between 0 and 10 m in the trophogenic zone with minimal and maximal values of 0.04 and 0.25 mg/l respectively. The lowest values in this zone were found during the stratification periods on September 1998, between November 1998 and January 1999 and from October until December 1999.

In general, high SRP concentration values were detected in the tropholytic zone, and they were even higher near the sediment-water interface during the stratification phases, when anoxic conditions in these deep layers prevailed, something that supports the release of phosphorus from the sediments (Boström et al., 1982; Boström et al., 1988).

Total Nitrogen (TN)

Concentrations of total nitrogen, TN, varied between 0.27 and 3.2 mg/l, with a mean value of 1.11 mg/l for the two years of analysis. These values are typical for mesotrophic lakes (Vollenweider, 1968) and can be considered high for a lake located above 2,500 m a.s.l. The temporal distribution of mean values for the trophogenic and tropholytic zones can be seen in Figure 4-16 that shows a high variation during 1998 and more constant values from November 1998 until August 1999. There clearly is a tendency to uniform concentration values throughout the water column during the overturn phases.

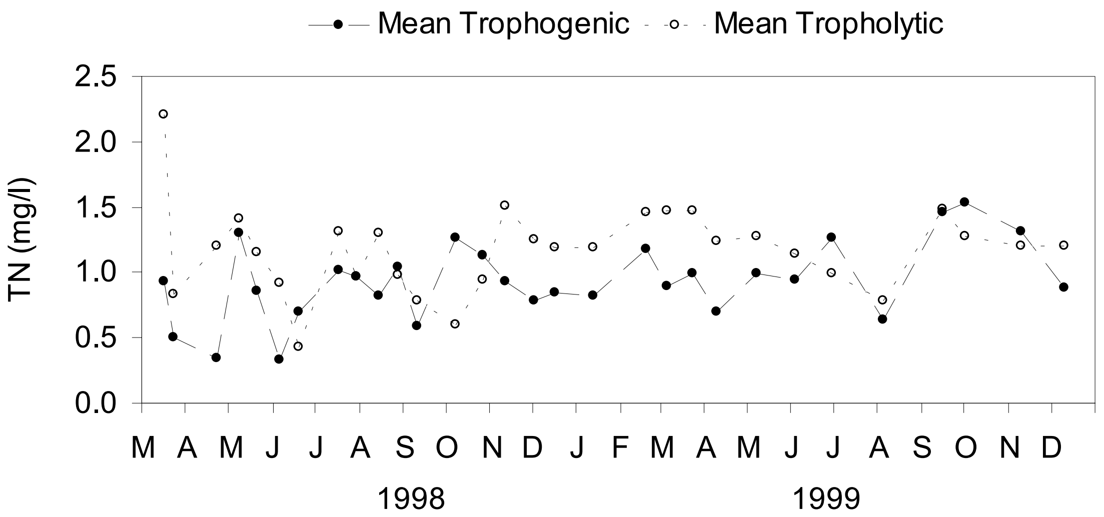


Figure 4-16. Total nitrogen concentration values (TN, mg/l) in Lake San Pablo. Here, the mean trophogenic and tropholytic values, calculated for each sampling date are represented. TN concentration tends to be uniform during overturn.

Dissolved Inorganic Nitrogen (DIN)

The concentrations of dissolved inorganic nitrogen, DIN, are shown in Figure 4-17. In general, these values can be considered moderate, with maximum peaks in the tropholytic zone and minimum ones in the trophogenic zone during the stratification periods. Ammonium was the chemical form of more significance within the inorganic nitrogen fraction, representing more than 90 % during the stratification, and sinking to less than 20 % during the overturn, as can be seen in Figure 4-18

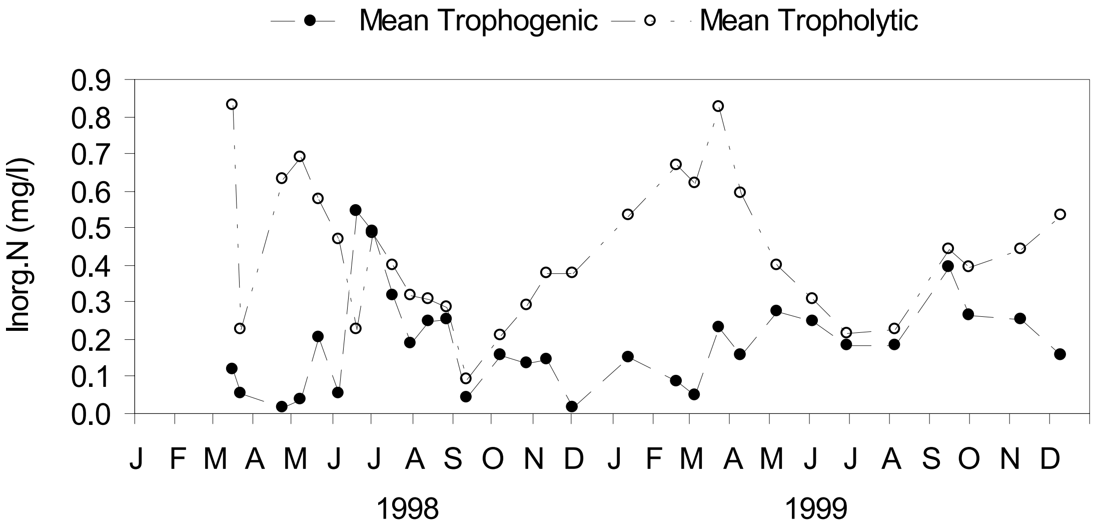


Figure 4-17. Mean values of dissolved inorganic nitrogen in the trophogenic and in the tropholytic zone. The lowest values were found in the upper layers during stratification period.

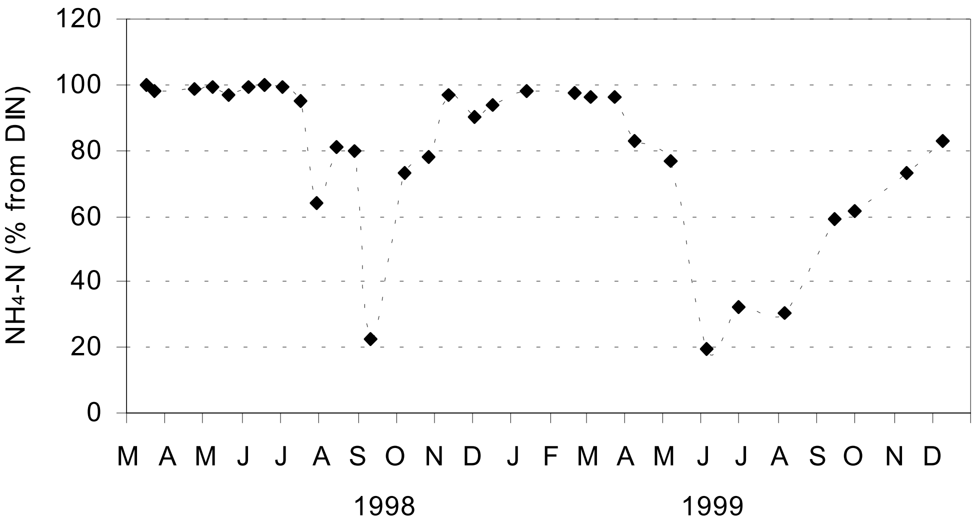


Figure 4-18. Ammonium content as percentage of total dissolved inorganic nitrogen (DIN). During stratification, ammonium represented more than 90 % of DIN, and amounted 20 % during overturn.

Nitrogen:Phosphorus Ratio (N:P ratio)

During part of the hydrological cycle of Lake San Pablo the relationship TN:TP expressed as weight did not reach a value of 10. This indicates a potential limitation of productivity due to nitrogen, as can be seen in Figure 4-19. However, the organic and other insoluble fractions of TN and TP, which are not directly available, are the main factors in this relationship. Since the productivity in a specific moment can be determined by the chemical fractions in solution (Wurtsbaugh et al., 1992), the relationship between DIN and SRP was calculated. This ratio provides useful and precise information about nutrients deficiencies (Figure 4-20). During 1998 and 1999 DIN:SRP ratio reached very low values in the trophogenic zone with a mean 0.18 from the surface down to 9 m depth, and higher values with a mean of 1.27 between depths of 14 and 30 m.

Silica

Values of silica, expressed as mg/l SiO_2, were between 31.7 and 82.5 mg/l, with a mean value of 50.2 mg/l. The values did not show a great variation between trophogenic and tropholytic layers, but did show fluctuations between overturn and stratification periods (Figure 4-21).

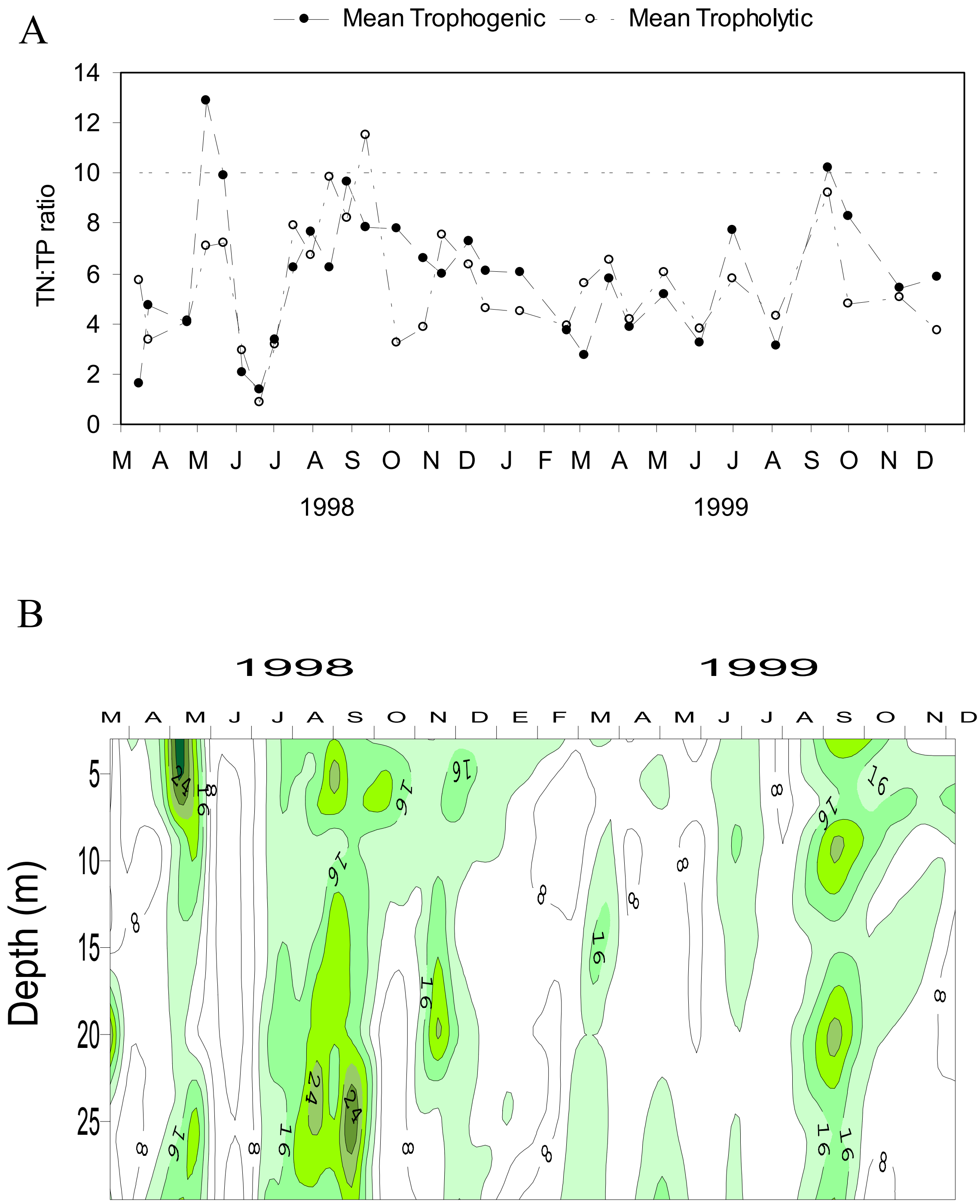


Figure 4-19. TN:TP ratio (weight). A) Ratio expressed as mean value in the trophogenic and in the tropholytic area was almost all the time under 10, indicating a possible limitation of phytoplankton production. B) TN:TP ratio represented as isopleths in order to show the depth-time distribution pattern.

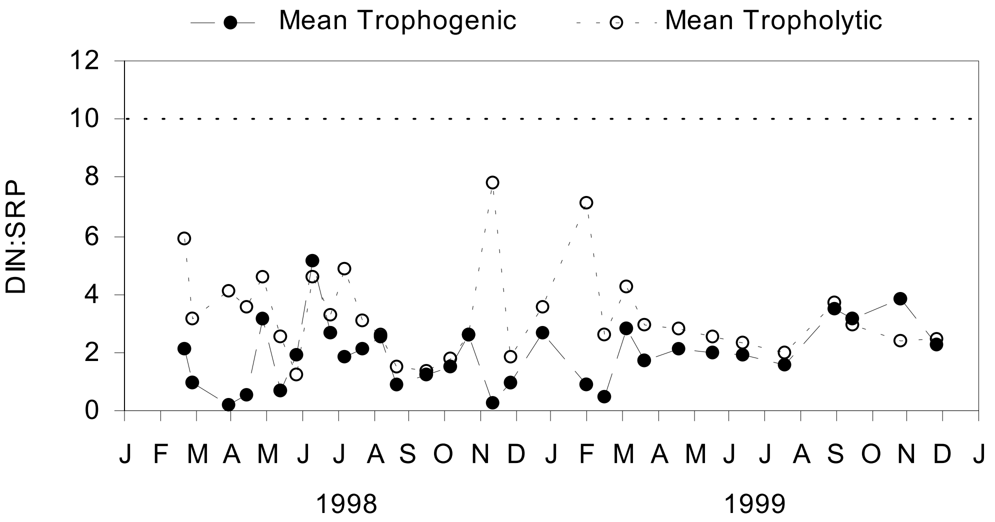


Figure 4-20. Ratio between dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP). The low levels of this relationship, especially in the trophogenic layers, indicate limitation of plankton production by nitrogen.

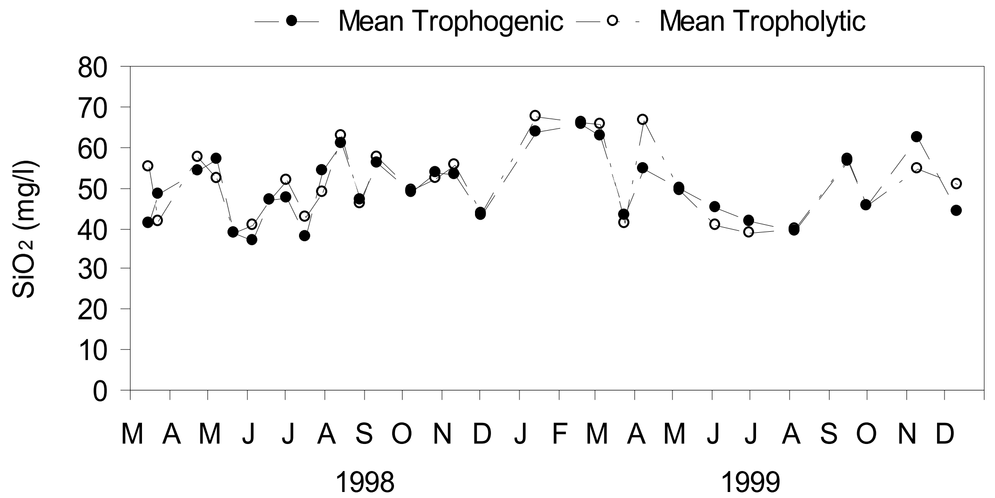


Figure 4-21. Concentrations of silica (SiO_2, mg/l)) in Lake San Pablo. Levels between trophogenic and tropholytic zones did not show high differences throughout the time of investigation. However, the temporal distribution showed the same trend observed for other parameters.

4.2.5 Biological parameters

4.2.5.1 Phytoplankton

Phytoplankton species found in Lake San Pablo, as well as a presence and abundance index is presented in Table 5. Additionally, pictures of *Aulacoseira granulata*, *Pediastrum boryanum*, *Microcystis aeruginosa*, *Neglectella sp*., *Planktosphaeria gelatinosa*, *Scenedesmus linearis* and *Elakatothrix gelatinosa* are presented in Appendix H.

Table 5. Presence and abundance of phytoplankton species found during the present study. The presence index was assigned based on the percentage of samples where the species were found: r = rare (0-25%), s = sporadic (25-50%), f = frequent (50-75%), p = permanent (75-100%). The abundance index was assigned based on the number of organisms of each species found during the two years of study referred to the total number of organisms: vl = very low, l = low, m = medium, h = high.

Species	Presence	Abundance
Cyanophyceae		
Microcystis aeruginosa Kützing 1833	s	l
Cryptophyceae		
Cryptomonas ovata. Ehrenberg	f	l
Cryptomonas sp. Ehrenberg 1838	r	l
Chroomonas acuta Hansgirg 1895	r	vl
Euglenophyceae		
Euglena sp. Ehrenberg 1830	r	vl
Trachelomonas volvocina Ehrenberg1833	f	h
Chlorophyceae, Chlorococcales		
Scenedesmus linearis Kom. 1974	p	h
Ankyra judayi (G.M. Smith) Fott 1957	f	l
Pediastrum boryanum var. *boryanum* (Turp.) Menegh.	p	m
Lagerheimia sp. Chodat 1895	s	l
Oocystis marssonii Lemm 1898	s	l
Oocystis naegelii A. Br. 1855	f	l
Nephrocytium schilleri (Kamm.) Comas 1980	r	vl
Neglectella sp. Vodenicarov & Benderliev 1971	p	l
Planktosphaeria gelatinosa G. M. Smith 1918	s	l
Sphaerocystis schroeteri Chod 1897	r	vl
Golenkinia radiata Chod 1894	r	vl
Monoraphidium komarkovae Komarkova-Legnerova 1969	r	vl
Lagerheimia sp. Chod 1895	r	vl
Elakatothrix gelatinosa (Snow) Printz Sensu Skuja 1948	r	l
Coelastrum microporum Näg. in A. Br. 1855	r	vl
C. pseudomicroporum	r	vl
Chlorophyceae, Volvocales		
Chlamydomonas sp.	r	h
Dynophyceae, Peridinales		
Peridinium sp. Ehrenberg 1838	r	l
Gymnodinium sp. Stein 1878	r	vl
Chlorophyceae, Zygnematales		
Cosmarium sp. Corda Ex Ralfs 1848	r	vl
Diatomeae		
Aulacoseira granulata (Ehrenberg) Simonsen 1979	p	h
Fragilaria ulna (Nitzsch) L-Bertalot 1980 var.ulna	r	vl
Nitzschia sp. Hassall 1845 nom. cons.	r	vl
Cocconeis sp. Ehrenberg 1838	r	vl
Cymbella sp. Agardh 1830	r	vl
Gyrosigma sp. Hassal 1843	r	vl

During the two years of research, only 32 phytoplankton species were identified. This can be considered a rather low species diversity. The flora consists of cosmopolitan species and its composition reflects eutrophic conditions. The majority of species belongs to Chlorophyta and Bacillariophyta and has a life-form typical of turbulent systems. The phytoplankton community is dominated by the Chlorophyta *Scenedesmus linearis* and *Pediastrum boryanum,* the diatom *Aulacoseira granulata,* and the Euglenophyta *Trachelomonas volvocina.* All of them showed a stable presence through the hydrological cycle and their abundance was moderate to high. Other species found almost all the time but in lower abundance were *Cryptomonas ovata*, *Ankyra juday*, *Oocystis naegelii* and *Neglectella sp.*. The occurrence of Cyanobacteria was sporadic and when occurring, was of low abundance, with *Microcystis aeruginosa* being the only species belonging to this group observed between July and December 1998 and in November 1999.

The mean value of abundance and biovolume of phytoplankton, calculated for the trophogenic and for the tropholytic zone is shown in Figures 4-22 and 4-23. The abundance varied between 1,000 and 12,000 n/ml in the trophogenic zone from 0.5 to 9 m depth, and between 200 and 7,500 n/ml in the tropholytic zone from 11 to 29.5 m.

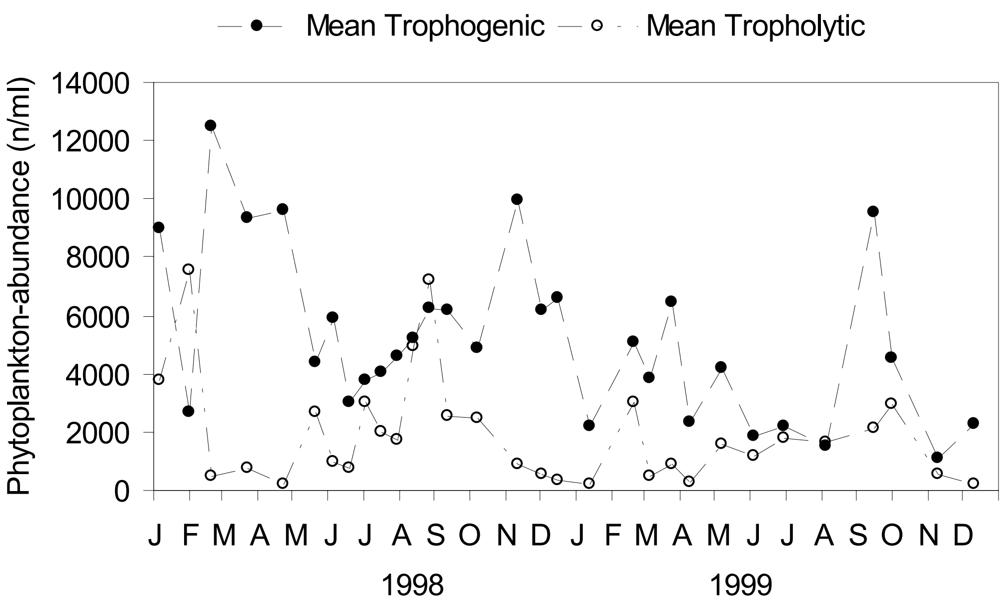


Figure 4-22. Temporal distribution of phytoplankton abundance in Lake San Pablo. Mean values for the trophogenic and the tropholytic zone are represented.

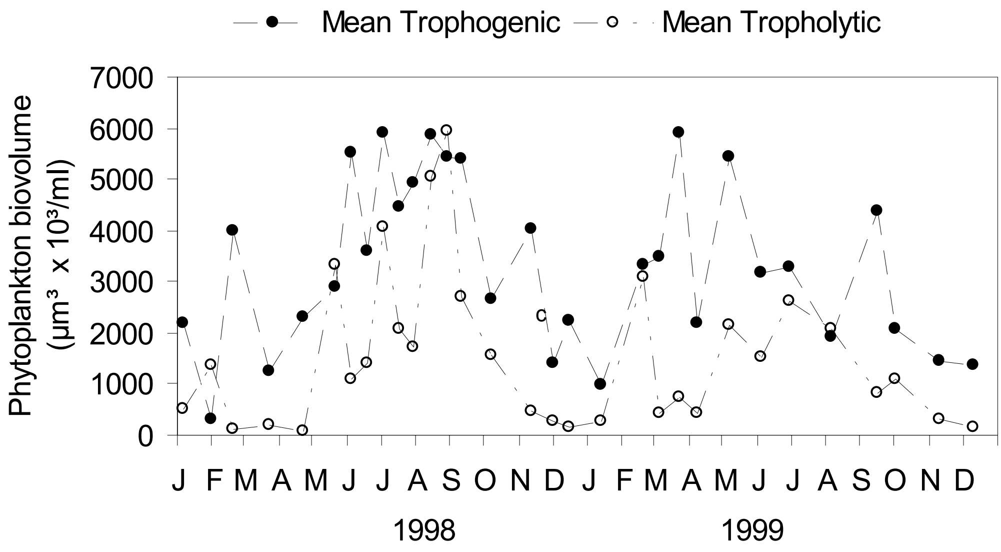


Figure 4-23. Seasonal variation in phytoplankton biovolume. Lower levels were found during stratification periods.

The calculated biovolume values varied between 70 x 10^3 and 6,000 x 10^3 µm^3/ml, as shown in Figure 4-23. Contrary to the abundance, maximum values of biovolume were detected during and after the overturn periods of both years. This apparent contradiction between abundance and biovolume is explained by the presence of *Trachelomonas volvocina* during the overturn periods (Figure 4-26 and 4-27), since its cellular volume is about 10 times greater than other species.

Phytoplankton abundance and biovolume are represented as isopleths in Figures 4-24 and 4-25, where spatial and temporal distribution can be better appreciated. Figure 4-24 shows that the highest abundance was found between 0 and 15 m depth during the thermal stratification in the first months of 1998, when high transparency values in the water column were registered. High abundance levels were also observed between August and November. The lowest abundance values were observed during the overturn in July, with a homogeneous level throughout the whole water column. Temporal and vertical distribution of phytoplankton in 1999 was light different than during 1998. The lowest levels of abundance in 1999 were detected between January and May and the highest level in September. Nevertheless, abundance levels during 1999 were lower and its vertical distribution was more uniform during the last months of this year than during the same period of 1998.

The time-depth diagram of biovolume distribution showed also a different behavior between these two years. In spite of high phytoplankton abundance during the first trimester of 1998 (Figure 4-24), biovlolume values during this same period were the lowest of this year (Figure 4-25). The highest biovolume values were reached between August and September with remarkable high levels towards the bottom of the lake. Levels and distribution of biovolume during 1999 were also different than during 1998 and they did not reflected the abundance pattern. Indeed, the highest biovolume values were found

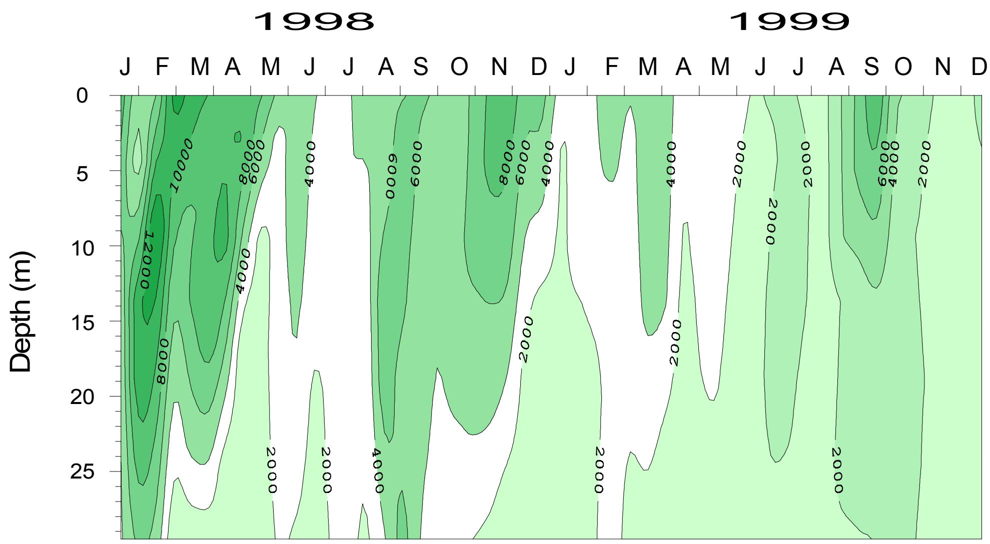


Figure 4-24. Isopleths of phytoplankton abundance (n/ml). Highest abundance was found between 0 and 15 m depth during thermal stratification in the first months of 1998. Lowest values were observed during overturn phases.

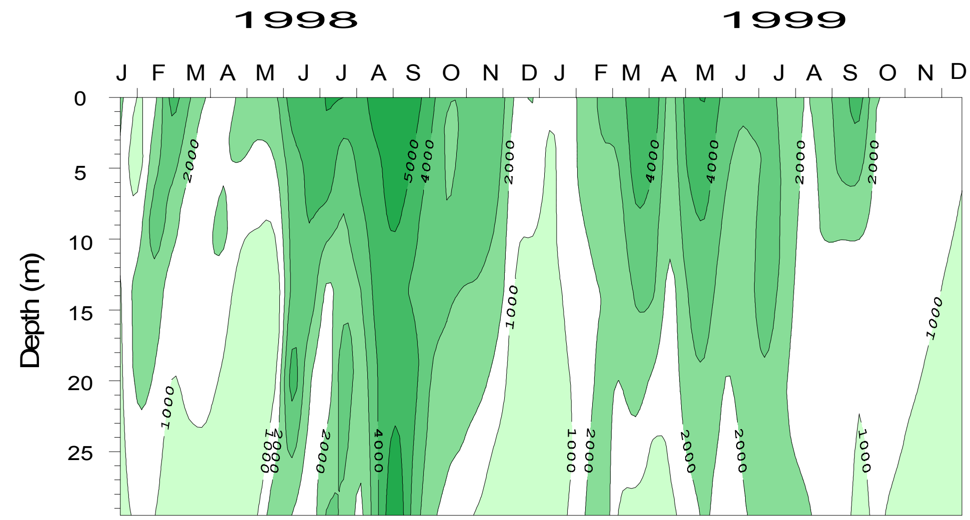


Figure 4-25. Isopleths of phytoplankton biovolume (μm^3 x 10^3 /ml). Maximal values were found during and after overturn periods.

between March and May, when low phytoplankton abundance was observed. On the other hand, moderate and uniform biovolume values were found between June and July and the lowest were found in January and between August and December.

The distribution patterns described for the abundance and the biovolume are obviously determined by the species composition. The contribution of the most important species to temporal distribution of abundance and biovolume are represented in Figures 4-26 and 4-27. Elevated values of total abundance observed between January and April 1998 as much in the trophogenic zone as in the tropholytic one were due principally to the occurrence of *Scenedesmus linearis*. This species reached its lowest level during the first semester of 1998 around May, and showed a new increase phase until September. At the same time, the increase of other species, especially of *Trachelomonas volvocina*,was notorious between April and November. During 1999, the major contribution to total abundance was also attributed to *Scenedesmus linearis*, although, *Aulacoseira granulata*, *Trachelomonas volvocina* and particularly *Pediastrum boryanum* were also abundant too, as shown in Figure 4-26.

As it was said before, the total biovolumen is largely determined by the species of high cellular volume, as it can be observed in Figure 4-27. Here, it can be seen that the greatest biovolumen variations were caused by the presence of *Trachelomonas volvocina.*

Due to the dominance of *Scenedesmus linearis*, *Pediastrum boryanum*, *Aulacoseira granulata* and *Trachelomonas volvocina*, time-depth diagrams were elaborated with data from 1999 to get a better view of the vertical distribution of abundance and the temporal succession between these four species (Figure 4-28). During the first months of the year a clear dominance of *Scenedesmus linearis* was observed. This species showed its highest abundance between the surface and 17 m deep. With the begin of overturn in April its presence decrease drastically. Toward the middle of the year, relatively high abundance of *Aulacoseira granulata* and *Trachelomonas volvocina* was observed, which reach high values up to deep layers. Furthermore, during the second semester of the year *Pediastrum boryanum* became the most important contributor to total abundance. Its highest abundance levels, which were detected around 15 m depth, coincided with the end of the overturn period. During this same period the presence of *Scenedesmus linearis* increased again in the lake, especially in the upper layers. At the same time, *Trachelomonas volvocina* showed its lowest abundance levels.

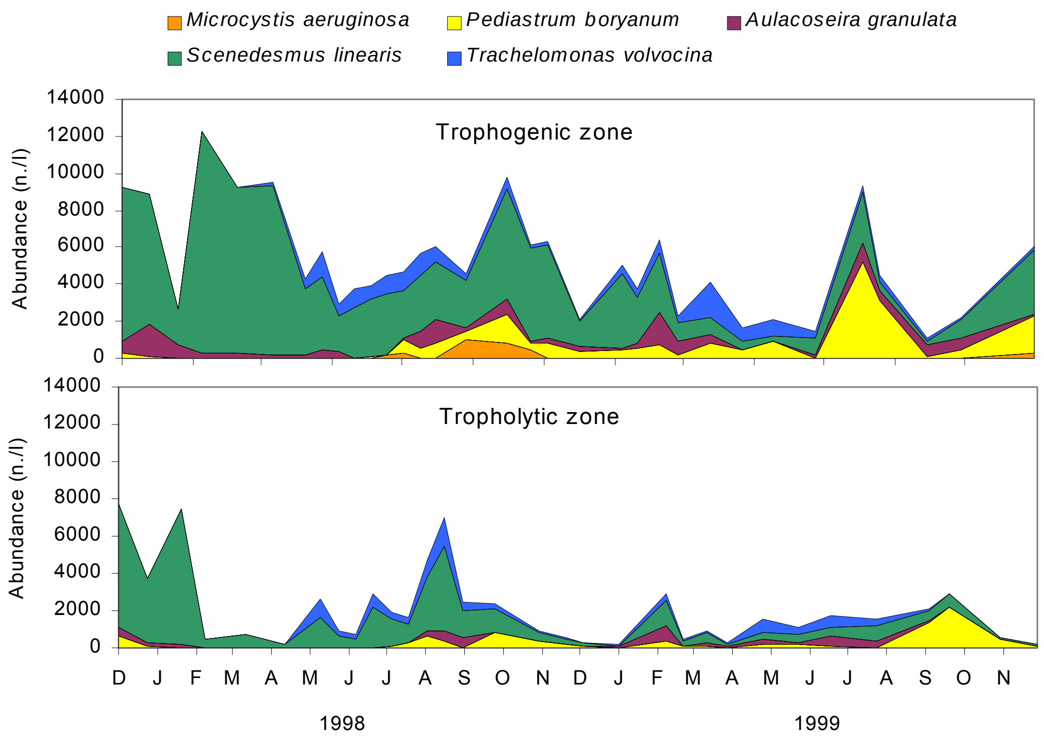


Figure 4-26. Seasonal abundance distribution of the most important phytoplankton species. Note the dominance of *S. linearis*.

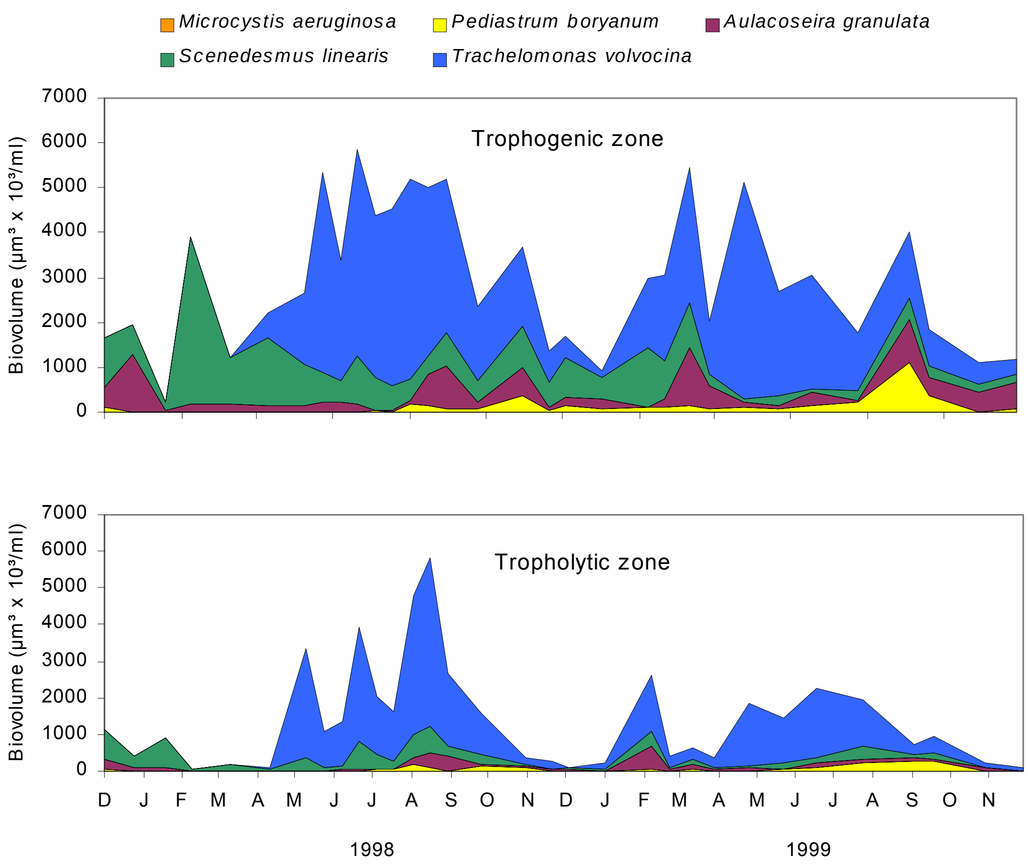
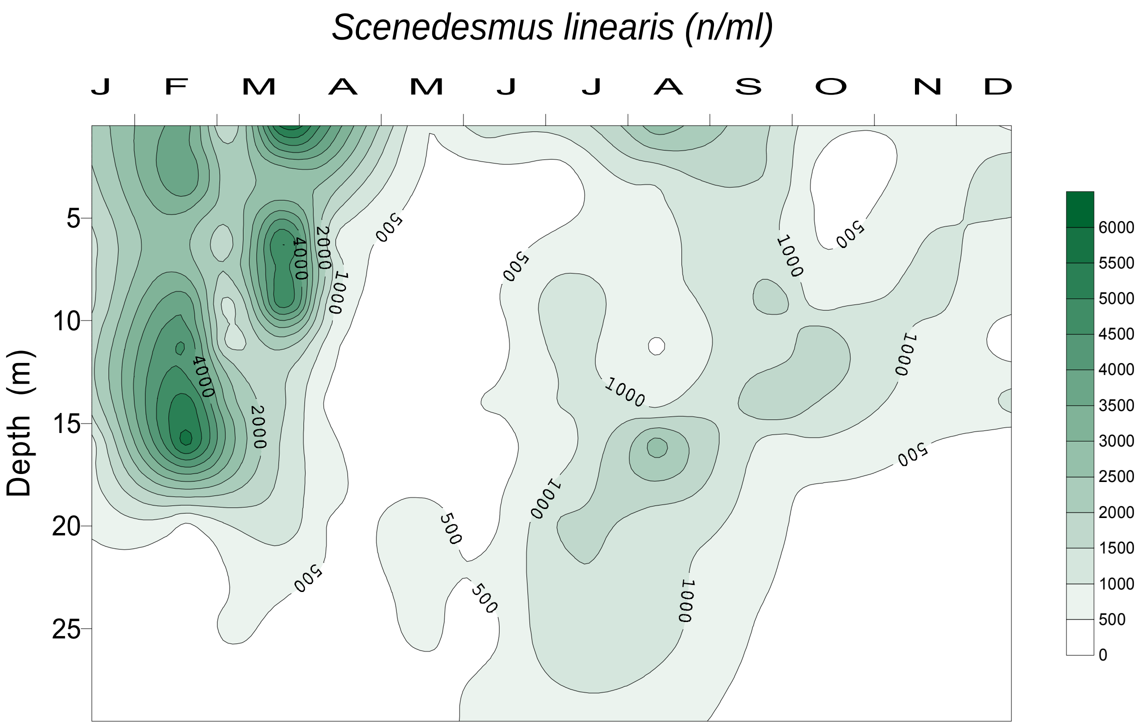
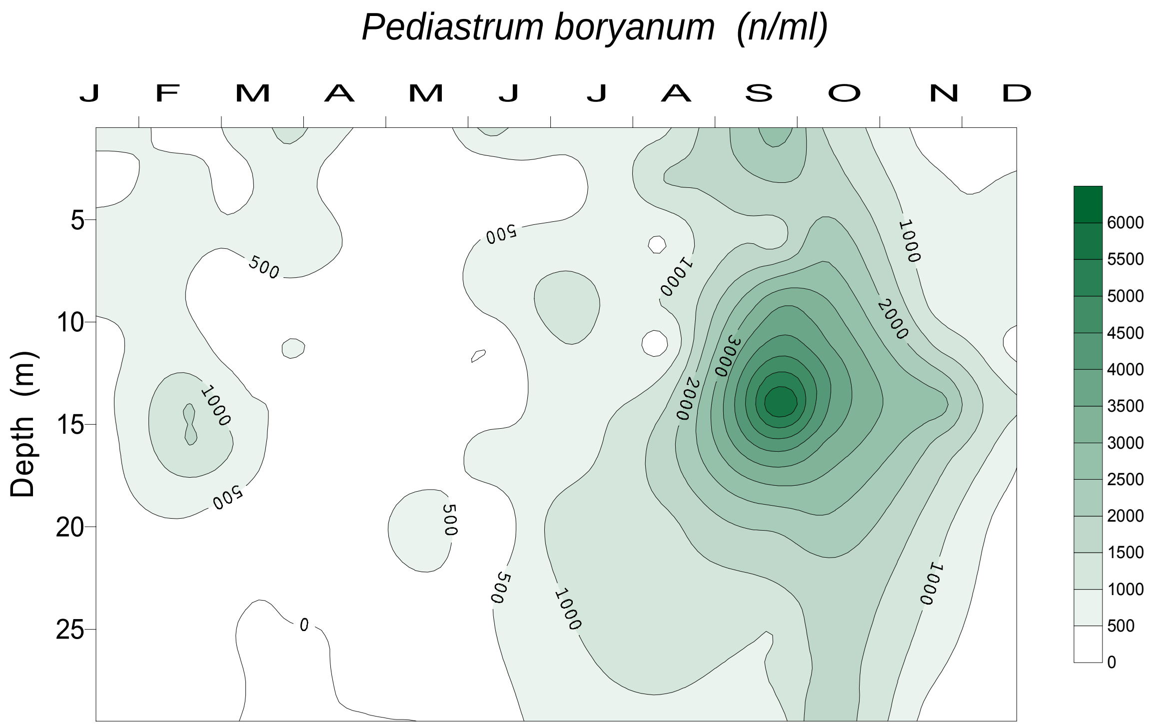
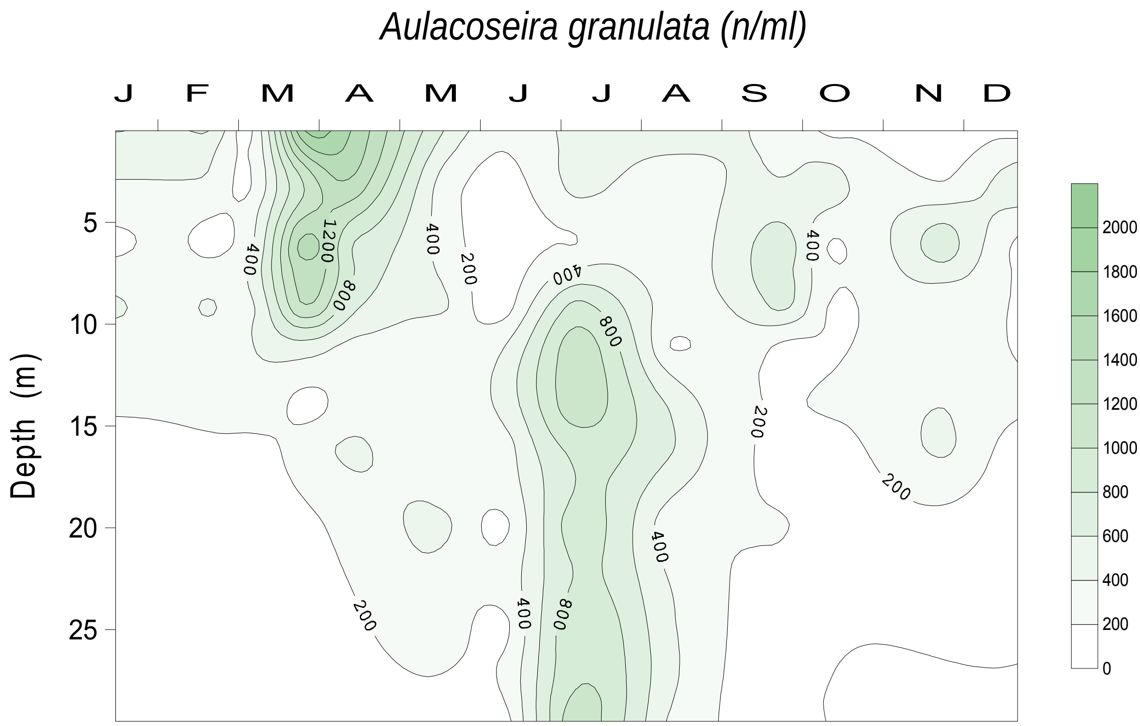


Figure 4-27. Seasonal biovolume distribution of the most important phytoplankton species.


Scenedesmus linearis (n/ml)
J F M A M J J A S O N D
Depth (m)
5
10
15
20
25
500
1000
2000
4000
6000
5500
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0


Pediastrum boryanum (n/ml)
J F M A M J J A S O N D
Depth (m)
5
10
15
20
25
0
500
1000
2000
3000
6000
5500
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0



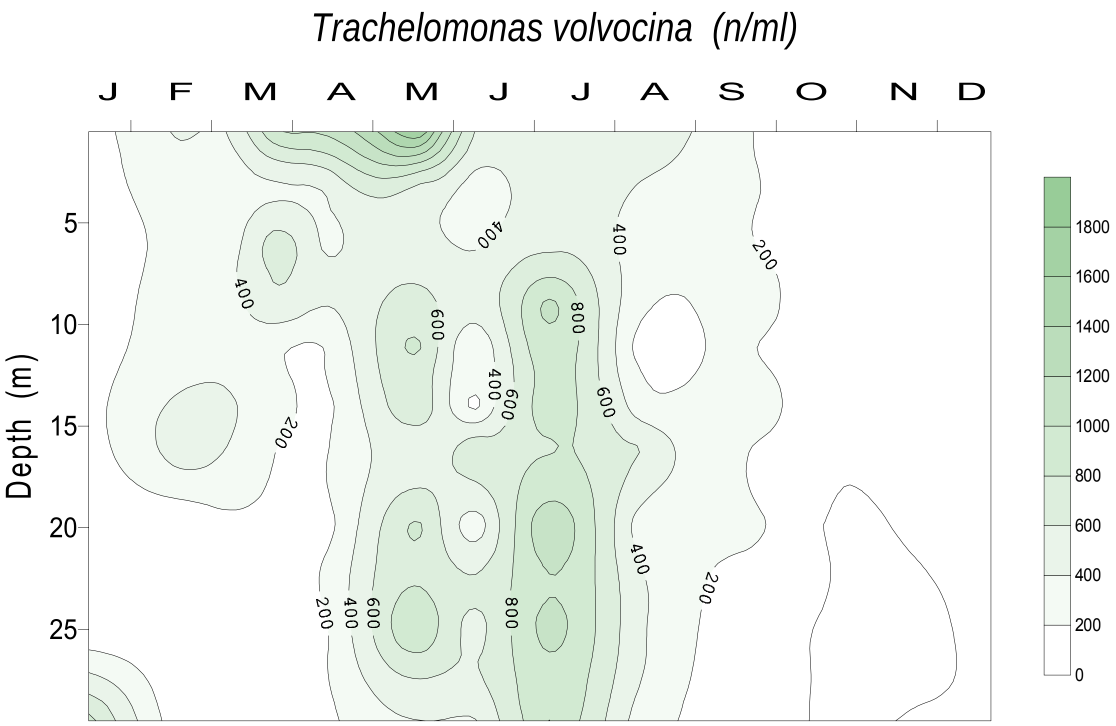


Figure 4-28. Vertical and temporal abundance distribution of the four most significant phytoplankton species.

The biovolume distribution pattern was confirmed by Chl. a data. The highest values of chlorophyll were reached during overturn periods, with a maximal value of 32.8 µg/l at a depth of 6 m in June of 1999, and with lower values during stratification, as shown in Figure 4-29. High concentrations of Chl. a were found at the bottom of the lake during the annual overturn, indicating the presence of a large amount of phytoplankton at these depths. This fact indicates loss of organisms, what causes a limitation of productivity.

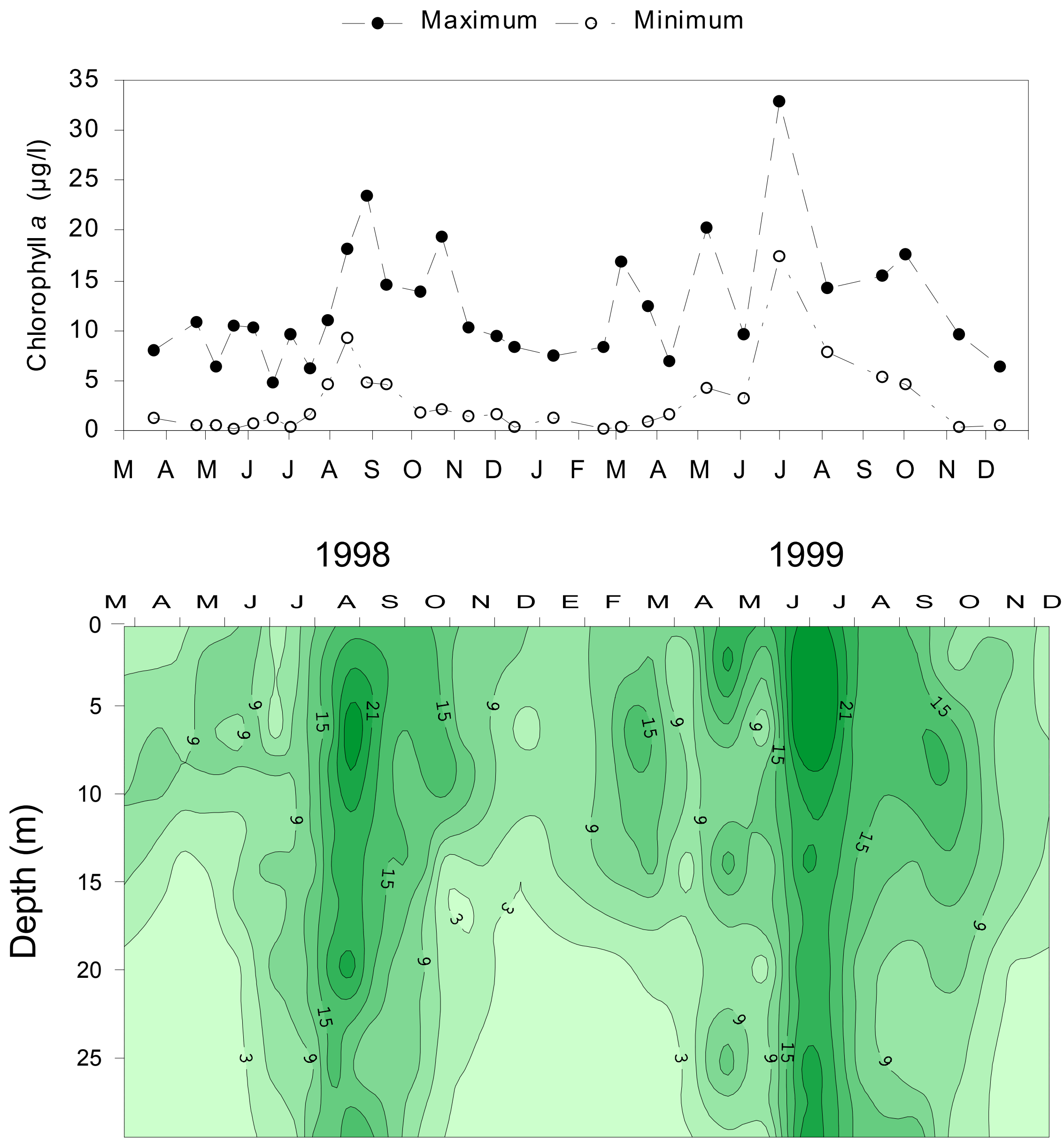


Figure 4-29. Vertical distribution of chlorophyll a (µg/l). Top: Maximal and minimal values. Bottom: Depth-time isopleths of chlorophyll a concentration.

4.2.5.2 Macrophytes

One of the most important biological components of the lake is the community of macrophytes. They are very present, covering almost 100% of the littoral. Only the area corresponding to the inflow of River Itambi is free of them. The macrophytes are not only the most conspicuous biological element in the lake but also constitute the most prominent primary producers. This community is dominated by *Schoenoplectus totora*, an emergent species; and four submerged species, *Ceratophyllum demersum*, *Myriophyllum quitense*, *Potamogeton illinoensis* and *Potamogeton striatus* (Appendix J). This group of submerged vegetation can cover wide shallow zones of the littoral up to a distance of 35 m from the shore reaching a depth of 7 m, representing almost 4 % of the lake area. Others species, like the floating water hyacinth *Eichhornia crassipes* and *Azolla* sp. are found only in patches and its biomass is not as significant as that of the dominant species. Table 6 shows the complete list of macrophytes found during the corresponding study carried out in October and November of 1996 (Gunkel, 2000; Kiersch et al., 2002).

Table 6. Littoral and surface vegetation in Lake San Pablo. Species found during samplings on October and November 1996 (Kiersch et al.**, 2002). Pictures of some of them in Appendix J**

Scientific name	Common name	Occurrence
Hydrocotyle ranunculoides L.	Pondweed	Emergent
Schoenoplectus totora (Knuth) Palla	Totora	Emergent
Azolla sp. Lamarck.	Fern	Floating
Lemma polyrrhiza L.	duck weed	Floating
Eichhornia crassipes Mart.	water hyacinth	Floating
Ceratophyllum demersum L.	hornwort / coontail	Submerged
Myriophyllum quitense Gaudich.	milfoil	Submerged
Potamogeton illinoensis Morong.	pondweed	Submerged
Potamogeton pusillus L.	pondweed	Submerged
Potamogeton striatus Ruiz & Pavon	pondweed	Submerged
Elodea matthewsii (Planch.) St.John	pondweed	Submerged

4.2.5.3 Zooplankton

A list of the pelagic zooplankton species found in Lake San Pablo is shown in Table 7. Pictures of *Daphnia pulicaria*, *Metacyclops mendocinus*, *Asplachna sp.*, *Trichocerva similes* and *Keratella tropica* are shown in Appendix I. With only 12 species, the diversity is extremely low for a lake with the characteristics of San Pablo. The zooplankton comprises two species of crustaceans, *Daphnia pulicaria* and *Metacyclops mendocinus*. These two species were permanent but with variations in their abundance during the time of investigations. Furthermore, 10 pelagic species of Rotatoria were found, from which only six were dominant with variations as to their permanency and respective levels of abundance. In the littoral area was found *Hyalella* sp., another crustacean, which growth in high abundance.

Table 7. List of pelagic zooplankton species observed in Lake San Pablo during 1998 and 1999. *) abundant and prevalent species.

Crustacea
Cladocera
Daphnidae
*) *Daphnia pulicaria* Forbes
Copepoda
Cyclopinae
*) *Metacyclops mendocinus* Wierzejski, 1893
Rotifera
Monogononta
Ploimida
Brachionidae
*) *Keratella tropica* Apstein, 1905
*) *Keratella cochlearis* Gosse, 1851
*) *Anuraeopsis fissa* Gosse, 1850
Euchlanidae
Euchlanis sp.
Lecanidae Bartos, 1959
Lecane luna O.F. Muller, 1776
Lecane Bulla
Trichocercidae Remane, 1933
*) *Trichocerca similes* Wierzejski, 1893
Synchaetidae
*) *Polyarthra vulgaris* Carlin, 1943
Asplanchnidae .
*) *Asplachna sp* .
Gnesiotrocha
Testudinellidae
Pompholyx complanata

Abundance and biomass

Mean, maximum, and minimum values and percentage values of abundance and biomass of organisms during the two years of analysis are shown in Table 8. Correlation curves between body size and biomass used for biomass estimation of *D. pulicaria* and *M. mendocinus* are shown in appendix G.

Table 8. Values of abundance and biomass of zooplankton found during the monitoring program. Dates of sampling corresponding to maximum and minimum values are shown in parentheses. Rotifera is represented as the sum of the six more frequent and abundant species. Values of *M. mendocinus* correspond to the sum of adults, copepodids and nauplii.

	Abundance (Ind x 10^3 m^{-2})	Abundance (Ind L^{-1})	Percent from total abundance	Biomass - dry weight (g m^{-2})	Percent from total biomass
Rotifera					
Mean value	1242	44.3	**61.1**	8.2	**0.4**
Maximum (2.7.98)	5522	197.2		26.7	
Minimum (23.4.98)	33	1.2		4.0	
Daphnia pulicaria					
Mean value	128	4.6	**6.3**	1288.5	**56.4**
Maximum (2.7.98)	342	12.2		3451.8	
Minimum (11.9.98)	14	0.5		1398.9	
M. mendocinus					
Mean value	663	23.7	**32.6**	989.7	**43.3**
Maximum (15.4.99)	1422	50.8		2113.5	
Minimum (11.9.98)	242	8.6		430.7	

Graphic representation of abundance and biomass during 1998 and 1999 is shown in Figure 4-30, where temporary variations, periods of more abundance and dominance of species can be observed. Abundance has been represented as ind/m² of lake surface. During the two years of study Rotifera species showed the highest levels of abundance followed by the copepod *M. mendocinus,* whereas *D. pulicaria* had the lowest levels. However, Rotifera were also the group with more variations in the abundance: during 1998 it showed peaks in April, July and October and low levels at the beginning and the end of the year, while during 1999 the highest levels of abundance appeared between February and March and lowest values in August. This variability was determined by the presence and abundance of the six more important species of Rotifera, as is showed in Figure 4-31. Here, seasonal presence of species throughout the two years of study can be observed: *T. similis* was the most abundant and permanent species of Rotifera found during the whole period (Figure 4-31), *P. vulgaris* was more abundant between July and November 1998 and during the first months of 1999, *A. fissa* was also important during 1998 and the first trimester of 1999, and also *K. tropica* showed a similar presence pattern but with lower abundance. On the other side *K. cochelaris* was absent during most of the time in 1998, but its presence was more notable during 1999. *Asplachna* sp., the unique rotifer predator in tropical waters, was found during most of the time. It was absent only between April-June

1998 and in January 1999 (Figure 4-31), showing high abundance variability, something directly related to the presence and abundance of prey.

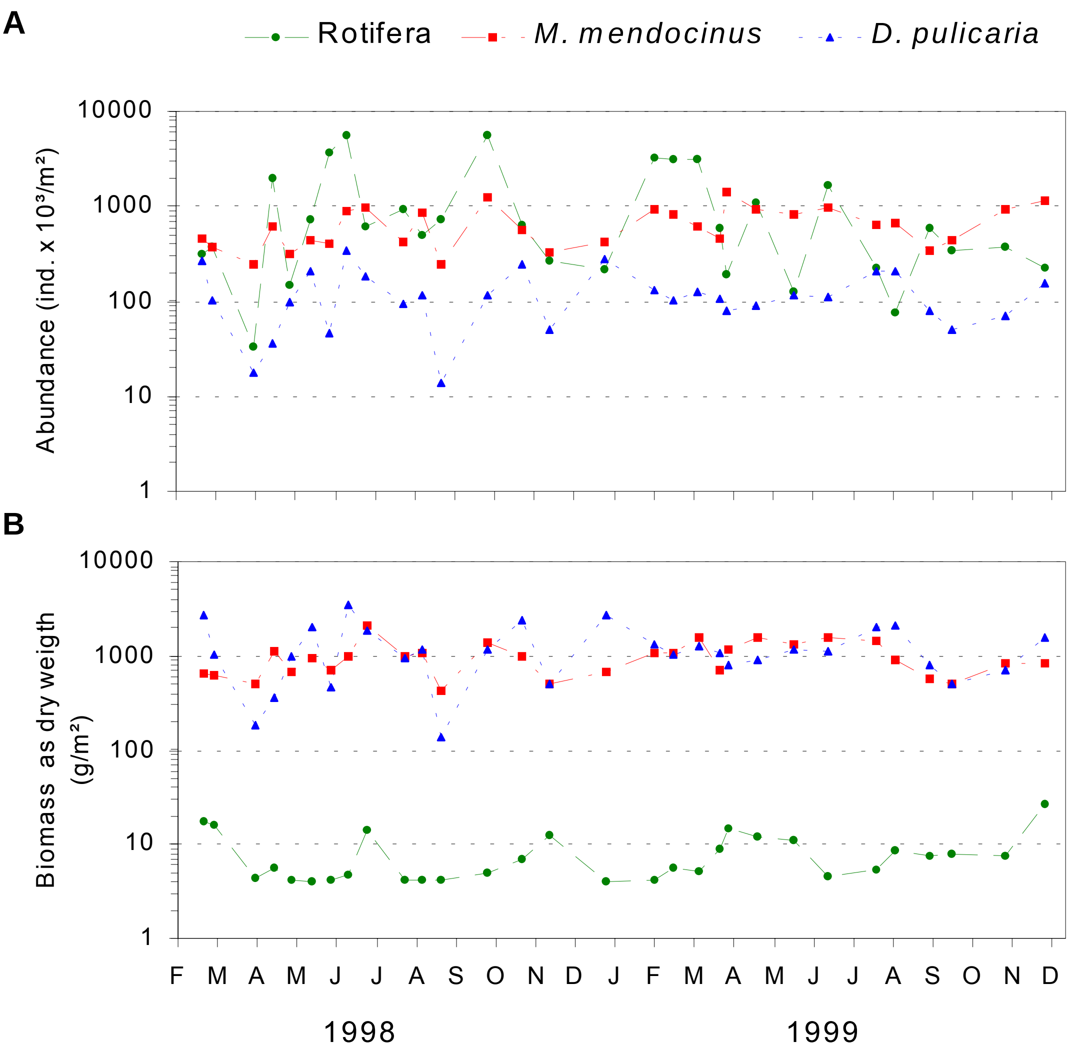


Figure 4-30. Seasonal abundance and biomass of zooplankton in Lake San Pablo. Rotifera species showed the highest and most variable levels of abundance. Nevertheless, its contribution to total biomass was low. *M. mendocinus* was the most stable population during the two years.

Abundance of *M. mendocinus* presented lower variations than other species, with values between 8.6 and 50.8 ind/L. *D. pulicaria* showed minimal abundance values and strong variations during 1998, while during 1999 the levels were more stable, as shown in Figure 4-30 A.

Looking at the values of biomass, Rotatoria constituted a very low percentage of the total biomass throughout the two years despite its high abundance (Table 8 and Figure 4-30 B). On the other hand, due to its size *D. pulicaria* represented most of total biomass, with peaks in March, July and November 1998 and August 1999. *M. mendocinus* showed the most constant presence within the zooplankton community, and also showed high values of biomass, with mean value of 43.3% of the total biomass.

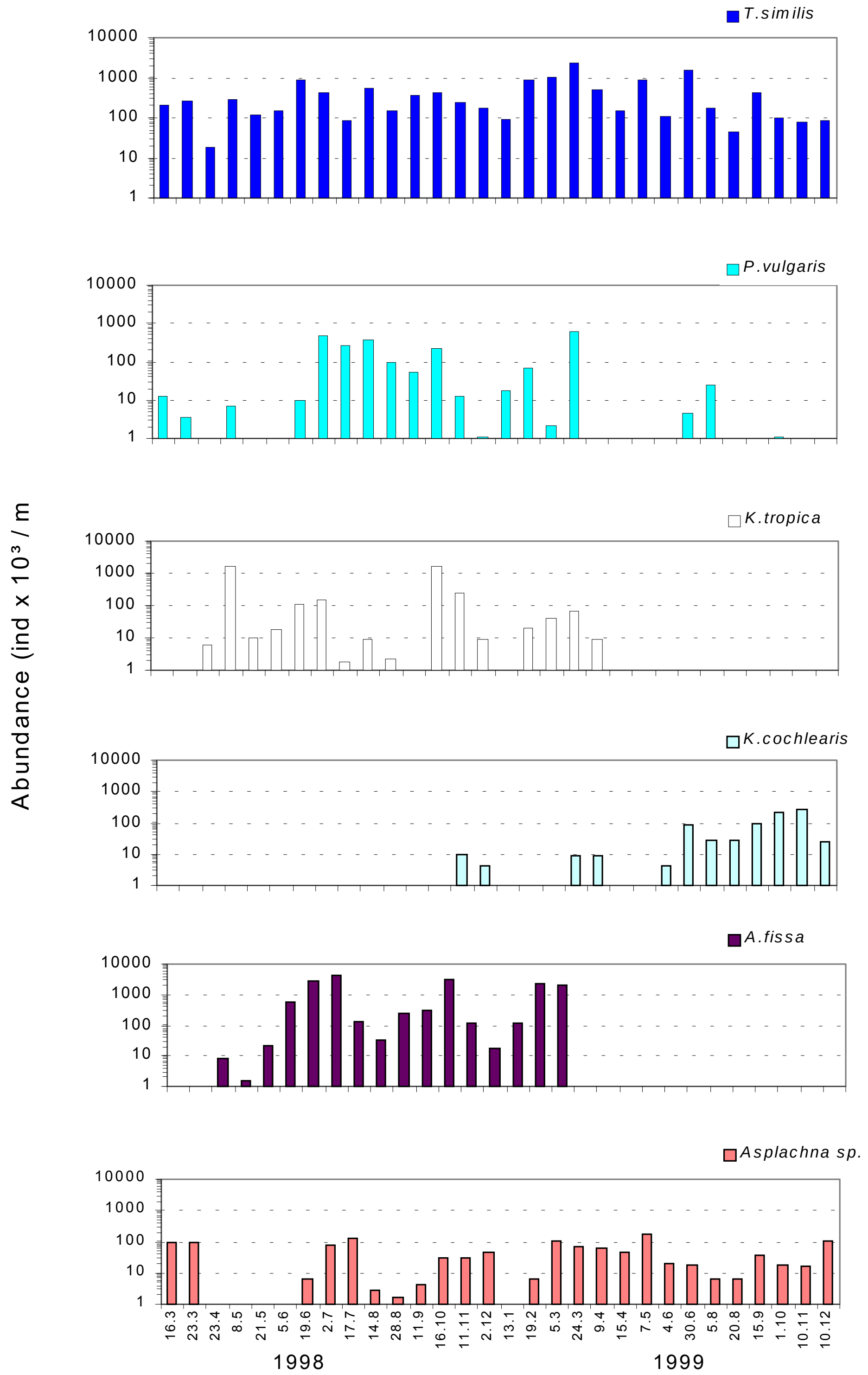


Figure 4-31. Temporal abundance distribution of the six most important Rotifera species.

Vertical distribution in the water column

Regarding vertical distribution of organisms in the water column at noon, high densities were observed in the upper strata between 0 and 10 m, and the lowest values in the deeper area, as shown in Table 9 and Figure 4-32. These levels showed some variations according to the season and, as in the case of *M. mendocinus,* according to the developmental stage (Table 9 and Figure 4-33). In the case of Rotifera, high abundances were observed in the inferior strata in Juni-July 1998 and in February, May and July 1999 (Figure 4-32).

D. pulicaria was very abundant in inferior strata in June-July and August 1998, with the highest abundance value between 20-28 m found on August 28. During 1999 its abundance values and distribution trend were more constant, with high abundance in deeper layers in August, coinciding with the final phase of thermal mixing.

M. mendocinus showed almost the same distribution pattern observed for *D. pulicaria*, as shown in Figure 4-32. The vertical distribution of *M. mendocinus* according to developmental stage (nauplii, copepodids, adults) and to depths is represented in Figure 4-33. It shows temporal distribution of abundance as ind/m² of lake surface. Nauplii showed the highest abundance levels and at the same time the highest variations.

Table. 9. Vertical zooplankton distribution during 1998 and 1999. Values for each group or species are given as percentage of the total in the water column. For *M. mendocinus,* percentage distribution among developmental stages is also shown.

	0 – 10 m	10 – 20 m	20 – 28 m
Rotifera	59.0	30.3	10.7
Daphnia pulicaria	62.7	25.9	11.4
M. mendocinus	60.3	25.3	14.4
Adults	22.0	28.4	19.5
Copepodids	25.6	21.9	16.0
Nauplii	52.4	49.7	64.5

In the upper 10 m, the vertical distribution during the first months of 1998 showed similar variation patterns for adults, copepodids and nauplii. However, nauplii abundance showed a strong increase beginning in August, while adults and copepodids had low levels until end of the year. At the beginning of 1999 and until March of that year, juvenile stadia (nauplii and copepodids) were dominant. From this month until end of the year, the abundance of all three stadia showed oscillations, with a strong increase of nauplii in December.

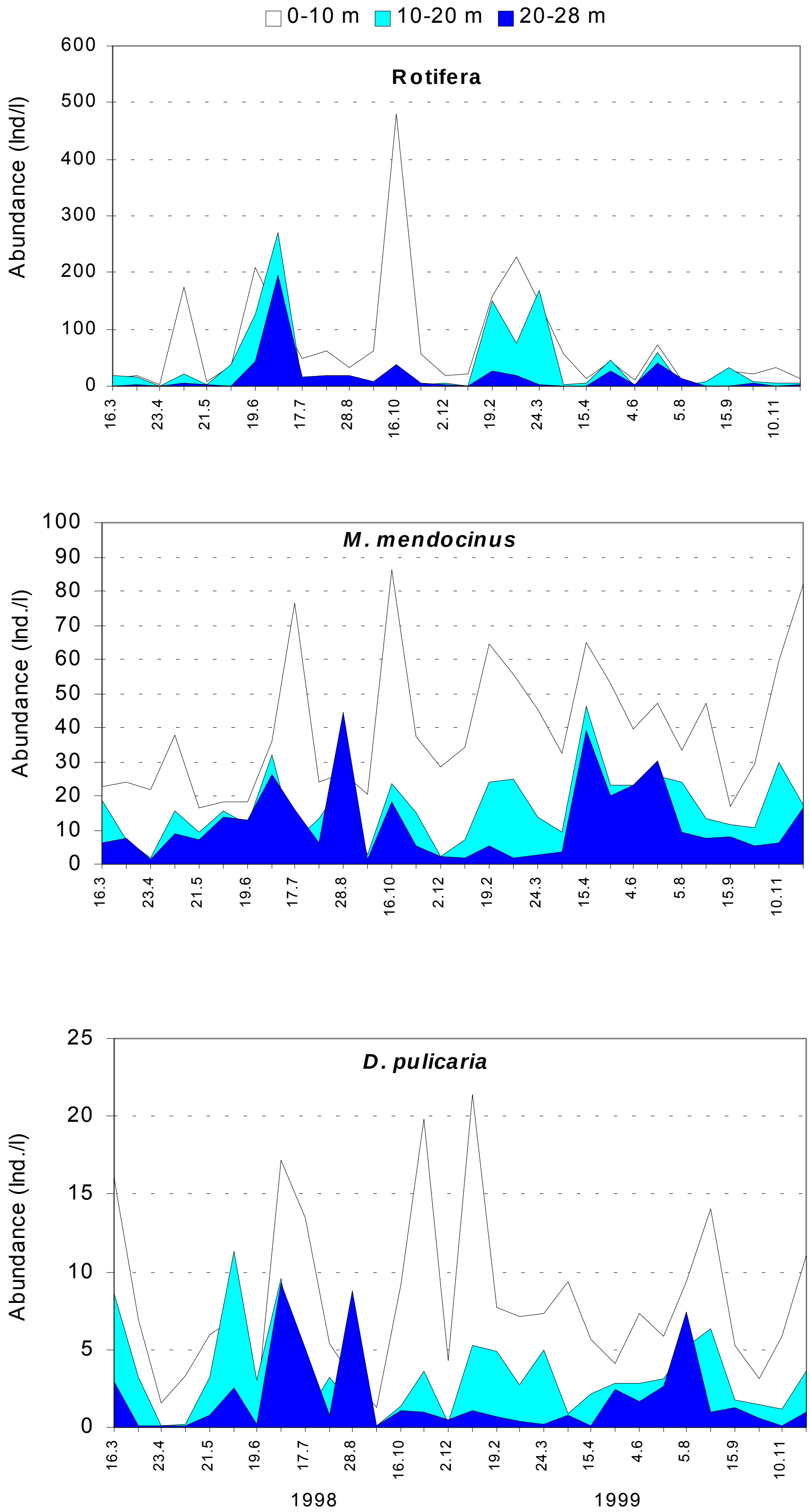


Figure 4-32. Time-depth abundance distribution of zooplankton. Rotifera is represented as the sum of its six most important species.

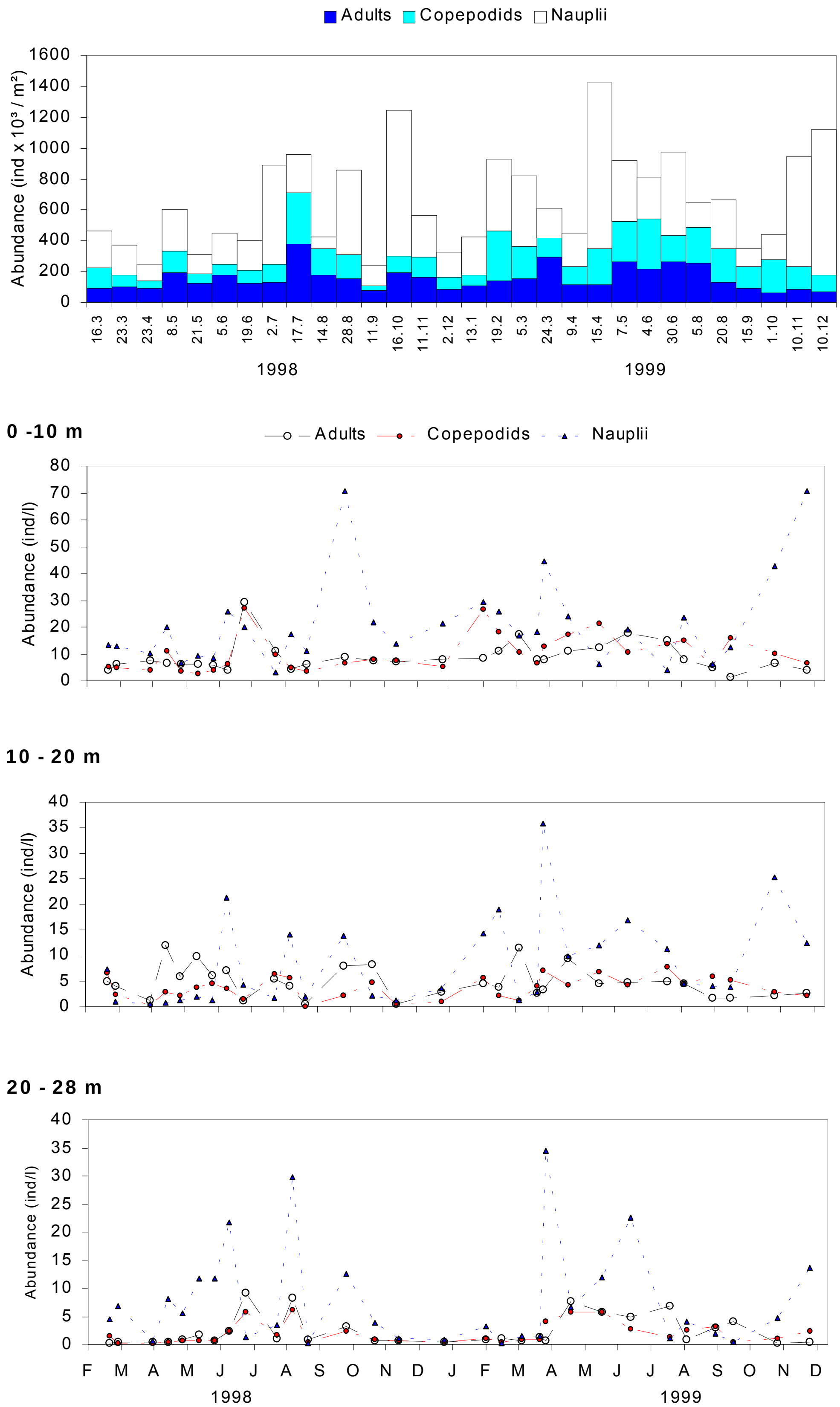


Figure 4-33. Time-depth abundance distribution of the life history stages of *Metacyclops mendocinus*. At the top: vertical distribution per m² of lake surface. Below: abundance distribution according to depth layers.

Between 10-20 m, adult organisms dominated during the first part of 1998 but their abundance decreased towards June, when the quantity of nauplii increased. From that month onwards, the abundance of adults and copepodids followed a similar oscillation pattern, with a period of more stability from May until December 1999, while the abundance of nauplii showed strong variations.

In the deepest stratum between 20-28 m the levels of abundance of all developmental stages were low compared with the values in other strata. Here, the dominance of nauplii was evident, showing almost the same variation pattern observed between 10-20 m.

4.2.5.4 Fish

Only two fish species were registered during this study. These species were identified as *Micropterus salmoides* (Largemouth bass, known as "Lobina" or "Trucha" in the area) and *Carassius carassius* x *C. auratus* , which were introduced to the lake several decades ago (Appendix I). Residents of the area reported also the presence of the rainbow trout (*Oncorhynchus mykiss*), a species introduced in many Andean countries. Apparently, the rainbow trout has been displaced totally by *M. salmoides*, since there is no current report of it neither was it observed during this study. Actually, the presence of *Micropterus* in the lake was detected in 1966 (Castro & Peñafiel, 2002). This benthopelagic predator species is native of the eastern United States. It adapts well to multiple environmental conditions, but normally inhabits shallow and clear lakes, ponds and swamps with submerged vegetation. This species has been introduced widely as a game fish and is now cosmopolitan. Many countries have reported adverse ecological impact after its introduction (Page & Burr, 2001).

4.3 Experimental Program

4.3.1 Enclosure experiments

4.3.1.1 Water thermal behavior and its influence on chemical and biological variables.

Measurements of water temperature profiles and Sechi disc transparency in the lake and in the enclosures throughout the experimental period provide not only valuable data on thermal behavior and convection currents in both systems, but also provide a measure of the reliability of experiments with this type of meso-cosmos.

Figure 4-34 A shows depth-time temperature isopleths (0 to 6.5 m depth) and Secchi disk transparency in each system from 28th March to 14th April 2000 during the stratification phase. The mentioned variables showed similar trends inside the two systems during the experiment: during the first six days there was a slight stratification followed by a mixing event between the seventh and eighth day. Then, there was a stronger stratification episode with higher temperatures. Transparency values also showed a similar trend in both cases, with values between 2.5 and 3.7 m in the enclosure and between 3.2 and 4 m in the lake. Figure 4-34 B show temperature profiles registered at different times on April 1st 2000 (fourth day of the experiment) in the enclosure and in the lake. Here, diurnal stratification and nocturnal mixing of the water column took place in both systems showing also a similar trend. The measurements at 11:20 and 12:35 hours show how the thermal structure in the superficial layers could change within short time intervals.

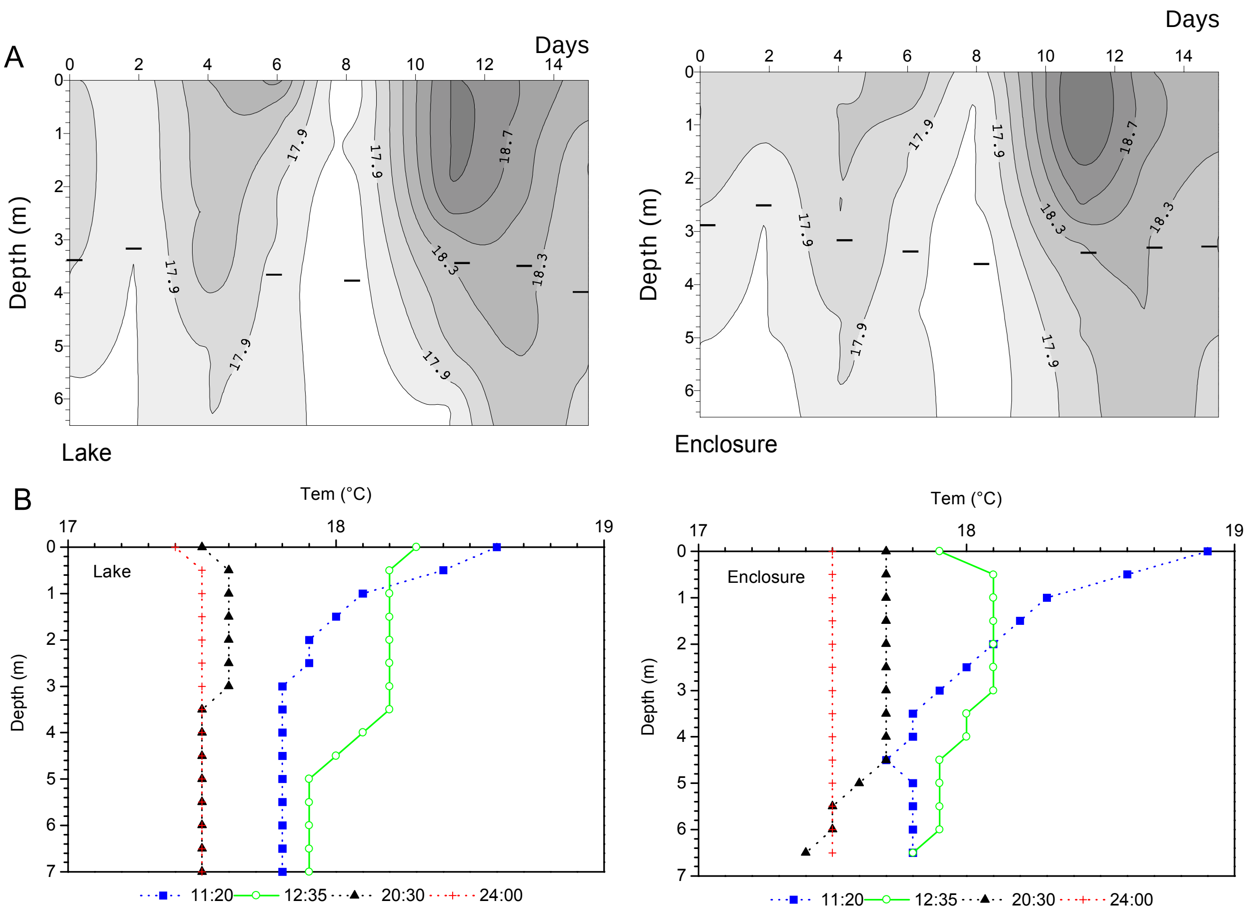


Figure 4-34. A) Time-depth diagrams of water temperature in the lake and in the enclosure during March-April 2000. Temperature was measured around noon. (−) Secchi disk transparency. B) Temperature profiles measured on 1st April 2000 at different times of the day. Similar day-night temperature pattern in the lake and in the enclosure was observed.

The observed thermal pattern has relevant implications for the concentration of nutrients and gases and for plankton productivity and distribution. To achieve a better appreciation of the thermal pattern during this trial, Figure 4-35 shows a model elaborated with the isotherms of the whole water column. During the first days moderate winds mix the upper strata and a secondary thermocline previously formed at 4.5 m is displaced towards the surface. During calm and sunny weather period superficial layers are heated with the formation of brief thermoclines over the secondary one. This latter together with the seasonal thermocline are then shifted down. After that, strong winds mix the upper strata, destroying the secondary thermocline and displacing the seasonal thermocline up again. In the evening the wind calms and air temperature decreases producing loss of heat, eventual thermal inversions and a stable and cooler mixed upper layer. After this short overturn period a new warming and stratification process begins again. The described thermal behavior is typical for tropical lakes and reservoirs (Payne, 1986) and was called "atelomixis" by Lewis (1973), who identified and described it working in lake Lanao (Philippines). In fact, the term atelomixis means "imperfect mixing" and describes any occurrence of vertical mixing of stratified lakes without the destruction of the hypolimnion. During such events the formation of secondary thermoclines occur above the main one due to calm and sunny weather periods and their posterior obliteration due to weather changes (cooling, rain, storms or wind). Such incomplete vertical mixing of a stratified lake can produce transfer of nutrients from deeper waters into the euphotic zone, often stimulating phytoplankton production (Lewis, 1973; Osborne, 2000), which was also observed in Lake San Pablo.

Chemical and biological variables can also show homogeneity in both systems during the whole experimental time or may show homogeneous levels only at the beginning with variations after some days due to the intrinsic conditions of each system. Figure 4-36 shows the pattern of some variables during March-April 2000: some nutrients such as SRP, NT and DIN and pH levels showed a similar trend throughout the whole experimental time both in the lake and the enclosure. On the other hand, Chl. a and oxygen content showed a different pattern between the two systems, with strong fluctuations in the lake whereas in the enclosure levels remained more stable. Another fact to note is that initial levels of almost all parameters were very similar in the lake and in the enclosure. The fluctuations observed in some of them -especially inorganic forms of nutrient- throughout the whole test are associated with the thermal trend: during the mixing of the superficial water layers on the eighth day of test (atelomixis) the levels of DIN went up, due to the input of ammonium from deeper layers. A strong decrease in oxygen content was also observed in the lake.

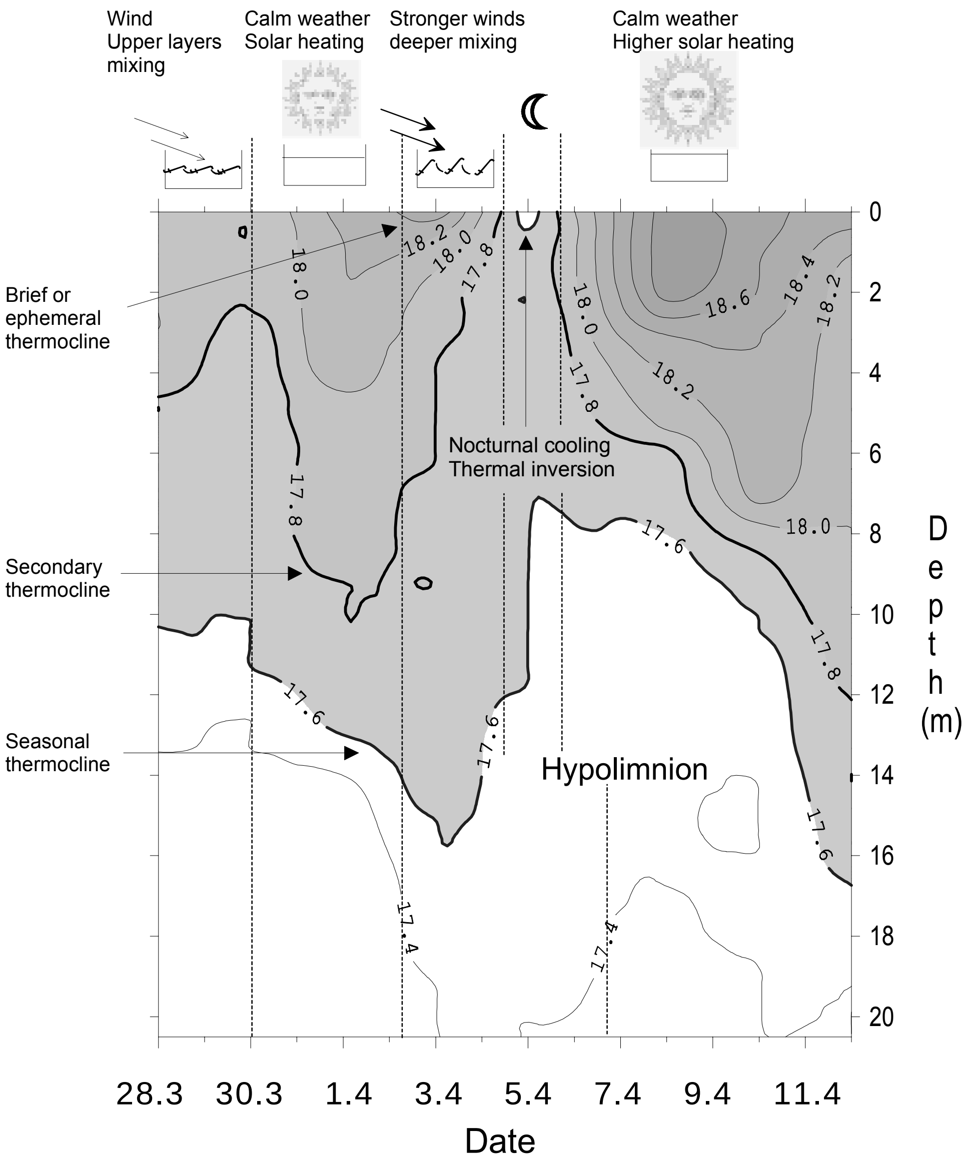


Figure 4-35. Model of the thermal behavior observed in Lake San Pablo during the stratification period on March-April 2000 (called "atelomixis"). During calm and sunny weather periods, a thin superficial layer is heated inducing the formation of a brief thermocline over a secondary one formed previously. Then, stark winds or bad weather periods mix the warm upper layers destroying the secondary thermocline and pushing the water masses down toward the seasonal thermocline. In the evening, the wind calms and air temperature decreases, producing loss of heat, eventual thermal inversions and a stable and cooler mixed upper layer. Modified from Goldman & Horne (1994).

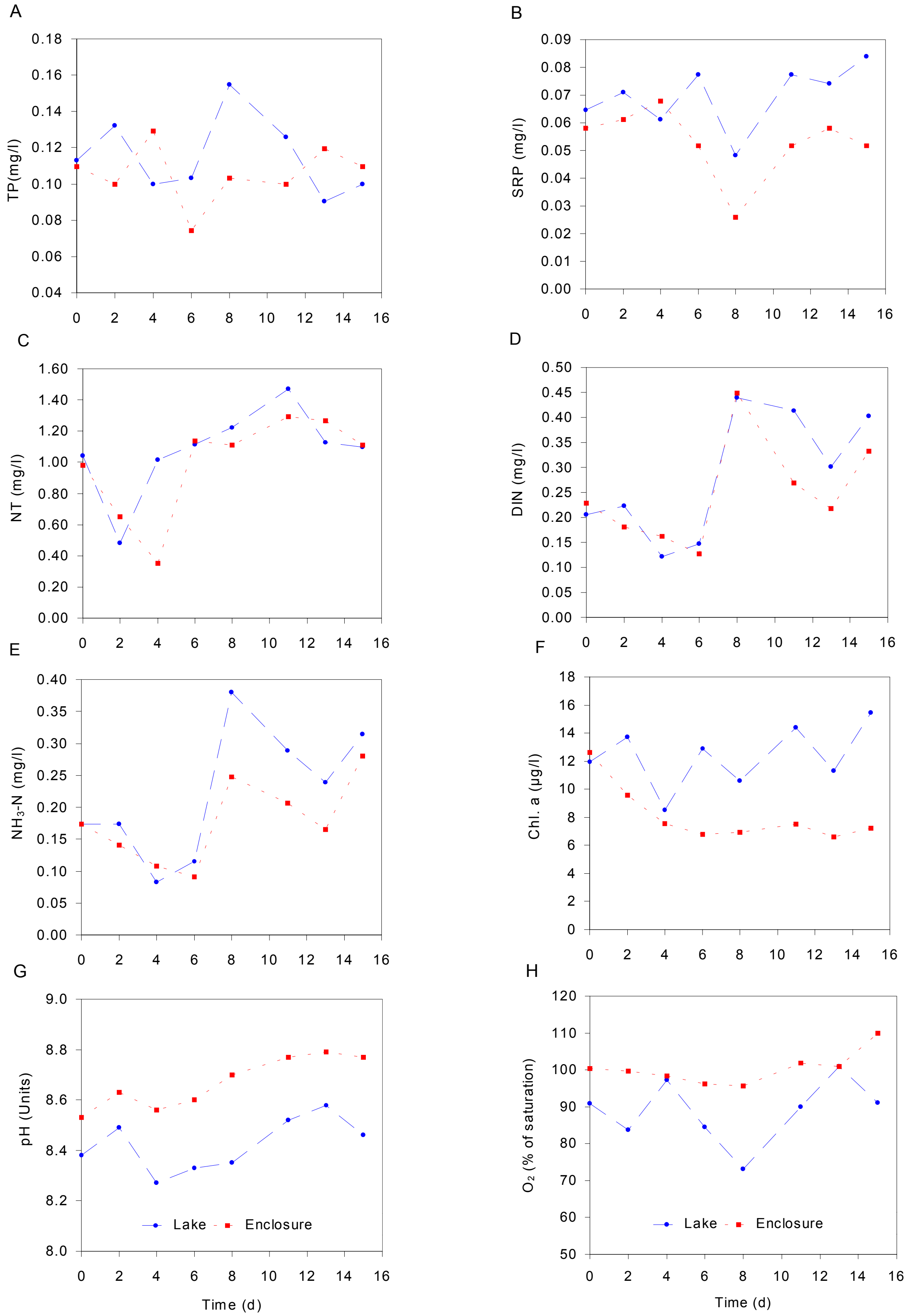


Figure 4-36. Nutrients content (TP, SRP, TN, DIN and NH_3-N), Chl. a, pH and oxygen saturation levels in the lake and in the enclosure between 28th March to 14th April 2000 during a stratification phase.

4.3.1.2 Physical factors controlling phytoplankton development: Effect of convection currents and UV radiation

The effect of convection currents and UV radiation on phytoplankton was tested during the two climatic seasons. Therefore, it was possible to quantify its effect during lake stratification (rainy season) and overturn (dry season).

During the experiment carried out between 5th and 17th August 2000, three of the enclosures suffered damage due to very strong afternoon winds. For this reason the enclosures “Control 2.5 m” and “Without UV 2.5 m” were suspended on the fourth day and the enclosure “Without UV 7 m” on the seventh day. However, data obtained up to the moment of the damage are presented here. The observations in the remaining enclosures and in the lake went on as initially planed.

Convection currents

Figure 4-36 F shows levels of Chl. a during the stagnation period in March-April 2000. Although initial Chl. a concentration was very similar in both lake and enclosure, chlorophyll values in the lake showed strong fluctuations throughout the experimental time. On the contrary, in the enclosure a continual decrease occurred from the initial value of 12.6 µg/l to 6.8 µg/l reached on the sixth day of test. After then, the values remained almost constant around 7 µg/l.

During the stratification period in March-April 2001 Chl. a values showed the same pattern observed the year before: similar initial values in both lake and enclosures, then strong oscillations in the lake and decreasing values in both enclosures throughout the test (Figure 4-37 A). Since nitrate content in the lake and in the enclosures at that time were below the detection limits of the used method, levels of total nitrogen are shown in Figure 4-37 A instead. Initial and final values of Chl. a obtained in the lake and in the enclosures ("Control") during both seasons, as well as the percent of variation between these values are given in Table 10.

A remarkable characteristic observed in both experiments carried out during stratification periods is that chlorophyll levels in the lake were always higher than those measured in the enclosures and a positive final increase was registered in the lake, whereas in the enclosures a strong decrease was found. During overturn a final increase was determined in both systems.

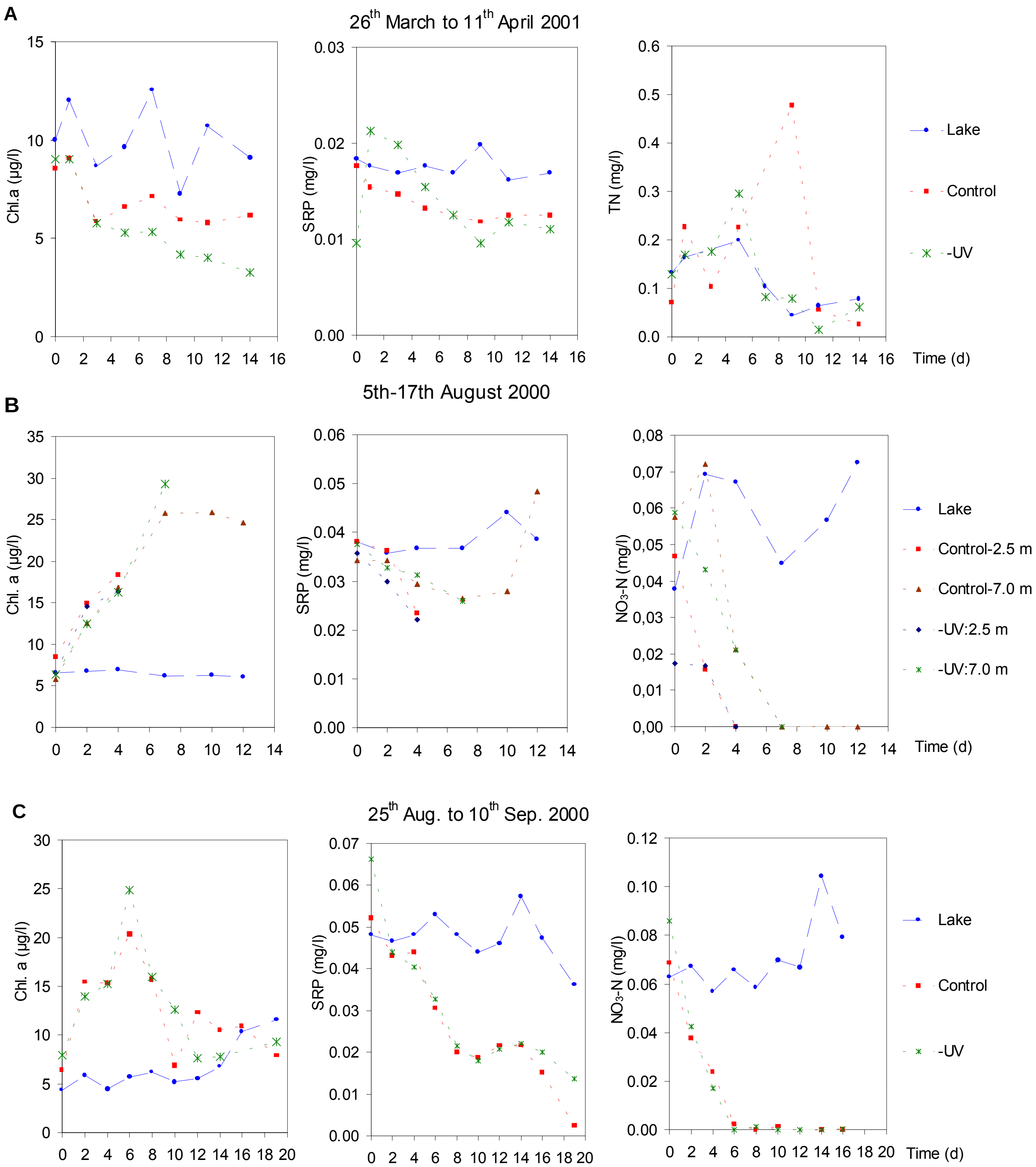


Figure 4-37. Levels of Chl. a and of nutrients in the lake and in the enclosures "Control" and "Without UV" (-UV) during the stratification period in March-April 2001 (A) and during overturn August-September 2000 (B and C). Trials were carried out to test the effect of convection currents and UV radiation on phytoplankton development.

Table 10. Initial and final values of Chl. a concentration (µg/l) in the lake and in the enclosure "Control". The percent of variation between initial and final values is given. Note the final increase in the lake during both seasons, whereas in the enclosures a strong decrease during stratification periods was observed.

System	Date	Stratification			Overturn		
		Initial	Final	% var.	Initial	Final	% var.
Lake	Mar-Apr 2000	11.9	15.4	29.4			
	Aug-Sep2000				4.3	11.6	169.1
	Mar-Apr 2001	10.0	9.11	8.9			
Enclosure	Mar-Apr 2000	12.6	7.2	- 42.9			
	Aug-Sep 2000				6.4	20.4*	218.7
	Mar-Apr 2001	8.6	6.2	-27.9			

* Maximal value reached before total depletion of nitrate.

When chlorophyll levels measured in the lake during both stratification and overturn are compared with each other, levels during stratification seem to be higher than during mixing, in spite of “lower” nitrate content (Figures 4-36 and 4-37 A and B). In fact, low nutrient levels during stratification are found only in superficial layers and for short time intervals, since reload of nutrients from deeper layers takes place due to daily mixing and atelomixis. In this way, intermittent increases of biomass in the lake are promoted and eventual losses of biomass due to sedimentation can be compensated. In the enclosures, although the same physical events also occur (nocturnal mixing, plankton sedimentation), a refill of nutrients does not take place. This is because, unlike the lake, there is no deep nutrients deposit and the only source of it is the initial amount in the enclosed water.

On the other hand, experiments carried out during overturn showed higher and increasing levels of Chl. a in the enclosures compared with those in the lake (Figure 4-37 B and C). These levels increased until the nitrate was exhausted. Additionally, values of Chl. a in the lake did not show the strong fluctuations observed during stratification periods. Instead, its levels were more stable throughout the experimental time, due to permanent mixing. That means in fact, a high amount of biomass distributed homogeneously through the whole water column, causing also a considerable loss of biomass since a fraction of phytoplankton is outside of the trophogenic zone and sinks. In the enclosures, the development of phytoplankton is promoted not only through higher nutrients contents at this time of the year but also through confinement in the trophogenic zone and the constant turbulence.

The behavior of Chl. a and nutrients levels during the two thermal seasons in both lake and enclosures demonstrates the effect of thermal patterns and convection currents upon the phytoplankton development.

UV radiation

In relation to the UV-radiation effects on Phytoplankton, the results would indicate that the elimination of ultraviolet radiation (in Figure 4-37 referred as "- UV") did not confer any advantage to phytoplankton. In the treatments "Without UV", chlorophyll values were very similar and occasionally even lower than those in the controls. Additionally, differences in chlorophyll values between enclosures of different length were not observed (Figure 4-37 B). This in turn may well indicate that longer exposure to typical light conditions has no effect on phytoplankton development. Sun radiation at Lake San Pablo during some days in August 2000 is shown in Figure 4-38, where the composition (UV-A, UV-B, PAR and infrared) and UV irradiance according to time of day and weather conditions are shown.

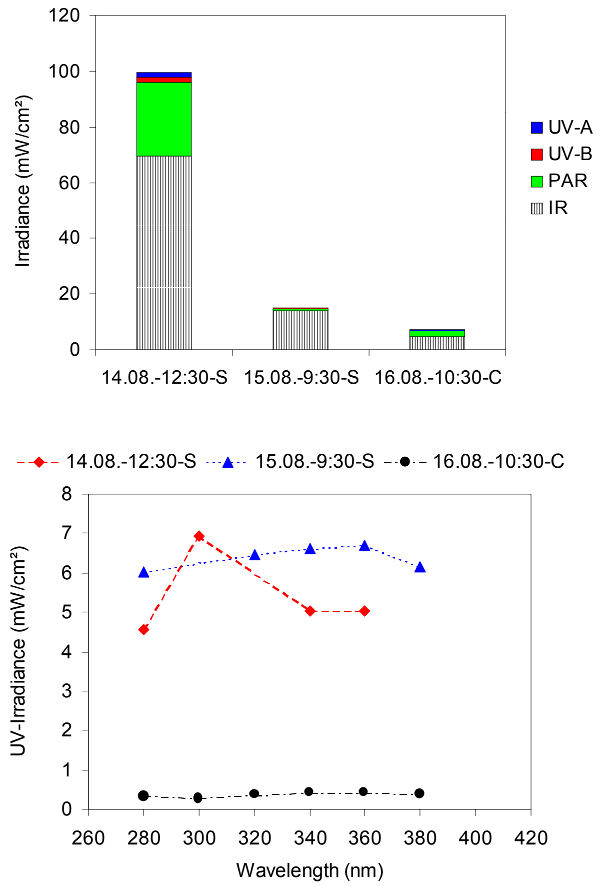


Figure 4-38. Solar radiation during some days in August 2000 at different times of day under sunny (S) or cloudy (C) conditions.

4.3.1.3 Nutrients relationship and its influence on biomass development

Changes in Chl. a concentrations during enclosure experiments were principally determined by the presence of nitrate as nitrogen source, even though ammonium was the most abundant nitrogen form. Ammonium represented approximately 80% of total DIN showing its dominance within this fraction. These high values can be explained by the mineralisation of organic matter and the excretion products of zooplankton. Ammonium also showed lower variation throughout the experiment time, a fact already observed during the monitoring program. Since the behavior of nutrients under natural conditions has been illustrated in an earlier section, only the results corresponding to those experiments where nutrients were added are presented here.

Figure 4-39 A shows chlorophyll and nutrient levels during August-September 2000. Initial concentration of chlorophyll was 4.3 µg/l in the lake and between 1.9 and 6.49 µg/l in the enclosures, with the highest value in the enclosure "Control" and the lowest in "N-supplemented". Initial concentration of SRP in the enclosure "P-supplemented" was 0.12 mg/l. In the other two enclosures and in the lake initial SRP values were around 0.05 mg/l. Levels of NO_3-N in the lake and in enclosures "Control" and "P-supplemented" lay between 0.06 and 0.08 mg/l at the beginning of the trial. In the enclosure "N-supplemented", after nitrogen addition, the initial value was 0.17 mg/l. Thus, addition of nutrients represented an increase in nitrate and SRP in the corresponding enclosure around 2.4 times the initial levels in the lake.

Chlorophyll values in the lake remained almost constant through the experiment, except for a significant increase towards the end of the test. In the enclosures, a progressive increase in Chl. a content was observed during the first days. This increase continued in the enclosures "Control" and "P-supplemented" until total consumption of nitrate. Greater Chl. a increase was observed in "N-supplemented", reaching a maximum of 43.5 µg/l on the 10^{th} day. At this time SRP stock was depleted in this enclosure, which was reflected in the strong chlorophyll reduction on day 12. On day 14 a light increase of nutrients occurred in the lake and in the enclosures. In fact, the light increase of SRP was reflected in an increase of Chl. a concentration in the lake and in those enclosures where enough nitrate was still available.

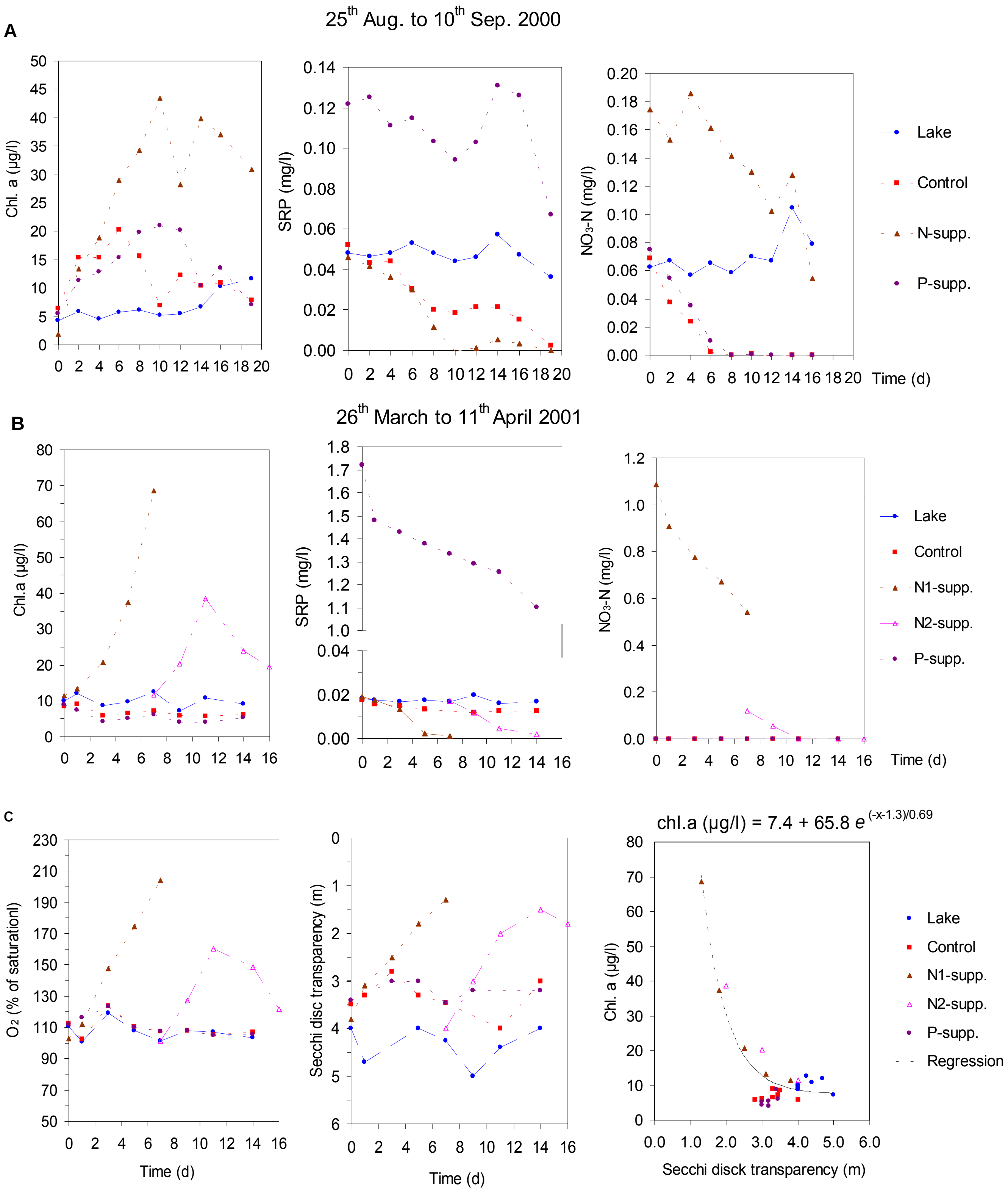


Figure 4-39. Levels of Chl. a and of nutrients during turnover in August-September 2000 (A) and during stratification period on March-April 2001 (B), when the effect of nutrient addition on phytoplankton development was studied. Changes on oxygen content and transparency during stratification 2001, as well as the correlation between transparency and Chl.a are also shown.

Similar results were achieved during stratification on March-April 2001 (Figure 4-39 B), when nutrient levels in the upper layers of the lake were very low. Initial values of SRP were around 0.02 mg/l both in the lake and in the enclosures, except in "P-supplemented", where the concentration rose to 1.72 mg/l after P addition. Initial nitrate levels in the lake were under detection limits and after N addition, nitrate concentration rose to 1.09 mg/l in "N1-supplemented" and to 0.12 mg/l in "N1-supplemented". Although initial nutrients levels in the lake were lower than during August-September 2000, chlorophyll values were higher. They lay between 8.6 and 10 µg/l in both the lake and the enclosures at the beginning of the trial.

A strong decrease in nitrate concentration was observed from the beginning in enclosure "N1-supplemented". On the seventh day total depletion of SRP was reached with a final nitrogen concentration of 0.54 mg/l. At the same time a maximum Chl. a level of 68.6 µg/l was measured, being six times the initial concentration. In enclosure "N2-supplemented" nitrate stock ran out in only 4 days with a maximal Chl. a concentration of 38.6 µg/l, 3.4 times the initial level.

In the "P-supplemented" enclosure the addition of phosphorus did not show an increase of biomass. Here, the chlorophyll levels were somewhat lower than the levels found in "Control". In the two last mentioned enclosures, levels of Chl. a were even lower than in the lake and showed only light variations during experimental time.

The changes in Chl. a content were also reflected in dissolved oxygen content and in water transparency, as shown in Figure 4-39 C. Here, oxygen levels in the two enclosures with nitrogen addition showed a strong increment from the beginning, reaching maximum values of 204 % in "N1-supplemented" and up to 160.2 % in "N2-supplemented". The decrease registered in "N2-supplemented" between the 11^{th} and 16^{th} days was probably caused by the depletion of phytoplankton and the subsequent reduction of photosynthesis. Changes in biomass levels as well as the effect of daily mixing patterns and consequent convergent currents generated variations in the transparency of the water column, something that might well be an additional factor for the limitation of plankton development. The increase in biomass in the enclosures with nitrogen addition generated a high decrease in transparency levels. In the lake and in the other enclosures, transparency values oscillated following the Chl. a. variation pattern (Figure 4-39 C). The relationship between Chl. a and transparency is illustrated in the same Figure, where a regression fitting is also shown. Here it can be observed more clearly that the lake showed the highest transparency values in comparison to "P-supplemented" and "Control" in spite of its higher Chl. a values. These results demonstrate that nitrogen, and more exactly nitrate, plays a central role as limiting factor of productivity.

4.3.1.4 Phytoplankton composition and abundance

Analysis of phytoplankton was carried out only during overturn 2000 and stratification 2001 in order to find out the possible effects of UV-radiation and nutrients addition upon especies composition .

During August-September 2000 the more abundant phytoplankton species were *Chlamydomonas sp*, *Pediastrum boryanum*, *Aulacoseira granulata* and *Trachelomonas volvocina*. (Figure 4-40 A). *Scenedesmus linearis*, having shown the highest abundance during the monitoring program, had very low abundance during this experiment, representing less than 0.2% of total abundance in the lake as well as in the enclosures. In the same way, the development of *Neglectella sp*. was very low, although its abundance in the lake was 12 times the abundance found in the enclosures. Of particularl interest was the presence and high abundance of *Chlamydomonas sp*. in the enclosures during this test. This species was found in the lake during the monitoring program only in June of 1999 in very low abundance, and showed again very low abundance in the lake during this test, when its contribution to total abundance was only 0.35%. Also remarkable was the development of *Pediastrum boryanum* and *Trachelomonas volvocina*, especially in the lake where these two species were much more abundant that in the enclosures. The abundance of *Microcystis aeruginosa* was notable only in the treatment “Without UV”, where the abundance of this species represented 27% of the total. In the other enclosures and in the lake its contribution to total abundance was below 0.2%. These facts indicate that the suppression of UV radiation may represent an advantage for the development of this species.

As far as biovolume is concerned, it turned out that this was mainly determined by the species of high cellular volume. This was also the outcome of the monitoring program. In this way and in spite of the dominance of *Pediastrum boryanum* in the lake, the biovolume was determined by the presence of *Trachelomonas volvocina*, due to its high cellular volume (Figure 4-40 B). In the enclosures the biovolume was determined by this same last species, as well as by the presence of *Chlamydomonas sp.*.

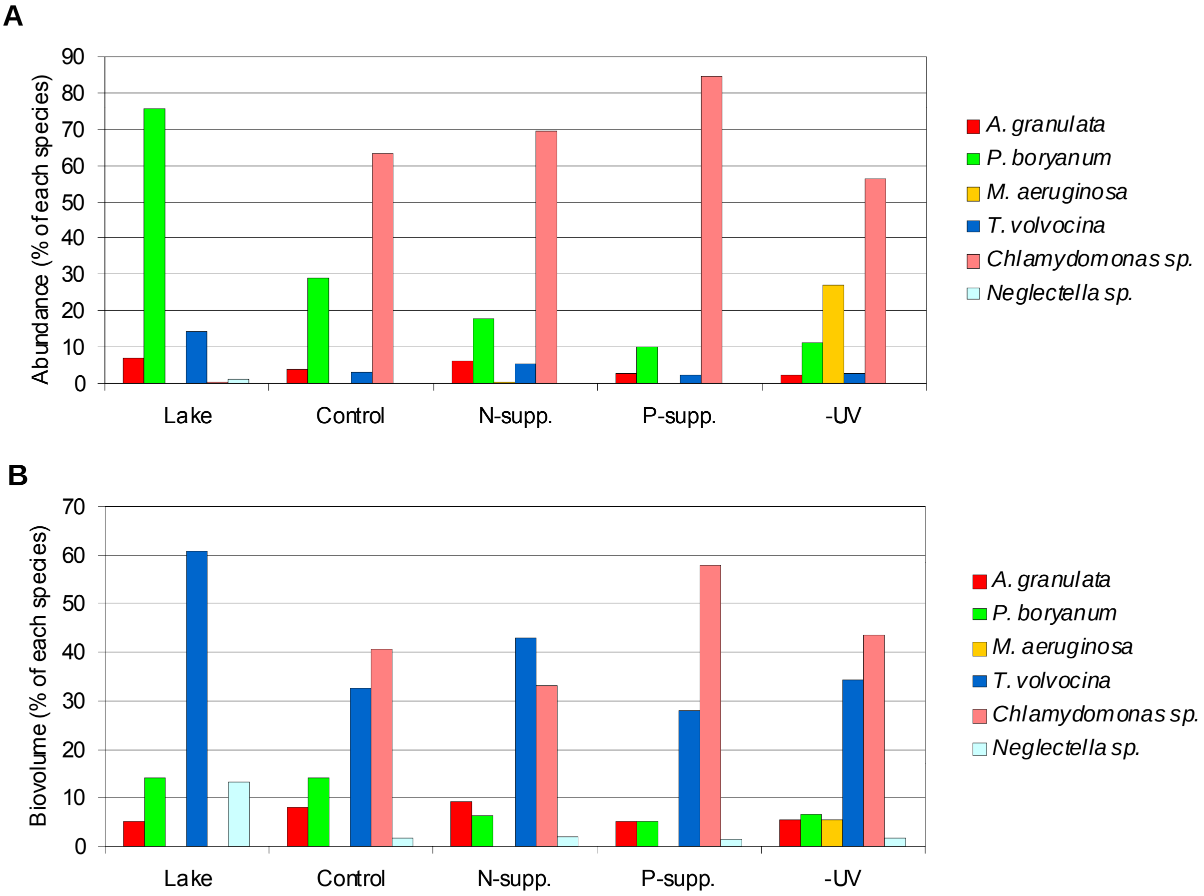


Figure 4-40. Abundance and biovolume of the most important phytoplankton species during enclosure experiments carried out in August-September 2000. Values given as percent with respect to the total amount registered through the time of study. Due to its high cellular volume, *T. volvocina* was important as component of total biovolume, especially in the lake, where *Clamydomonas* sp. was absent.

Abundance and biovolume during March-April 2001 in the lake and in each one of the enclosures are shown in Figure 4-41 A. Here, high abundance and biovolume levels was observed in the enclosures where nitrogen was added, whereas in the lake and the other enclosures these levels were much lower. The same trends were observed for Chl. a levels, as described earlier.

Additionally, abundance and biovolume of the six predominant species are represented in Figure 4-41 B as percentage of the sum of values registered during the sampling period in the lake and in each enclosure. From these data, it can be deduced which species could have a competitive advantage under experimental conditions. *P. boryanum* was the most abundant species, representing more than 40 % of the total abundance in the lake and in each enclosure. *A. granulata* also showed good development, especially in the enclosures with nutrient addition and in “Without UV”. Total biovolume was also strongly determined by this species. The Cyanobacteria *M. aeruginosa* was very abundant in the lake, with 34.7 % of total abundance. In the enclosures its abundance was much higher than during overturn lying between 8.2 and 16 %. The contribution of *Neglectella sp*. to the total abundance was low in all cases, with a maximum of 4.1 % in "Control". However, due to its large size this species represented the highest biovolume values, reaching up to 61.6 % in "Control". During this trial *Clamydomonas sp.*, which was the principal component of biovolume during overturn 2000, was practically absent.

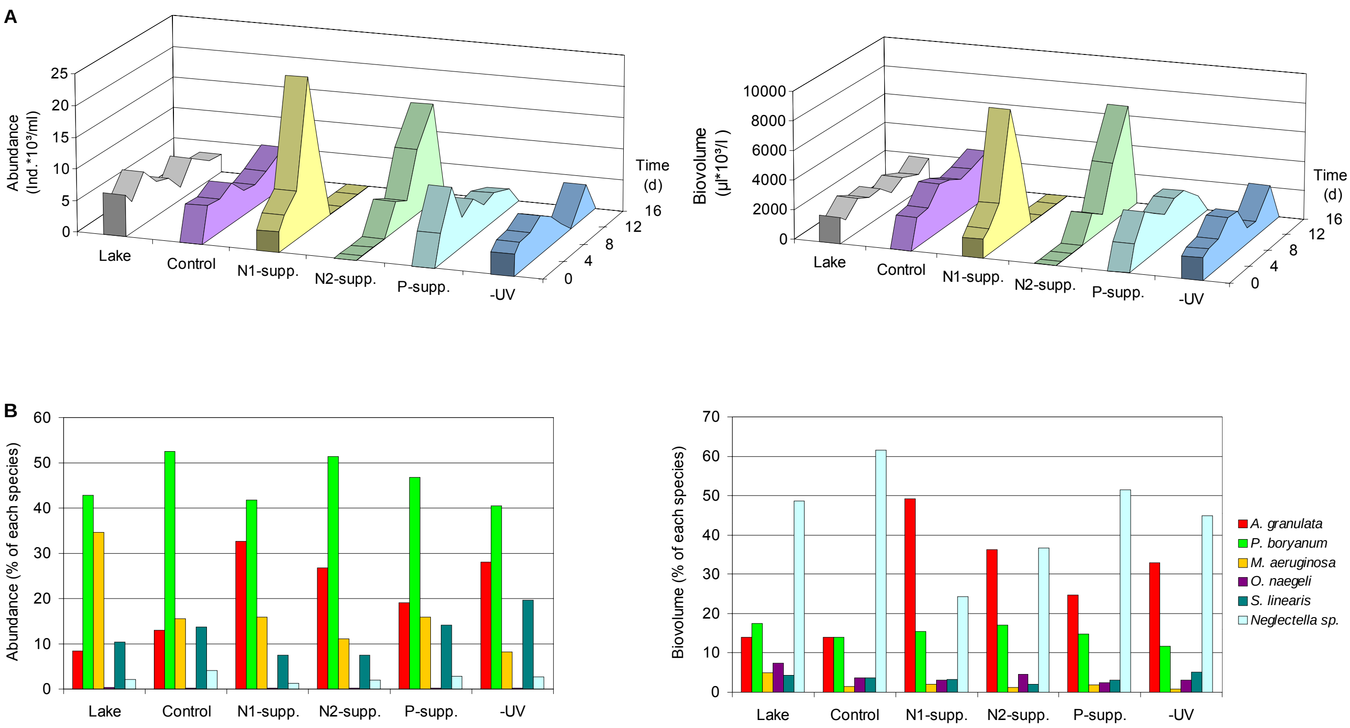


Figure 4-41. (A) Temporal distribution of abundance and biovolume of phytoplankton in the lake and in each one of enclosures during March-April 2001. Higher abundance and biovolume were found in the enclosures where nitrogen was added. (B) Abundance and biovolume of the six most important species. Values are given as percent with respect to the total amount registered throughout the test. This time, *Clamydomonas sp*. was not found and *M. aeruginosa* showed high relative abundance in the lake and in all enclosures in comparison to the results from Ausgust-Serptember 2000.

4.3.1.5 Nitrate versus chlorophyll a : Elaboration of an Eutrophication model

In order to obtain a mathematical model that describes the relationship between nitrate content and chlorophyll levels, a regression analysis was carried out with the highest Chl. a values registered in the enclosures and in the lake during all enclosure experiments and the corresponding initial concentrations of nitrate. Nitrate values were chosen for the elaboration of the model, since it was determined through the monitoring program and the enclosure experiments that this form of nitrogen is the one that plays a preponderant role as limiting factor for phytoplankton production. Thus, the Figure 4-42 shows data used for the regression fitting, the regression equation, and the corresponding curve. Additionally, mean values of nitrate and Chl. a. calculated for the trophogenic zone with data from the monitoring program are represented in this Figure. Such data fit well within the regression curve.

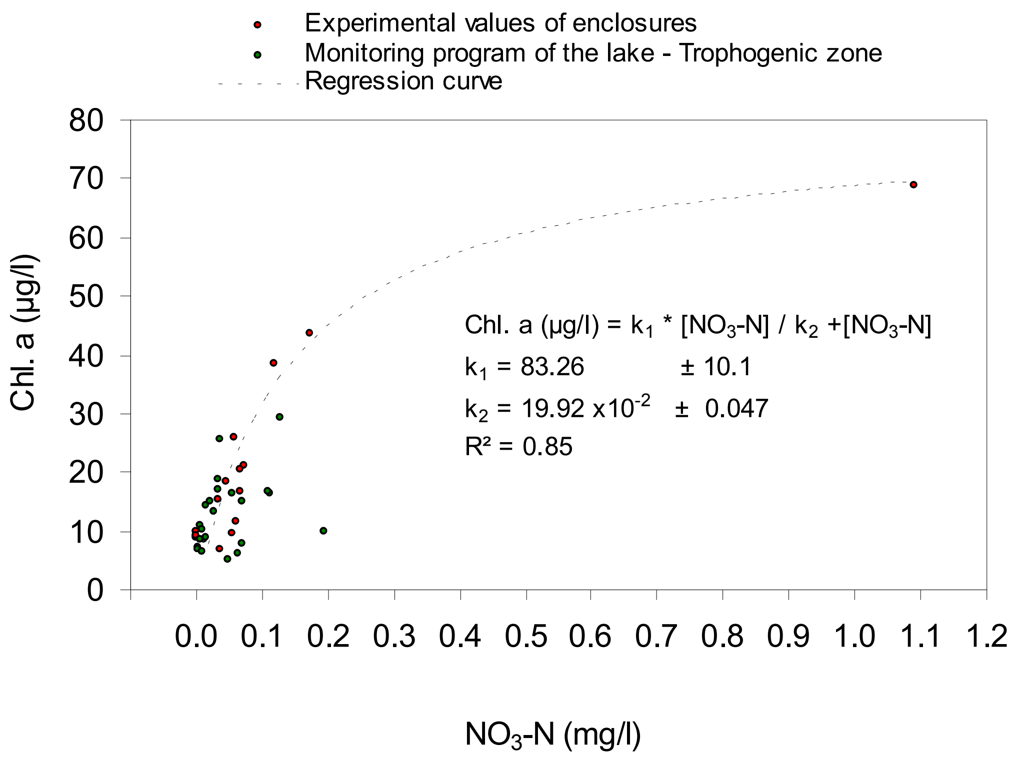


Figure 4-42. Correlation between initial nitrate content and final chlorophyll levels. Experimental data from enclosure experiments were used to fit a regression curve. Mean values of nitrate and Chl. a for the trophogenic zone calculated with data from the monitoring program of the lake are also shown.

A model of this type, as well as that presented in Figure 4-39 C (transparency vs. Chl. a), would be useful in the elaboration of eutrophication control and management programs for the lake, since through the determination of nitrate inputs into the lake, e.g. as consequence of agricultural use of fertilizers, it would be possible to estimate the chlorophyll level that would be reached and its negative effects on the system.

4.3.2 24-hours sampling series

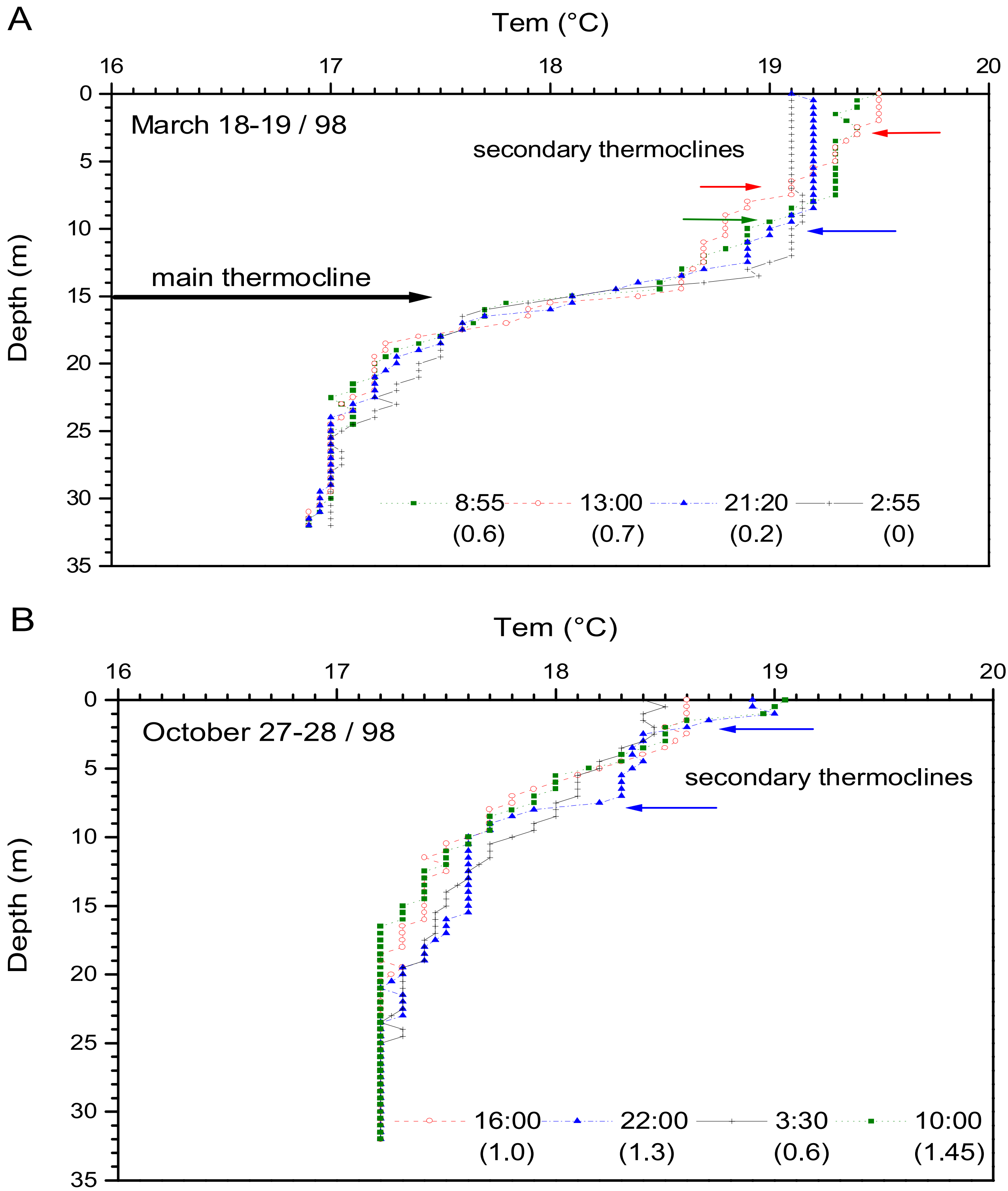
Dates of the three sampling series are shown in Figure 4-5 where the corresponding thermal state of the lake at the moment of the sampling can be also observed. Temperature profiles obtained during these three 24-hours-samplings are shown in Figure 4-43.

4.3.2.1 Daily Thermal behavior

The first sampling series between 18th and 19th of March 1998 was performed during the rainy season, when thermal stratification and high stability of the thermocline occurred. Here, the four profiles registered at 8:55, 13:00, 21:20 and 2:55 hours (Figure 4-43 A) showed the typical stratification pattern of temperate lakes during summer, with higher temperatures in the superficial layers, a stable thermocline between 14 and 18 m, and lower temperatures in the deeper strata.

However, examining the behavior of temperatures in the upper 15 m, it can be observed a stratification and mixing process developed during the day-night cycle. Here, the temperature profile at 8:55 already showed an incipient stratification process in the first meters, with the formation of a secondary thermocline between 8 and 12 m depth (green arrow). The profile at 13:00 showed a more defined thermal stratification in the first 15 m with formation of secondary thermoclines above the main one (red arrows). In the same strata, the profile at 21:20 showed a uniform temperature until 9 m, indicating a mixing process from the surface down until this depth, and a secondary thermocline between 9 and 12 m (blue arrow). After midnight, at 2:55, a lower and uniform temperature was registered until 12 m, indicating the disappearance of secondary thermoclines and a total mixing of these superficial strata. Below 15 m, the main thermocline remained invariable through all four measuring periods, causing the isolation of the deeper layers from the superficial ones. This thermal behavior is a clear example of atelomixis.

The second sampling series was carried out between 27th and 28th October 1998, after the complete mixing in the lake occurred in July. At the moment of this sampling the stability of the lake was still low (Figure 4-7).



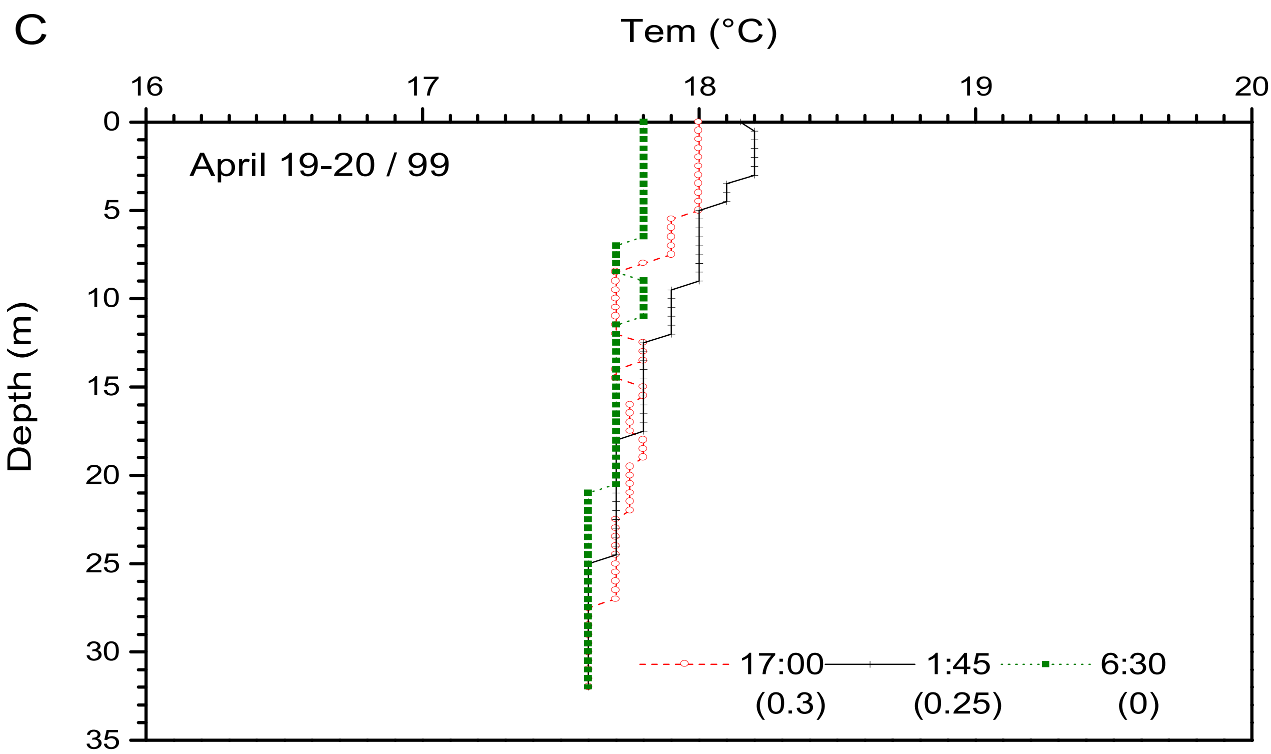


Figure 4-43. Temperature profiles registered during the 24-hours sampling series. A, C: rainy season; B: dry season. The arrows indicate the formation of secondary thermoclines. Values in parentheses show thermal resistance to mixing between surface and 10 m depth (relative units; Wetzel, R.G., 1991).

Temperature profiles measurements at 16:00, 22:00, 3:30, and 10:00 hours (Figure 4-43 B) showed an incipient development of the seasonal stratification along the column of water. In the upper layers thermal differences between day and night were measured, with a slight tendency to thermal homogeneity at 22:00 hours between 2 and 7 m depth and the formation of temporary thermoclines (blue arrows). Comparing the temperatures from the first 10 meters of this sampling with those of March 18th, it can be observed that in October the temperatures were somewhat lower than in March but the temperature differences among adjacent layers were higher, which implicates a higher thermal stability and higher resistance to mixing in the upper strata in October. Furthermore, the thermal resistance to mixing in the upper 10 m at 22:00 hours was 6.5 times higher in October than in March. Howerer, if the whole water column is considered, the stability and the resistence to mixing were higher in March.

The third sampling series between 19th and 20th April 1999 was carried out during the rainy season. The measurements at 6:30, 17:00 and 1:45 hours showed an almost homogeneous temperature profile and therefore low stability in the lake, with a temperature difference of only 0.6°C between the maximum and the minimum values registered (Figure 4-43 C). In spite of this small difference, an unusual nocturnal weak stratification at 1:45 hours was observed. This fact was corroborated with data from the automatic temperature data-logger device as is shown in Figure 4-8 B. This graphic shows a very irregular pattern of stratification and overturn at the time. On 19th April a midday stratification was registered, a stark decrease of water temperatures around 17:00 hours because of very strong winds and the formation of the above mentioned weak stratification at 1:45 hours. More uniform temperatures were reached at 6:30 a.m., due to calm weather at nighttime and the effect of thermal inversion. Thus, this survey coincided with a short period of mixing within a period of transition (see Figure 4-5). This explains an atypical behavior with strong variations of the patterns in a very short time period, something that was not observed during more stable phases, as Figure 4-8 A and B show.

4.3.2.2 Chemical characteristics

Values of dissolved oxygen and pH obtained during each of the 24-hours sampling series are represented in Figure 4-44. These parameters showed almost the same trend observed for temperature and confirmed the observations about diurnal mixing processes.

<u>Oxygen</u>

In all registered profiles on 18-19 March 1998 (rainy and stratification season), oxygen reached levels only just above saturation in the upper 6 m depth. From this depth on, oxygen content decreased during the day and part of the night, except for the profile at 2:55 a.m., which showed almost constant oxygen content between the surface and 12 m depth due to nocturnal mixing of the superficial layers.

On 27-28 October 1998 (rainy season; stratification process), oxygen content was much higher near the surface due to photosynthetic activity, which was high during this period, as can be seen in Figure 4-28. and 4-49. Towards deeper layers oxygen levels dropped off until reaching complete anoxia. Contrary to the observations in March, uniform oxygen content on the superficial layers of the water column was not observed during this sampling series.

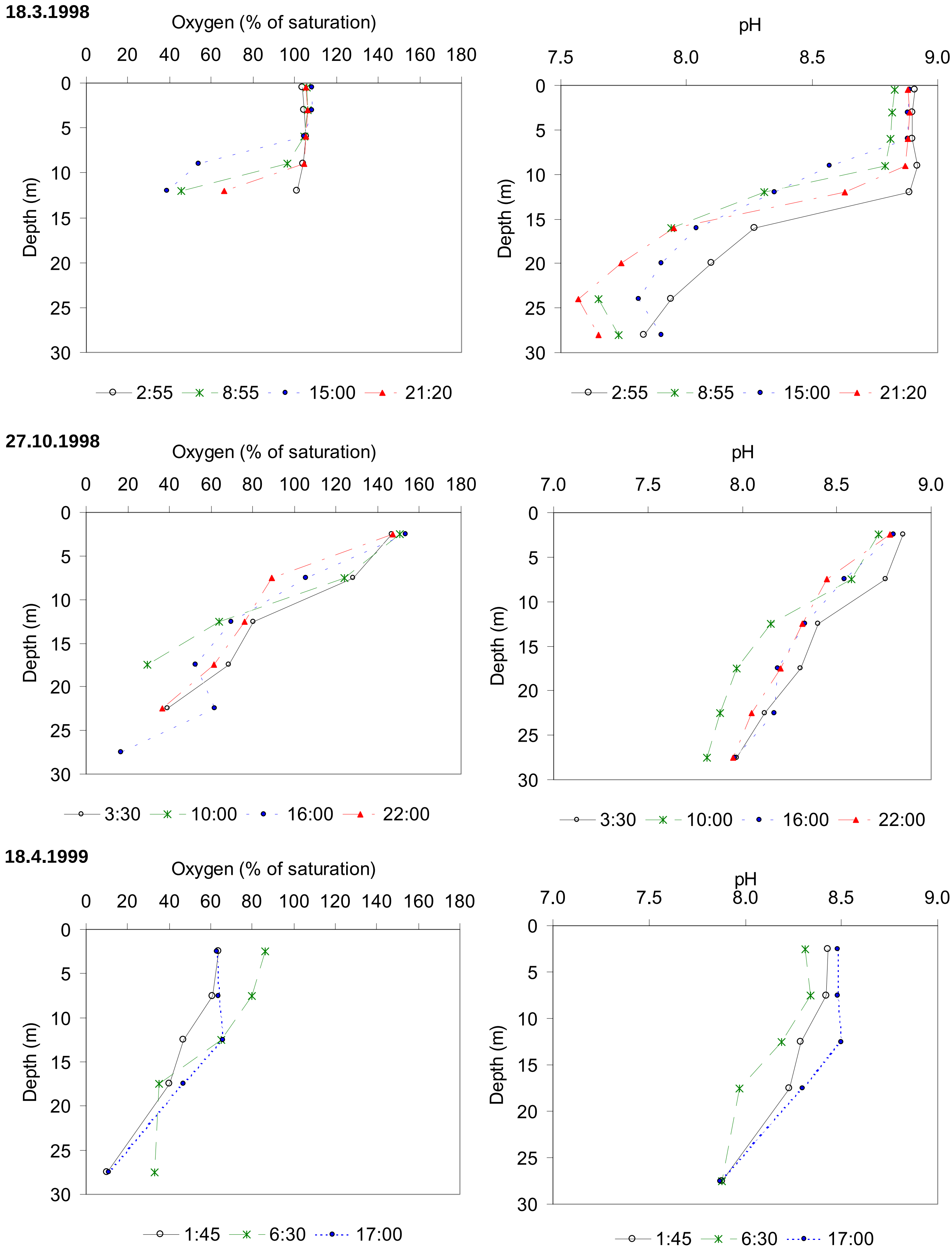


Figure 4-44. Values of dissolved oxygen and pH measured during each one of the 24-hours sampling series.

During the last sampling on 19-20 April 1999 (rainy season), oxygen concentrations were the lowest among the three samplings carried out, showing during the morning hours the highest level in the superficial area and lower levels in deeper strata. In the afternoon and in the night the concentration trend was similar to the one registered at 6:30 a.m., but with lower values.

pH values

During all three sampling dates, pH values showed a daily distribution pattern very similar to the one described for oxygen. In March of 1998 pH values were near to 9.0 in superficial layers to 7 m depth with variations depending on the sampling hour, while below 20 m pH values were between 7.5 and 8.0. On October 1998 and April 1999 pH values showed a narrower range.

Nutrients

Levels of nutrients found during the third sampling in April 1999 are shown in Figure 4-45.

TP values showed strong variations throughout the water column in the three profiles analyzed within a defined pattern: lower concentrations at the surface and between 10 and 15 m, with higher values at the bottom of the lake. TP concentrations at 17:00 hours were notably higher than during the night and early in the morning.

TN concentrations showed strong variations too, but a uniform pattern for the three samplings was not observed. In general, low concentrations were detected in superficial layers with a significant increase at 17:00 hours, while higher levels were found at the bottom of the lake.

Concentrations of SRP and inorganic nitrogen showed similar patterns. At 17:00 hours SRP concentration was 0.13 mg/l near the surface, falling to 0.03 mg/l at 6:30 a.m. on the next day. During midnight, SRP values were almost uniform up to a depth of 13 m. The levels diminished toward the deeper zones of the lake, reaching values close to 0.2 mg/l in all three measurements. Inorganic nitrogen showed values between 0.1 and 0.15 mg/l in the superficial zones and much higher values in the deepest zones. Within inorganic nitrogen, ammonium was again the most important fraction, representing 25% near the surface and up to 94.5% near the bottom of the lake. These high levels of SRP and NH_4 at the bottom of the lake are related to the anoxic conditions and mineralisation processes in these strata.

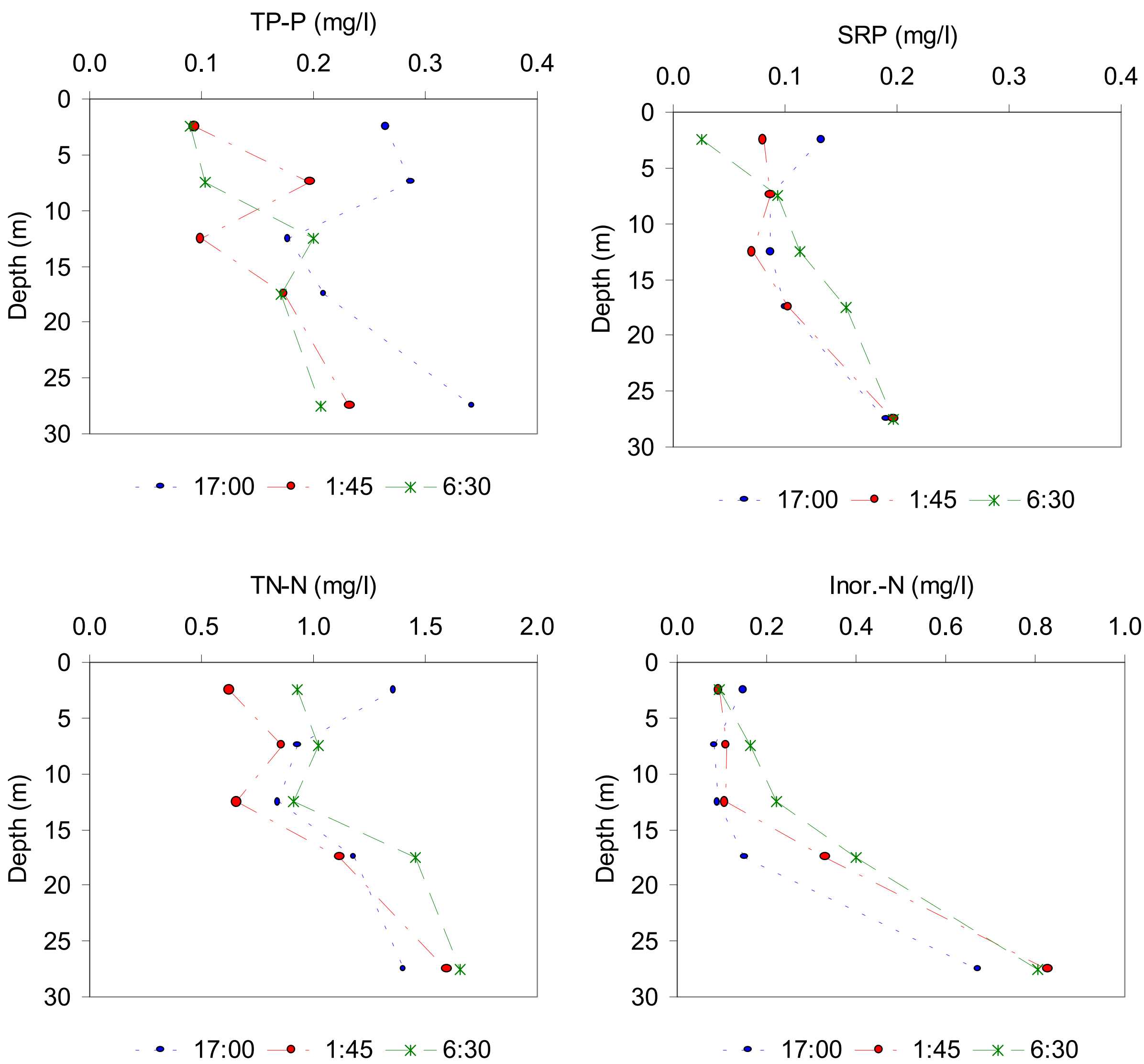


Figure 4-45. Vertical nutrients profiles during the 24-hours sampling in April 1999, during the rainy season.

Zooplankton

Figures 4-46 to 4-48 show daily vertical distribution of zooplankton abundance for each one of the sampling dates.

None of the samplings showed higher zooplankton abundance in deep zones during the night, which would indicate that daily vertical migration of zooplankton does not take place during any time of the year. However, the differences in abundance levels and distribution of zooplankton according to the sampling period are noteworthy.

The sampling done on March 18^{th} 1998 (Figure 4-46) occurred within a season of low zooplankton abundance (see Figure 4-30). The organisms were concentrated in the first 16 meters, coinciding with the thermocline location. In other words, the strong thermal stratification and the associated low oxygen level in deep layers influenced the vertical distribution of the zooplankton. On the other hand, a high relative abundance of adults and copedodites of *M. mendocinus* was observed in the area corresponding to the thermocline during the morning hours. In the case of *Asplachna sp*., there was a significant high abundance at the thermocline level, as much in the morning as in the night.

During the sampling on October 1998 (Figure 4-47), higher abundance of organisms was observed in superficial layers until 5 m depth, and a more regular distribution between 5 and 28 m. Noticeable was the higher abundance of *D. pulicaria* during the night, which could be an indication of horizontal migration of this species. Also noteworthy is the vertical and seasonal population distribution of *M. mendocinus*. In March, the population composition was more homogeneous, while during October there was much higher abundance of nauplii. They also had a more homogeneous vertical distribution during the night. During this same sampling the presence of *Asplachna sp*. was extremely low.

In the sampling on April 1999 (Figure 4-48), *D. pulicaria* and *Asplachna sp.* showed higher abundance between 15 and 20 m both in the morning and in the afternoon. However, *M. mendocinus* showed higher abundance levels at the surface with decreasing quantities toward deeper layers.

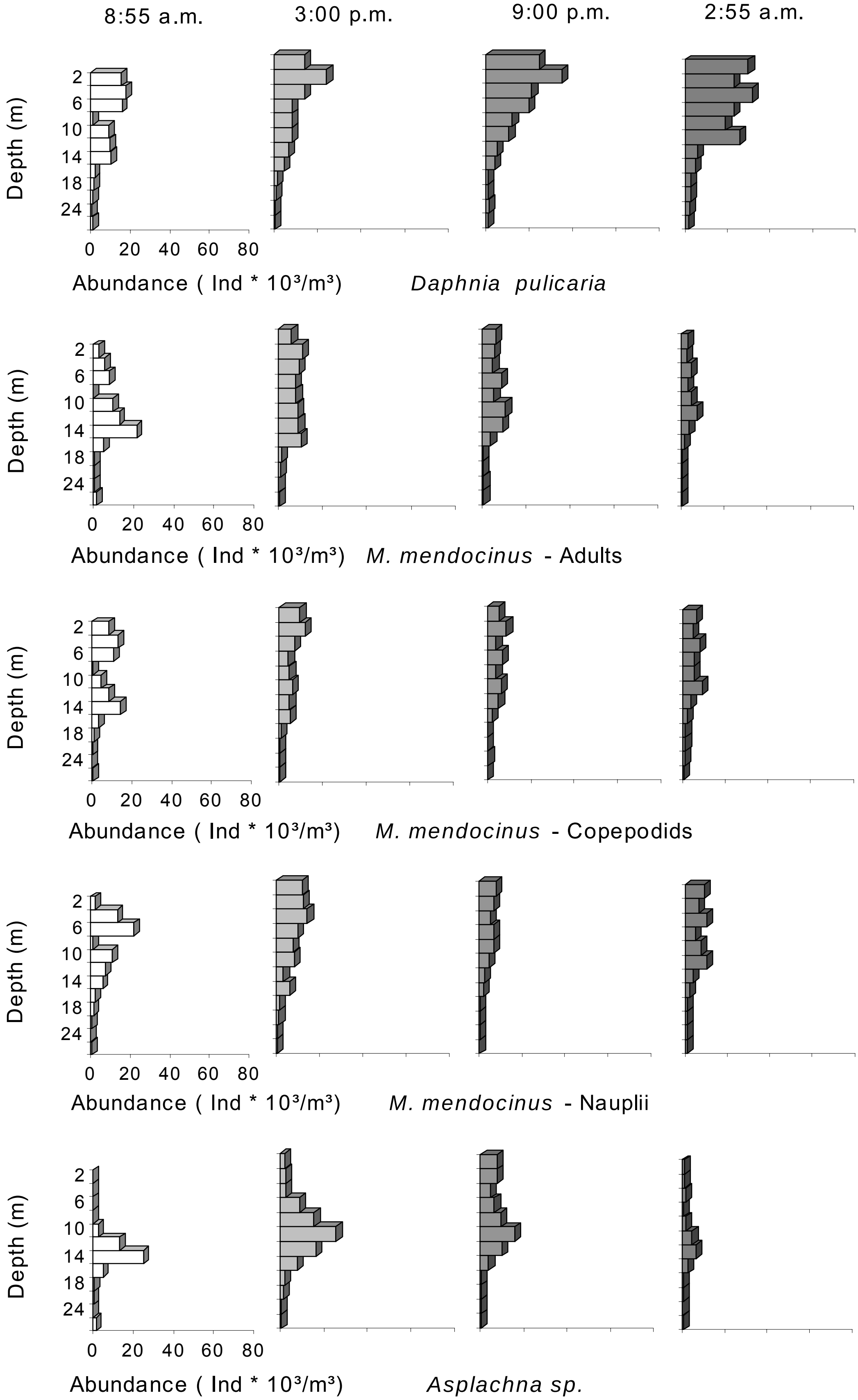


Figure 4-46. Daily vertical distribution of zooplankton on 18-19 March 1998. Note the concentration of organisms at the thermocline location.

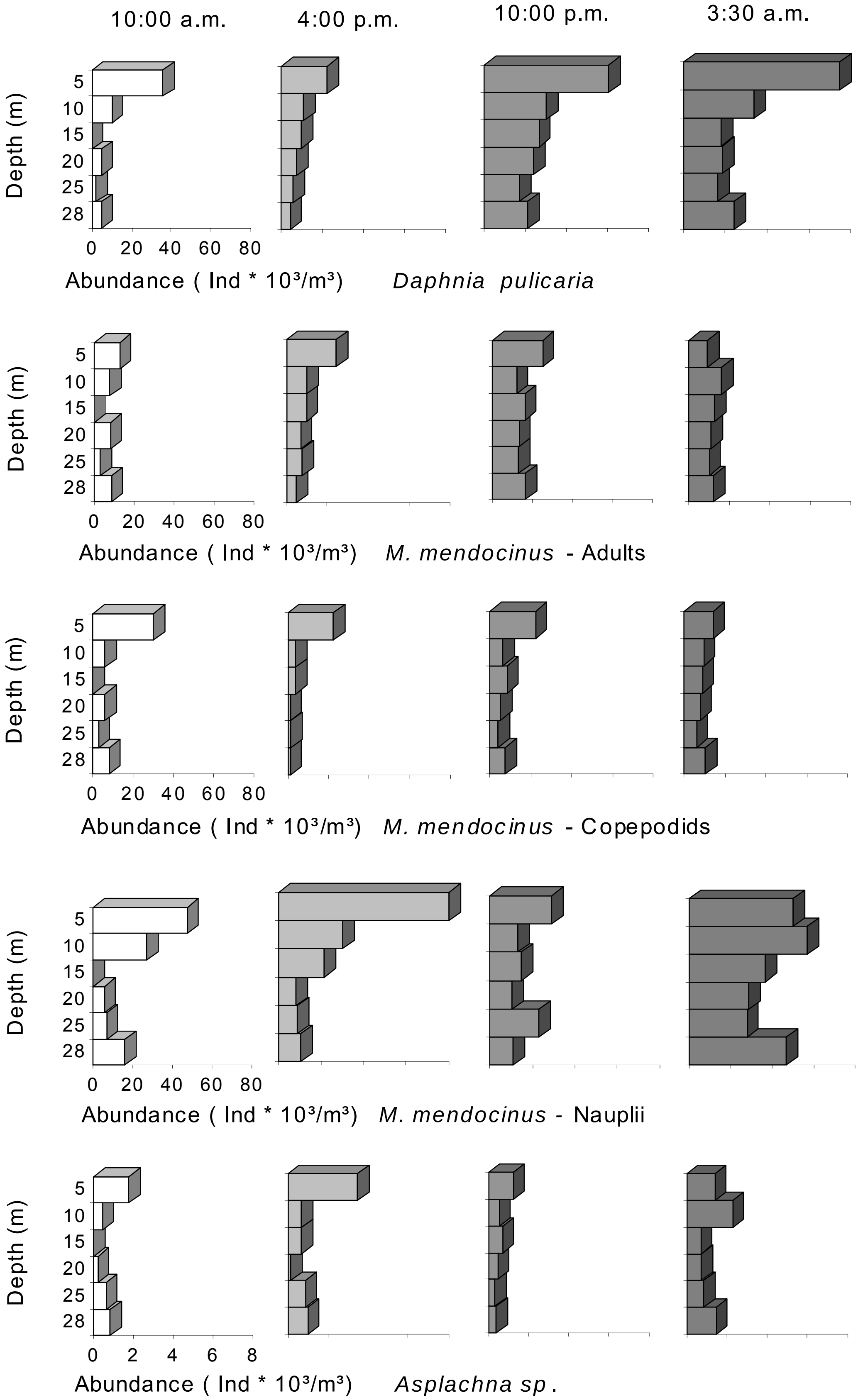


Figure 4-47. Daily vertical distribution of zooplankton on 27-28 October 1998.

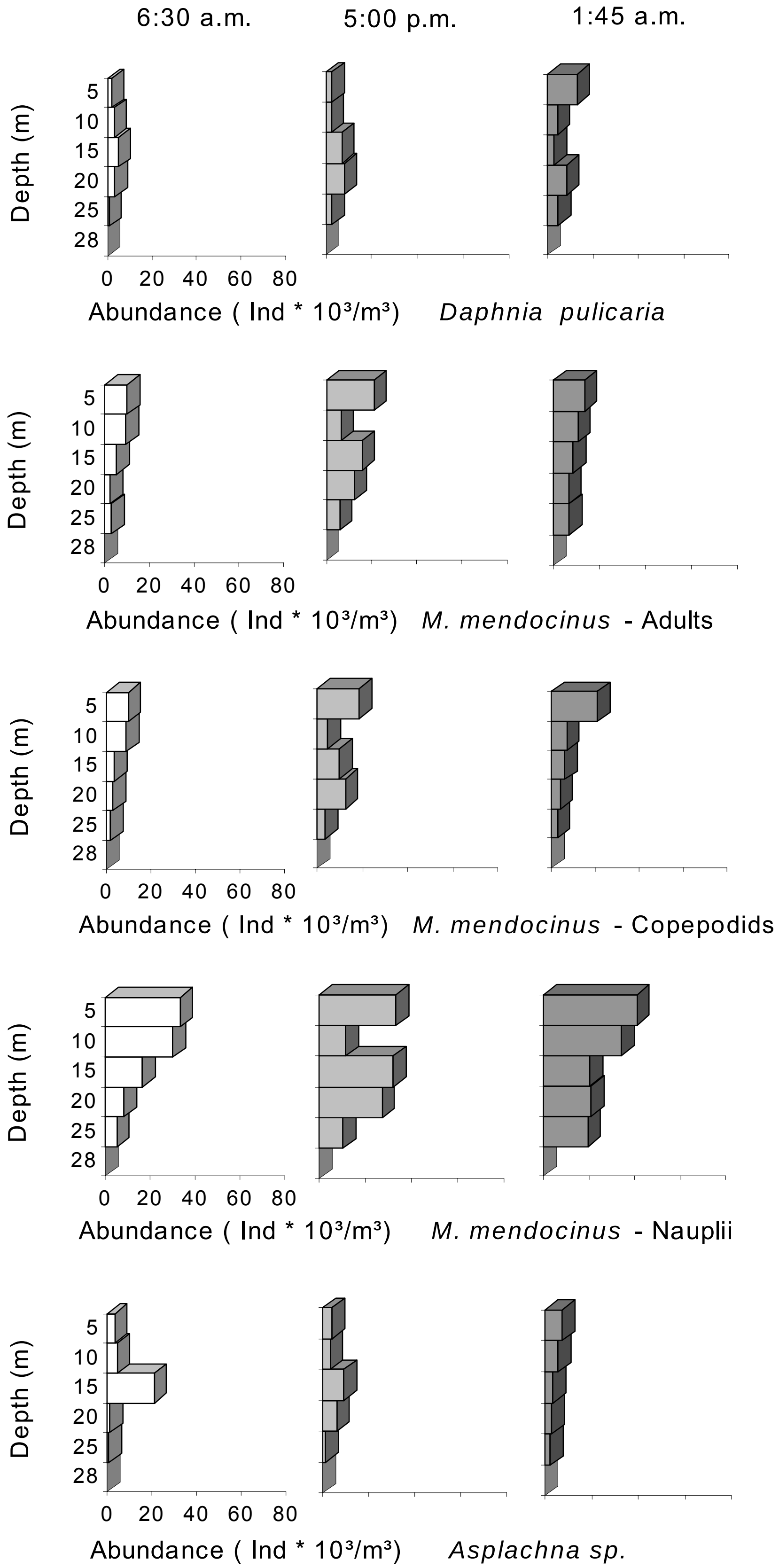


Figure 4-48. Daily vertical distribution of zooplankton on 19-20 April 1999.

Chlorophyll analysis was carried out only during the sampling in October 1998. The results are presented in the Figure 4-49. Higher Chl. a concentrations were detected in the trophogenic area, with the highest concentration between 2.5 and 7.5 m, and lower concentrations toward the bottom of the lake both during the day and the night. The lowest levels were registered at 10:00 a.m., something that could indicate an important decrease of phytoplankton during the night. In fact, high abundance of *D. pulicaria* was registered in upper strata during the night, which could cause this decrease of Chl. a due to feeding. The vertical distribution of Chl. a concentration would also indicate a low rate of phytoplankton lost due to sinking and lower zooplankton feeding rates during daytime.

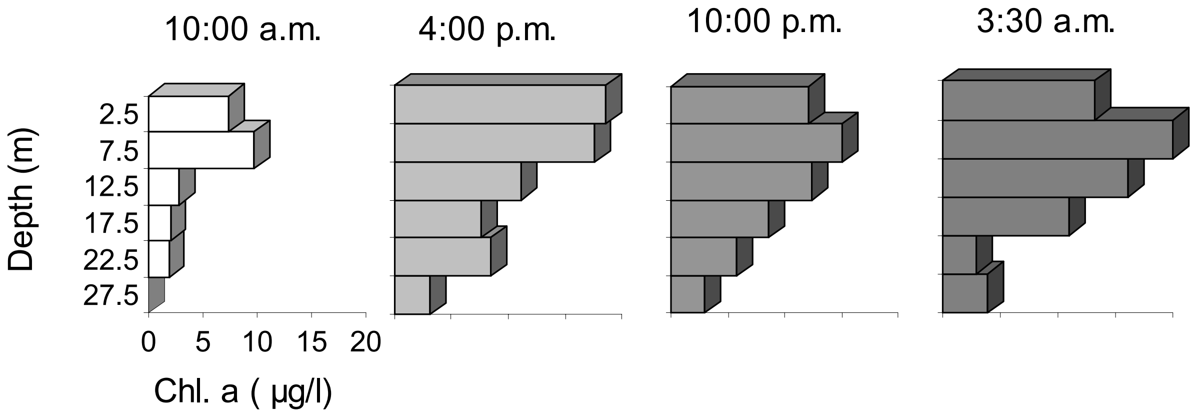


Figure 4-49. Vertical Chl. a distribution during the 24-hours sampling in October 1998. A similar pattern was observed along the four profiles: highest values between 2.5 and 7.5 m and decreasing levels toward deeper layers.

5 Discussion

5.1 Thermal characteristics of the lake

Climatic conditions in the tropics, mainly determined by latitude and altitude, together with the morphometry of the lake basin, are decisive factors in the thermal regimes in water bodies (1994; Arai, 1981; Osborne, 2000). Furthermore, thermal structure, heat content, and water movements are three of the most important characteristics of a lake. These parameters are closely related and are of fundamental importance for the physiology, metabolism, distribution, and behavior of the organisms that inhabit an aquatic system. They can also determine the behavior of other variables, such as the distribution of nutrients and the content of dissolved gases. For these reasons, the determination of the thermal structure, the heat content and the water movements are of fundamental importance in limnological studies.

The principal source of energy in water is solar radiation, but some transfer of heat, although of minor magnitude, can occur from the air, sediments and input waters. The absorption of solar energy and its dissipation as heat in the water body clearly affects the thermal structure and the circulation patterns of water masses in lakes, reservoirs, and streams (Wetzel & Likens, 1991). Additionally, solar energy absorption is influenced by physical, chemical and, in some cases, biological characteristics of the water (Wetzel, 1983). The retention of the acquired heat in a lake or reservoir depends partially on factors that influence its distribution within the water body, like water losses, the physical effects of wind energy and currents and other water movements. The interaction of all these factors is of major importance for the biota and the productivity of a lake.

The thermal behavior observed in Lake San Pablo throughout each studied hydrological cycle is characterized by a period of stratification during the rainy season, and a period of mixing during the dry season. The stratification shows a low temperature variation along the water column; therefore, it can be considered weak. The beginning of the dry season by the middle of the year and the consequent appearance of strong winds in the afternoons provides sufficient energy to break down the weak stratification. This initiates a period of total circulation of the masses of water begins. In this process, intensity and duration of the winds are decisive factors for the energy balance in the lake, determining the duration of the overturn period and the temperature of the water column during this period.

It should be noted that the necessary temperature difference between layers in a water body that makes a stratification formation possible becomes gradually smaller towards the equator (Lewis, 1995). These gradients are especially low in the tropics, due to the small temporal variation in daily irradiance, air temperature and evaporation ratios (Lewis, 1987). These characteristics are also responsible for the low heat budgets of tropical lakes, which are easily observed in equatorial regions (Cole, 1988). The annual heat budget of Lake San Pablo (350 cal/cm²) is very low compared with those of lakes in temperate regions: Lake Tom Wallace (2.34 ha, surface and 8.7 m depth) and Lake Michigan have values of 6,940 cal/m² and 52,400 cal/m² respectively. Annual temperature differences determine these high values, although the morphology and volume of the lake are also important (Cole, 1988). It appears to be that in tropical regions altitude also has an influence on the heat budget: for the high mountain lake El Sol (4,120 m a.s.l.) in Mexico, Banderas et al. (1991) calculated a value of 5,988cal/m². In this case, like in Lake San Pablo, the comparative low values are the result of the combination of high altitude and low latitude.

Another important characteristic of Lake San Pablo is the observed daily mixing pattern (atelomixis). Here, stratification is generated during the hours of higher sun radiation (diurnal warming). In the afternoon, the diminution of the environmental temperature causes loss of heat in the top layers of the water column, and a total disappearance of stratification as well thermal inversions around midnight due to nocturnal cooling. These abrupt changes of temperature during the night produce cooler and denser surface waters, generating convection currents and water mixing that can reachts 20 m depth, as shown in Figure 4-9. This daily mixing pattern was observed during stratification and overturn periods, but does not occur every night, since such an event depends on prevailing daily climatic conditions (Gunkel & Casallas, 2002b).

The described thermal behavior, when occuring over a long time interval -days or even weeks- correspond to an atelomictic process (Figure 4-35). Typical for these thermal events is the formation and disappearance of secondary thermoclines during seasonal stratification, producing irregular and partial mixing in the upper strata without affecting the underlying layers. These water movements have essential implications for the chemistry and biology of water bodies, as will be discussed later.

Based on the described characteristics and Lewis's mixing classification system (1983), Lake San Pablo can be classified as a warm monomictic lake, since it shows a single period of overturn through the year with water temperatures above 16° C, daily mixing patterns occurring during great part of the year with a partial, and probably total mixing. This indicates a continuous warm polymictic regimen, something that is also considered characteristic of tropical mountain lakes (Lewis, 1987; Roldán, 1992). Taking these facts into account, it may be assumed that Lake San Pablo represents an intermediate or transitional thermal category between the tropical warm lakes of low areas and the high mountain lakes located over 3,500 m a.s.l. in the Paramo region. In any case, it demonstrates the complexity of thermal pattern in tropical systems.

On this aspect, Lewis (2000) points to the confusion that still exists in relation to the seasonality of mixing cycles in tropical lakes. According to him, this confusion has its origin in the typology of tropical lakes developed by Hutchinson & Löffler (1956). This classification gave rise to the idea that tropical lakes can only be either polymictic or oligomictic. Actually, studies carried out years after this classical work of Hutchinson & Löffler have demonstrated that this typology is inaccurate when applied to tropical regions. These later studies have demonstrated that tropical lakes are basically monomictic, with variations toward polymixis or meromixis depending on the relative depth. Steinitz-Kannan et al.(1983) have also pointed out that although the generalization about the polymixis of high mountain lakes in tropical areas of Africa and America is broadly accepted, it is not completely satisfactory when applied to the Ecuadorian lakes, since all of these stratify from time to time and most can also mix as a consequence of rains and winds, especially during the night.

In the described thermal processes, the morphometry of the lake basin as well as the regional weather, and specially the wind patterns, play a preponderant role. The calculated values of stability and heat content during monitoring demonstrate how those elements are decisive for the energy balance, since they determine the gains, transfers, and losses of heat, which in turn establish the circulation and mixing patterns. Just as Nilssen affirmed (1984), wind is the decisive factor for circulation in many types of tropical lakes, having a larger influence than the seasonal fluctuation of sun radiation and the atmospheric temperature.

5.2 Content and distribution of nutrients and their implications on plankton development

Stratification and overturn determine also the concentration and distribution of nutrients (e.g. SRP, DIN), gases (e.g. oxygen, carbon dioxide) and other chemical substances (e.g. organic matter, toxic compounds, etc.) throughout the whole lake. The interaction of these processes determines when and in what magnitude the highest values of biomass are reached. The amount of pelagic biomass in the lake is then determined by the periods of mixing during the season of strong winds, when oxygenation of deeper layers occurs, and nutrients accumulated in deeper layers and in the sediments during stratification are available again to the primary producers.

To analyse nutrient content and its relationship with phytoplankton and biomass peaks in the lake, it is important to look closely at the question of nutrient sources in lakes, especially in the tropical ones. Nutrients in lakes usually tend to be supplied with dissolved substances mainly through their tributary rivers and, to a lesser degree, from rainwater. In Lake Titicaca for example, more than twice the total nitrogen, and 16 times the total phosphorus entered the lake through river inputs than by direct precipitation on the lake (Wurtsbaugh et al., 1992). Although phosphorus is frequently the most important nutrient limiting phytoplankton in lakes, it seems unrealistic to suppose that all lakes are limited by the same nutrient, because nutrient supply is affected by the biogeochemistry of the drainage basin, atmospheric pollutants as well as by lacustrine processes. In fact, some authors suggest that phytoplankton in tropical lakes are more frequently limited by nitrogen than by phosphorus (Vincent et al., 1984; Wurtsbaugh et al., 1992).

Phosphate in tropical regions is principally derived from weathering of rocks, in special igneous types like apatite, and from volcanic rocks. However, the availability of phosphorus and other important nutrients can vary according to factors such as soil and vegetation. This is especially important with respect to nitrogen concentrations in runoff waters. Intense and prolonged sunlight, high temperatures, and high rainfall, at least during a part of the year, produce weathered ferrulite soils, which are poor in ions (Payne, 1986)

Silicate levels are high in the tropics due to the pH of soils. This is because its solubility, like that of iron and aluminum, is pH dependent. Under acidic conditions, larger quantities of aluminum and iron are dissolved whereas under neutral conditions more silica passes into solution. High temperatures also contribute to the weathering of silica and consequently to its high levels observed in tropical lakes and rivers (Payne, 1986). This was also observed in Lake San Pablo.

Mountain lakes in the altiplano regions of the Andes have their own chemical characteristics. The salt content of the high rainfall is generally very low, although a wide range may be found. There, the salt content of waters is highly influenced by the geological composition of the rocks and soil in the catchment area (Löffler, 1964; Steinitz-Kannan et al., 1983).

Miller et al. (1984) paid attention to the alkalinity and total salts content in Lake San Pablo and found that both remain low because rainfall is much greater than evaporation. However, nutrient levels in Lake San Pablo are high when compared to other Andean lakes (Table 11), especially with those of the "Paramo" region (i.e. the region above 3,000 m a.s.l.), where no human interference has taken place. Steinitz-Kannan et al. (1983) found that Ecuadorian lakes lying below the Paramo have higher pH and dissolved nutrients levels than those lying above the Paramo. However, they found these differences striking since all these lakes are localized in the same volcanic rock formations. The authors consider that these differences are due principally to temperature. This means that a variation of 5 °C resulting from 1,000 m of altitude difference is decisive for the weathering intensity and consequently for the nutrients content of the lakes. Additionally, human influence plays an important role on nutrients content in water bodies localized in inter-Andean plateaus, since a high percent of the human population has settled in these regions causing a strong pressure on natural resources and cultural eutrophication of lakes and rivers (Dumont, 1994; Galárraga et al., 1992). The high inputs of TP and TN in Lake San Pablo through its main tributary, the River Itambi, reflect that situation. Moreover, Ecuadorian lakes lying at similar altitude and under similar influences as Lake San Pablo also show high nutrient levels (Steinitz-Kannan et al., 1983). Human eutrophication of lakes and reservoirs has been detected not only in Ecuador, but also in other countries in the Andean area (Roldán, 1992).

5.3 Controlling factors of species richness, abundance and productivity

In tropical areas, rain regime is also a climatic aspect of great importance. In lakes and reservoirs, it determines important increments of water inputs with high levels of dissolved nutrients and suspended matter and has influence on the occurrence of overturn and stratification patterns as well. Moreover, a relationship between the hydrological cycle and productivity has been observed as much in tropical warm lakes (Masundire, 1994b; Melack, 1979; Wright, 1927) as in high mountain lakes (Donato, 1991b; Mora M. & Téllez B., 1991). According to these studies, peaks of biomass coincide with the rainy season and circulation periods, whereas the lowest levels relate to dry periods and overturn. Nevertheless, in the case of Lake San Pablo, although peaks of phytoplankton biomass occur during and after the overturn, these periods do not coincide with the rainy season.

Table 11. Comparison of limnological characteristics of Lake San Pablo and those of other mountain lakes in the Andes Region. Sources: (Dejaoux & Iltis, 1992; Barros, 1999; Donato, 1991b; Koste & Böttger, 1992; Mora M. & Téllez B., 1991; Roldán & Ruiz, 2001)

	NO_3^- mg/l	NO_2^- mg/l	NH_4^+ mg/l	PO_4^{-3} mg/l	Phytoplankton Species number Abundance	Chl. a µg/l	Zooplankton Species number Abundance
Lake Tota 3,015 m - Colombia	2.2	0.02	0.001	0.12	[n]67 [a]28		[cl]12, [c]5, [r]6 [a]4, 17, 14
Lagoon Chingaza 3,265 m - Colombia	0.12		0.08	0.2	56 100-450		
Lake Cocha 3,000 m - Colombia	0.2	0.01	0.07	0.03			
Lake Titicaca 3,803 m - Peru-Bolivia	0.28	<DL	<DL	0.07	125 300-1,600	0.5-5.9	31, 7, 7 69, 175, 90
Lagoon Toreadora 3,900 - Ecuador	0.026		<0.05	0.01		1.86	3, 2, 5
Lake San Pablo 2,660 m - Ecuador	**0.24**	**0.03**	**0.16**	**0.28**	**32 200-12,000**	**9.4-32.3**	**1, 1, 10 5, 24, 44**

[n] Species quantity, [a] Abundance in n/l; species quantity of [cl] Cladocera, [c] Copepoda, [r] Rotatoria
<DL below detection limits

With the arrival of the dry and windy season and the subsequent overturn, nutrients are released from the sediments and distributed in the water column starting a new pelagic production. This particular pattern of input and recycling of nutrients, contrary to the observations pointed out above for other lakes, could actually play a role as a limiting factor of productivity in Lake San Pablo. According to Melack's classification system (1979), the described seasonal changes classify the lake into the pattern "A", in which are grouped lakes that show pronounced seasonal fluctuations caused generally by weather changes, rains, river inputs or vertical mixing.

5.3.1.1 Composition, abundance and biomass of phytoplankton and limiting factors of productivity and biomass increase

With only 32 pelagic species, phytoplankton richness in Lake San Pablo is relatively low when compared to other mountain lakes of the South American Andes (Table 11). Nevertheless, some species have been reported in other investigations (Rott, 1981a; Steinitz-Kannan et al., 1983; Steinitz-Kannan, 1997) that were not found during this one. The phytoplankton composition in Lake San Pablo is very similar to that found in some Andean lakes (1992; Mora M. & Téllez B., 1991): Like in Lake Tota and in Lake Titicaca, a high percent of the species found in Lake San Pablo have morphological characteristics typical of turbulent systems.

The low number of pelagic species of phytoplankton, the succession pattern and the amount of biomass found in Lake San Pablo can be influenced by some factors observed already in other water systems, such as nutrient limitation (Payne, 1986; Wurtsbaugh et al., 1992; Wurtsbaugh & Vincent, 1985), water mixing processes (Murphy, 1962; Reynolds et al., 1983; Reynolds et al., 1984), the effect of ultraviolet radiation (Häder, 1995; Häder, 1999; Hessen et al., 1997; Kinzie III et al., 1998; Löffler, 1964), high light intensity (1992; Tilzer, 1973; Vincent et al., 1984), and zooplankton grazing (Carpenter et al., 1993; Cruz-Pizarro et al., 1994).

The low species diversity in Lake San Pablo can be explained by a rapid turnover in combination with thermal patterns. In the eutrophic and very productive Lake George the low plankton diversity appears to be associated with these same factors. Since thermal events show little variation throughout the year, the existent plankton species must have a wide tolerance to the daily fluctuations. Under such conditions no succession of species occurs during the year and consequently the number of niches is limited. The daily perturbation of the system could keep it “immature” but productive (Payne, 1986). In fact, Miller et al. (1984) determined a productivity of 2.6 g C/m² day in Lake San Pablo, which could be considered very high. In comparison, the productivity in Lake Titicaca attains values above 1 g C/m² day (1992), and in temperate lakes rates of primer production rarely exceed 3 g C/m² day, even in shallow eutrophic waters (Talling, 1965). The predominance of passive life-forms of phytoplankton -that means no motile species- observed in Lake San Pablo and also found in other Andean mountain lakes (Donato, 1991b; Iltis, 1992; Mora M. & Téllez B., 1991) confirm observations made about survival strategies of phytoplankton and the effects upon species diversity in such turbulent systems. In view of the above, it can be stated that turbulence and mixing appear to be associated with low diversity of species because a turbulent system implies a low number of niches in the ecosystem and a low equitability of resources distribution coupled with an inefficient use of them.

Although a slight succession of species was observed (Figure 4-26), this is not so marked as in temperate lakes, where a typical sequence in the occurrence of taxa can be observed e.g. Diatomeen during mixing, Chlorophyceen at the beginning and part of stratification, and Cyanophyceen when stable stratification and low nutrient levels are reached. Instead of an evident succession of taxa in Lake San Pablo there is a variation in the abundance and vertical distribution of the few dominant species, as could be observed in the time-depth diagrams of abundance distribution of the most important species (Figure 4-28). On this aspect Margalef (1983) points out that tropical lakes show a more limited dynamism due to the lack of the strong changes that induce the successions in temperate lakes.

In Lake San Pablo abundance and biomass of organisms, this last measured as Chl. a, can be regarded as moderate considering the high nutrients content. Actually, the TN:TP ratio indicates a potential limitation of productivity due to nitrogen. This sort of limitation has been already observed in some tropical mountain lakes (1992; Banderas Tarabay et al., 1991; Donato, 1991b; Roldán, 1992; Wright, 1927; Wurtsbaugh & Vincent, 1985) and could be confirmed for Lake San Pablo throughout the enclosures experiments: nitrogen addition produced an increase of Chl. a levels five times higher with respect to the control enclosure, whereas supplement of phosphorus did not cause any change. Similar results were found in a series of bioassay experiments carried out in Lake Titicaca, where nitrogen stimulated four times the carbon fixation and five times the chlorophyll production, whereas a phosphorus addition did not (Wurtsbaugh et al., 1992). Nevertheless, in Lake Titicaca the phytoplankton appeared to be limited by nitrogen during most of the stratified period, but not during periods of deep mixing. Additionally, nitrogen limitation would allow a competitive advantage to Cyanobacteria species, since they are able to fix atmospheric nitrogen. Consequently, a high increment in its abundance would be likely. However, this was not observed during the monitoring in 1998 and 1999 at Lake San Pablo. Only during the third and fourth enclosure experiments in September 2000 and March 2001 was a high relative abundance of *Microcystis aeruginosa* observed: in the first case in the lake and in the second one in the enclosure “Without UV”. The low presence and development of Cyanobacteria in systems limited by nitrogen has already been reported for some tropical lakes and seems to be related to the high light intensity, which inhibits the fixation of atmospheric nitrogen (Henry et al., 1978; Lewis & Weibezahn, 1987; Richerson et al., 1986).

Phytoplankton in Lake San Pablo seems to be limited by daily and seasonal mixing processes. The high values of Chl. a registered at deep layers as well as the vertical distribution of some species during 1999 (Figures 4-29 and 4-28) indicate the presence of a large amount of phytoplankton in deep layers. This would indicate a loss of phytoplankton from surface layers due to convergence currents and later sedimentation. In fact, enclosure experiments demonstrated that the prevention of phytoplankton loss toward deep layers (> 7 m) caused a considerable increase of biomass in the enclosures. This occurred, however, only during overturn but not during stratification periods (Table 10). Furthermore, some investigations have shown that daily stratification patterns can play a significant role in the phytoplankton dynamic (Wetzel, 1983). Water movements are important not only for the physical movement of algae out of the euphotic zone and back into the same, but they are also significant in the vertical transport of mineralized matter from lower depths and littoral regions to the open waters. In this way, the degree of turbulence and water movements are crucial in the regulation of algal distribution, periodicity, and production. In this context, the combination of turbulence and sedimentation is considered the most important factor in plankton ecosystems, where the survival of populations can be seen as the result of a temporary equilibrium between remaining afloat and unavoidable sinking (Margalef, 1978). Here, not only the density of plankton organisms but also the individual size, form and physiological state play an important role. The simplest theory about sedimentation speed of passive organisms is based on Stokes’ law. According to it, the sinking speed of spherical particles with a mean diameter of no more than 0.5 mm varies inversely to the viscosity of the medium. In other words, relatively large particles sink faster that small ones. The density of most freshwater plankton organisms lies between 1.01 and 1.03 times that of the water, causing plankton to sink in undisturbed water. Actually, to sink out of the euphotic zone is clearly a disadvantage for photosynthetic algae. However, the movement of a cell through water has the advantage of disturbing nutrient gradients around the cell, increasing the chances of contact with nutrient molecules. Consequently, the disadvantage of sinking out of the euphotic zone, which is usually fatal, is compensated by the advantage of increased nutrient incorporation (Titman & Kilham, 1976; Wetzel, 1983). Reynolds (1982) pointed out that in general non-motile species with high sinking rates, predominantly diatoms, are dependent upon deep mixed layers, if adequate nutrients and light conditions are available. This seems to be the situation for the phytoplankton species living in Lake San Palo.

It should be pointed out that the exclusion of UV-radiation did not show strong effects either on the composition or on the abundance of phytoplankton, in spite of the differential sensibility to UV among phytoplankton species. Some investigations have demonstrated that this differential sensibility plays a role on phytoplankton composition (Birge, 1916; Cabrera et al., 1997; Davidson et al., 1996; Häder, 1999; Jokiel & York, 1984; Lütz et al., 1997; Olesen & Maberly, 2001). The decrease of primary production under UV-radiation has also been observed (Hessen et al., 1997; Kinzie III et al., 1998). However, results of some investigations seem to be contradictory with respect to UV-radiation effects: Halac et al. (1997) did not find negative effects of UV-radiation on the phytoplankton in the oligotrophic high mountain lake Gossenköll (2,417 m a.s.l in the central Alps) and pointed out that the species appears to be well adapted to the high UV-B radiation. Some authors have even found that some species can tolerate and even take advantage of high levels of UV-radiation. Working with mesocosms in the oligotrophic Andean lake Laguna Negra, Cabrera et al. (1997) found that the Chlorophyta *Ankyra juday* reached the highest density when it was exposed to UV-B radiation, with an increase in Chl. a concentration.

In Lake San Pablo a remarkably higher abundance of *Microcystis aeruginosa* in relation to the Control enclosure and to the lake was detected only during the enclosures experiment carried out in August-September 2000. These results would indicate that the exclusion of UV-radiation gives a competitive advantage to this species during overturn. In fact, Cyanobacteria are extreme sensible to UV-B radiation (Häder, 1999) and research has shown that it inhibits some of the specific enzymes responsible for the assimilation of atmospheric nitrogen, principally glutamin synthetase (Guderian & Gunkel, 2000).

One other point to make about UV radiation is its relation to the mixed layer, since its depth and stability can operate as a regulator against photoinhibition (Kinzie III et al., 1998). In any case, it is evident that the existent species in the lake have acquired adequate protection mechanisms against the deleterious effects of high UV-radiation. Consequently, ultraviolet radiation probably plays only a secondary role as limiting factor on phytoplankton development in Lake San Pablo.

It is evident that most of the phytoplankton species observed in the lake require special physical and chemical conditions for growth and survival. Moreover, some of them can be used as environmental bioindicators of water quality, as is the case of *Pediastrum boryanum*, which is considered as an indicator of mesotrophy (Löffler, 1964) and *Microcystis aeruginosa,* as an indicator of eutrophy. Similar observations were made by Rott (1981a), who found that water transparency and floristic composition of phytoplankton and periphyton in Lake San Pablo were an indication of eutrophic conditions.

5.3.1.2 Zooplankton composition and abundance

With only two pelagic species of Crustacea and ten of Rotifera species, diversity in the lake can be considered very low when compared with that of other Andean lakes. For example, seventeen Crustacea species are known from Lake Tota, an oligotrophic lake in Colombia, and 38 species have been registered in Lake Titicaca (Table 11). In relation to the composition of tropical zooplankton, Fernando (1980b; 1980a) noted the low diversity of limnetic crustaceans and the rarity of *Daphnia* species. Pennak (1957) compared the limnetic zooplankton community of 27 lakes from Colorado (USA) and 42 lakes from other parts of the world and found that they contained between 1-4 species of cladocera, 1-3 species of copepods and 3-7 species of rotifers. These values seem to be common also for some tropical lakes (Cole, 1988). In this way, herbivore communities in tropical lakes are similar in composition to those of temperate lakes, differing from them in the rarity of large zooplankton species (Fernando, 1980b; Fernando, 1980a). Steinitz-Kannan et. al (1983) reported a low zooplankton species for some mountain lakes of Ecuador with only two or three species per lake, with *M. mendocinus* and *D. pulex* as the most common zooplankters in the lakes below the Paramo region. In this sense, the low number of species in Lake San Pablo corresponds well with these last observations.

Originally, the Cladocera species found in the Lake San Pablo was identified as *Daphnia pulex* by Steinitz-kannan et at. (1983). In a review of the distribution of the genus *Daphnia* in high mountain and temperate lakes of South America, Villalobos (1994) could establish that the species in Lake San Pablo corresponds in fact to *D. pulicaria* (Forbes), which was reported also for the Ecuadorian lake Cuicocha. In a study of the freshwater zooplankton of Central America and the Caribbean, Collado et al. (1984) reported the presence of this species only in Cuba, where components from North and South America as well as endemic fauna are found.

The other crustacean, *Metacyclops mendocinus,* the only species of Copepoda found in the lake, has a distribution limited to the neotropical area (Gaviria, 1994), and has been recorded in nearly every country in South America, Central America and the Antilles (Reid, 1985). The genus *Metacyclops*, as is the case with *Thermocyclops*, *Mesocyclops* and *Tropocyclops*, has the major number of its species in the tropics and it is possible that this genus originated there. With respect to the distribution of the genus *Metacyclops* according to altitude in Colombia, Gaviria (1994) makes an interesting observation: in the warm waters (above 23° C) of the low region called "Los Llanos" is found *M. tradecimus*; *M. mendocinus* and *M. laticornis* are found in lagoons of the Andean forest at 2,600 m a.s.l., whilst *M. leptopus* (*toténsis*) is found in the Paramo region, above 3,500 m a.s.l., where water temperatures are below 12° C. Thus, temperature seems to be the determining factor for the distribution of this genus.

M. mendocinus has been sometimes confused with a very similar species, *M. leptopus*. In spite of their similarities the two species appear to be ecologically distinct: *M. mendocinus* is eurytopic species with often dense populations in saline or highly eutrophic waters (Ringhelet 1958, Sendacz & Kubo 1982, cited by Raid et. al., 1990) while members of the *M. leptopus*-complex seem to inhabit relatively clean, mostly high altitude lakes (Reid et al., 1990).

As for the distribution of *M. mendocinus* in Ecuador, it is present in other lakes below the Paramo zone, like Lake Cuicocha and Lake Yaguarcocha, while it has not been observed in the region of the tropical humid forest nor in the waters of the high mountain region of Antisana (Steinitz-Kannan et al., 1983).

Observing the general low abundance of *D. pulicaria*, the most important phytoplankton consumer in the lake, and its fluctuations during 1998 and 1999 no clear tendency can be defined in relation to the development of phytoplankton. Early in March 1998, a decrease in the abundance of *D. pulicaria* was registered, despite the high values of phytoplankton biomass at that time. Although a slight increase of *Daphnia* was noted at the beginning of the dry season in June, it decreased thereafter and reached its lowest value in August when chlorophyll a values were highest. During 1999 the abundance of Daphnia was much more stable than during 1998 in spite of the fact that phytoplankton showed a pattern similar to that observed during 1998. Nevertheless, in many aquatic systems a direct positive relationship has been established between the seasonal variations of these two communities, influenced by input of nutrients during the rainy season (Cisneros & Mangas, 1991; Infante, 1982; Payne, 1986).

Another fact that has been observed between these two communities is that the biomass of zooplankton relative to phytoplankton is lower in the tropics and therefore, zooplankton does not control phytoplankton biomass in these regions (Fernando, 1994). Herbivory appears to be no more efficient in tropical plankton communities than in temperate ones (Osborne, 2000). On the other hand, in some planktonic systems a time-shift among phytoplankton and zooplankton peaks has been observed (Zauke et al., 1992). Although phytoplankton constitutes the nutritious base of herbivore zooplankton, it does not always cover its nutritional necessities (Gonzáles de Infante, 1988). In an oligotrophic high mountain lake in Spain, where *D. pulicaria* constitutes 98 % of the heterotrophic biomass and its abundance is comparable to that found in Lake San Pablo, Cruz-Pizarro et al. (1994) found that the food supplies are not enough to cover the nutritional necessities of this species. Additionally, for some systems it has also been found that phytoplankton blooms have negative effects on the development of some species of *Daphnia* (Gasiunaite & Olenina, 1998). Thus, for the development of zooplankton species not only the quantity of food plays an important role but also its quality is fundamental. Studying the effect of nutrient limited algae (N and P) on the feeding and growth of *D. pulex*, Lürling & VanDonk (1997) found a reduction in growth rates, body length, brood sizes, size at maturity and increased age at first reproduction. Algae exposed to UV-B radiation and fed to *D. pulex* had almost the same negative effect described above for algae poor in nutrients (De Lange & Van Donk, 1997). In a similar way, the quality of food supply in Lake San Pablo, as well as the effect of possible predation of *M. mendocinus* on *D. pulicaria* could be limiting the development of *Daphnia*.

The predator-prey interactions have been considered the principal mechanism in shaping zooplankton communities (Gliwicz, 1994). Since large herbivores like *Daphnia* are more perceptible than smaller zooplankton organisms, they are more susceptible to predation by visually-oriented planktivorous fishes. Therefore, they are the first to be decimated or even locally eradicated (1996; Brooks & Dodson, 1965; Hrbacek et al., 1961; Lazzaro, 1987). In habitats where new species of planktivorous fishes have been introduced the disappearance of the more conspicuous, large-bodied zooplankters are most noticeable. For instance, Brooks & Dodson (1965) observed that the introduction of *Alosa* resulted in extermination of large-bodied calanoids in the Great Lakes in America. It was also observed that the introduction of brook char in fish-free alpine lakes in the Tatra Mountains caused permanent extinction of all cladoceran and most copepod species (Gliwicz, 1967; Gliwicz & Rowan, 1984 in Gliwicz, 1994). Additionally, it was found that after a selective elimination of fishes, the small crustacean species were substituted for bigger ones with a decrease of rotifers (Wetzel, 1983). Thus, the presence of *D. pulicaria*, a relatively large-size crustacean, points to the absence or low abundance of pelagic fishes in Lake San Pablo.

In addition, results obtained during 24-hour sampling did not show any evident vertical migrations of zooplankton. This fact also indicates an absence or low abundance of pelagic fishes. Contrary to the results presented here, Steinitz-Kannan et al. (1983) reported a pronounced vertical migration of zooplankton in Lake San Pablo, principally of *Daphnia*. Apparently, their conclusion was based only on day-night qualitative surveys since no experimental data were presented. Daily vertical migration of zooplankton is a behaviour that has been intensively studied in the last years (Armengol & Miracle, 2000; Bohrer, 1980; Leibold, 1990). It has been found that one of its principal causes is the presence of planktivorous fishes. (Carpenter & Kitchell, 1996; Lampert, 1989). Since fishes in Lake San Pablo prefer the shore areas where the nutritious offer is higher (Dumont, 1994), there seems to be a situation that their abundance in the pelagic areas is too low to create a depredation pressure on zooplankton. Some investigations demonstrate that daily migration is partly due to competition between species (Carpenter & Kitchell, 1996), and a behavior related to light intensity, concentration and distribution of food and to physiological advantages like reduction of metabolism (Haney et al., 1990; Leibold, 1990; Payne, 1986).

Thus, vertical migration in Lake San Pablo does not give the zooplankton any survival or metabolic advantage; on the contrary, it would require higher energy consumption.

The presence of a thermocline also seems to reduce the diurnal movements of zooplankton due to the anaerobic condition in the hypolimnion of a stratificated lake. In such cases, the majority of zooplankters remain above the thermocline (Bohrer, 1980; Payne, 1986). This behavior was detected in Lake San Pablo only during strong stratification periods.

With respect to rotifers, an increase in their abundance was observed during the dry season, something that certainly has to do with an increase of suspended material due to overturn. It has been observed that in tropical lakes rotifers can be present in any environment without a particular relationship to the trophic state of the lake in question (Esteves, 1988). During a three years study of Lake Xolotlán (Nicaragua), Cisneros & Mangas (1991) observed that the population trend of rotifers was very variable, and its maximum abundance was associated with the beginning of the rainy season and the consequent input of nutrients and suspended material. Besides the importance of food availability, also temperature and salinity, as well as size and localization (altitude a.s.l) of the water body can determine the development and the characteristic associations of rotifers (Green, 1994).

5.4 Trophic State

Determining the current trophic state of Lake San Pablo based on the analyzed variables and with the available data and models is a complex task. According to the systems established by the OECD (1982) and the CEPIS (1990), chlorophyll a values would indicate a eutrophic state, but at the same time, the concentrations of total nitrogen would classify the Lake San Pablo as mesotrophic (Table 12). Furthermore, due to its high phosphorus levels, the lake could also be classified as hypertrophic. Oxygen concentration trends in the lake during stratification showed an anoxic hypolimnion, which by itself is also an indication of the eutrophic grade.

Table 12. Trophic state classification system (OECD, 1982). Data correspond to stratificated lakes from temperate zones. Values for Lake San Pablo correspond to mean values from experimental data (1998-1999).

Parameter	Oligotrophic	Mesotrophic	Eutrophic	Lake San Pablo
TP, mean (μg/l) SD	8.0 4.9 - 13.3	26.7 14.5 - 49	84.4 38 - 189	215
TN, mean (mg/l) SD	0.66 0.37 - 1.18	0.75 0.49 - 1.17	1.87 0.86 - 4.08	1.03
Chl. a, mean (μg/l) SD	1.7 0.8 - 3.4	4.7 3.0 - 7.4	14.3 6.7 - 31	9.4
Chl. a, maximum (μg/l) SD	4.2 2.6 - 7.6	16.1 8.9 - 29	42.6 16.9 - 107	32.3
Secchi Disk, mean (m) SD	9.9 5.9 - 16.5	4.2 2.4 - 7.4	2.45 1.5 - 4.0	3.2

Although productivity measurements were not carried out during the present study, available data indicate that Lake San Pablo is a highly productive system (Miller et al., 1984), where physical factors, principally wind and diurnal water mixing, are the crucial mechanisms controlling plankton biomass. Additionally, it is evident that deforestation, agricultural activity, erosion processes and the absence of waste water treatment in the area have produced alterations in the balance of the water system, affecting the biomass development and the trophic chains, certainly carrying the lake toward an accelerated eutrophication process.

A good knowledge and comprehension of the structure and dynamics of tropical lakes and reservoirs is essential for the evaluation of the trophic state of these systems. As von Sperling (1997) pointed out, the special characteristics of tropical aquatic systems indicate complex relationships between nutrients content and biomass formation. In this respect, Lewis (1996) identified four characteristic features in tropical lakes in comparison to temperate lakes: a) greater efficiency in producing phytoplankton biomass for a given nutrient supply; b) a tendency towards nitrogen, rather than phosphorus limitation of primary production; c) lower efficiency in passing primary production to higher trophic levels; and d) greater non-seasonal variation superimposed on a seasonal cycle.

For the reasons expressed above, a careful and detailed analysis is required before the most convenient form is chosen to express the trophic grade. Frequently, a choice is made with very few data obtained during a specific period, reflecting only a momentary state. Moreover, it is known that a given water body can show variable conditions in a period of 24 hours changing from an oligotrophic to an eutrophic condition. Von Sperling (1997) considers that eutrophication problems are in fact caused by the formation of biomass and not from the simple presence of nutrients. Since the quantity of biomass formed per unit of nutrient depends on the growth rate of phytoplankton (Sommer, 1993), in tropical lakes and reservoirs the loss of biomass due to grazing and sedimentation must be compensated by high growth rates. Therefore, the utilization of physico-chemical and biological indicators for the evaluation of the trophic state has strong limitations, since they do not really show the processes that lead to the configuration of the different trophic levels. Consequently, it seems more convenient to use criteria that illustrate the association and interaction of organisms and the performance of several organic functions (von Sperling, 1997). Additionally, the dependence and interaction of the organisms with their physical environment should be another important criterion for the determination of the trophic state.

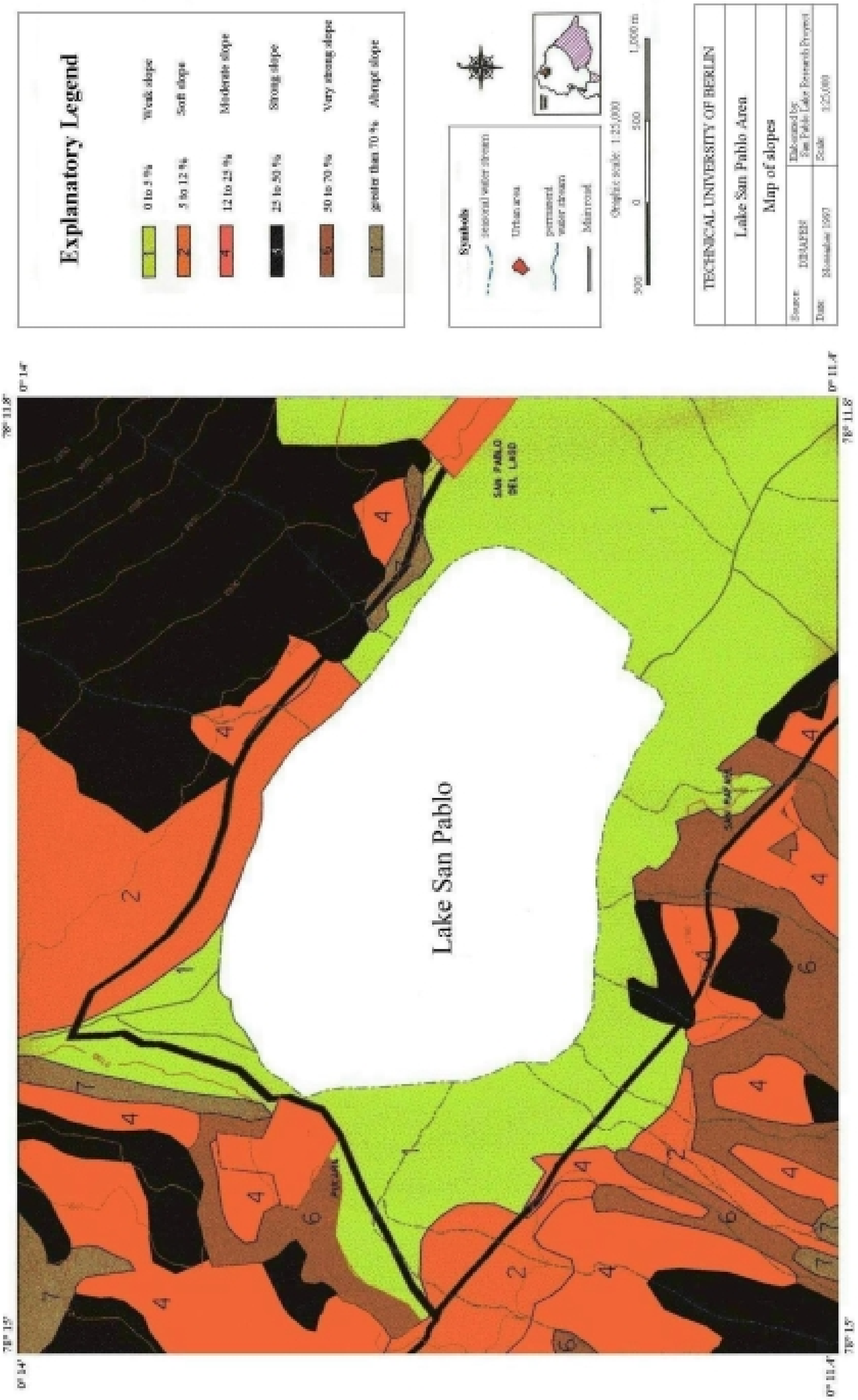
All the exposed characteristics make clear that tropical aquatic mountain systems can not be analyzed and explained with the models developed for the tropical lakes of low areas (Zaret, 2000), neither with those developed for lakes of temperate regions (Baigún & Marinone, 1995; Lewis, 1987; Vollenweider, 1968). Furthermore, since tropical lakes and reservoirs are more susceptible to eutrophication than those of temperate regions (Lewis, 2000), it is of crucial importance to improve knowledge about these systems to create models that will allow precise diagnoses their evolution. In that way, appropriate procedures can be implemented to mitigate and even control eutrophication processes. In this sense, the results obtained in this investigation are a contribution and a support for the elaboration of such programs for the region of Lake San Pablo.

6 Appendices

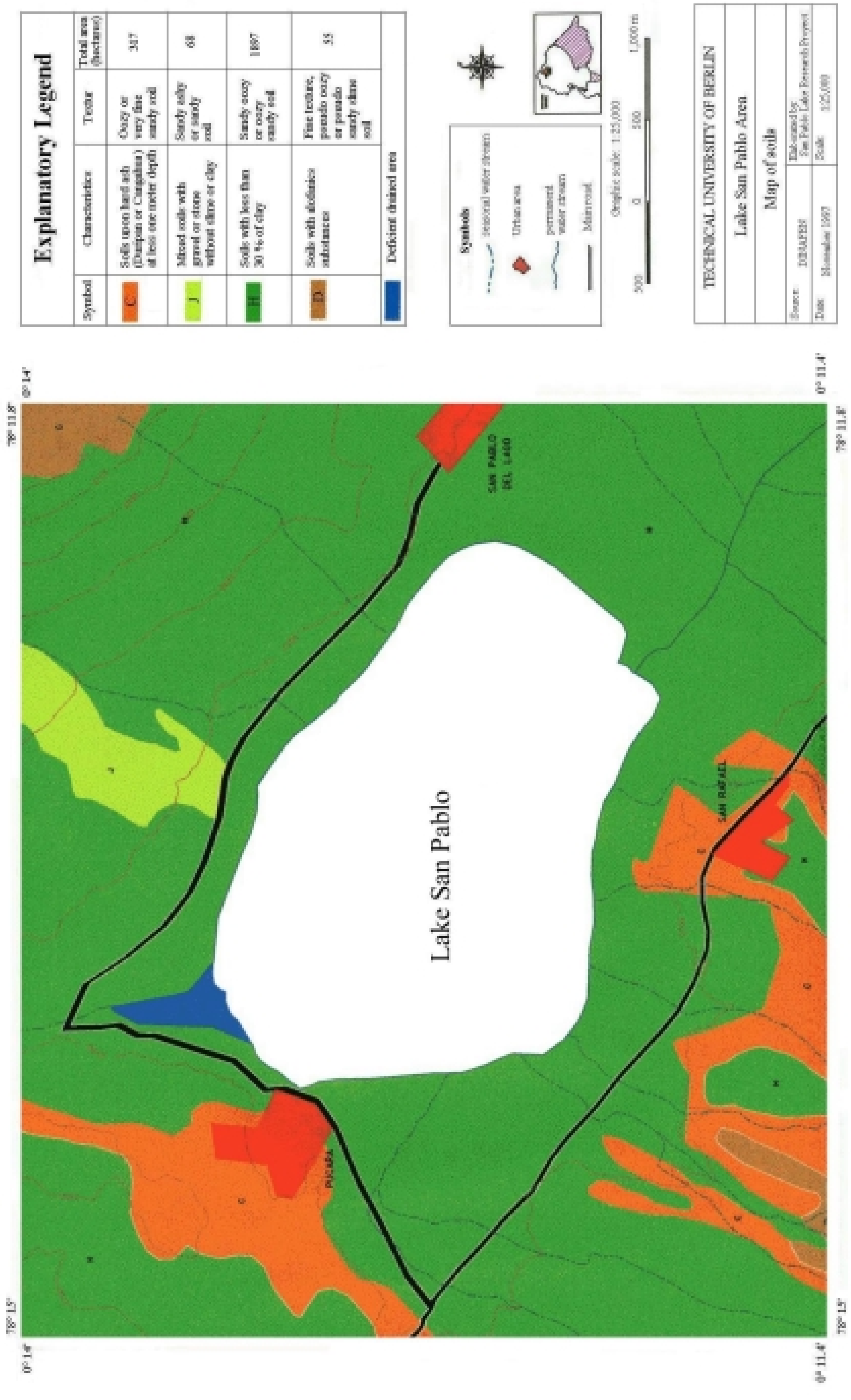
Appendix A. Abbreviations and units

BOD5	:	Biological oxygen demand
DIN	:	Dissolved Inorganic Nitrogen
PAR	:	Photosynthetically active radiation
SRP	:	Soluble reactive phosphorus
TC	:	Total carbon
TIC	:	Total inorganic carbon
TN	:	Total nitrogen
TOC	:	Total organic carbon
TP	:	Total phosphorus
UV	:	Ultraviolet ratiation
nm	:	nanometer
µm	:	micrometer
mm	:	millimeter
cm	:	centimeter
m	:	meter
km	:	kilometer
ha	:	hectare
µg	:	microgram
mg	:	milligram
g	:	gram
t	:	tons
ml	:	milliliter
l	:	liter
s	:	second
min	:	minute
h	:	hour
d	:	day
y	:	year
%	.	per cent
°C	:	degrees centigrade
cal	:	calorie (1 cal = 4.185 J)
J	:	Joule (kg m^2 s^{-2})
µS	:	micro-siemens
a.s.l.	:	above sea level
e.g.	:	e.g. (*exampli gratia*)
et al.	:	and others (*et alii*)
i.e.	:	that is (*id est*)
sp.	:	species (singular)
<	:	less than
>	:	greater than
≈	:	approximately
±	:	more or less

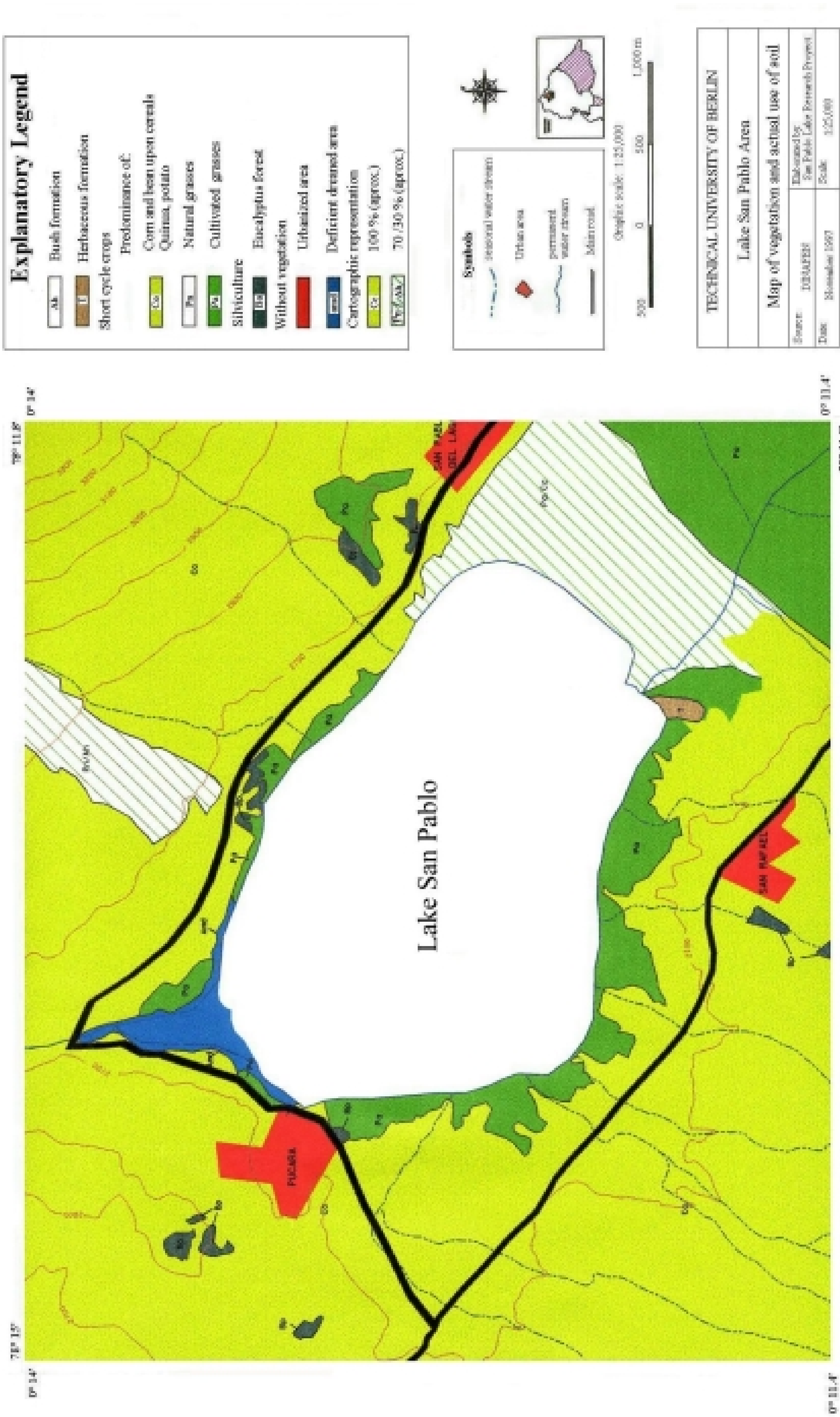
Appendix B. Area of Lake San Pablo - Map of slopes



Appendix C. Area of Lake San Pablo - Map of soils



Appendix D. Area of Lake San Pablo - Map of actual use of soils



Appendix E. Determination of size, biovolume and quantity of phytoplankton cells

For a detailed study of phytoplanktonic populations, it is necessary to make an estimate of the abundance and the biovolumen of each species. However, the number of individuals does not represent the true biomass due to the considerable variation in the size of the cells among the different species and inside each one of them. This discrepancy can be solved multiplying the number of cells of a given species by its cellular average volume. In addition, when species with colonial forms are counted, it is important to estimate the mean number of cells per colony. Nevertheless, this number can vary spatially and seasonally within a lake, due to changes in the availability of nutrients. Thus, the abundance and the biovolume were estimated for each one of the samples using standard methodology (Lund et al., 1958; Rott, 1981b; Utermöhl, 1958; Wetzel & Likens, 1991)

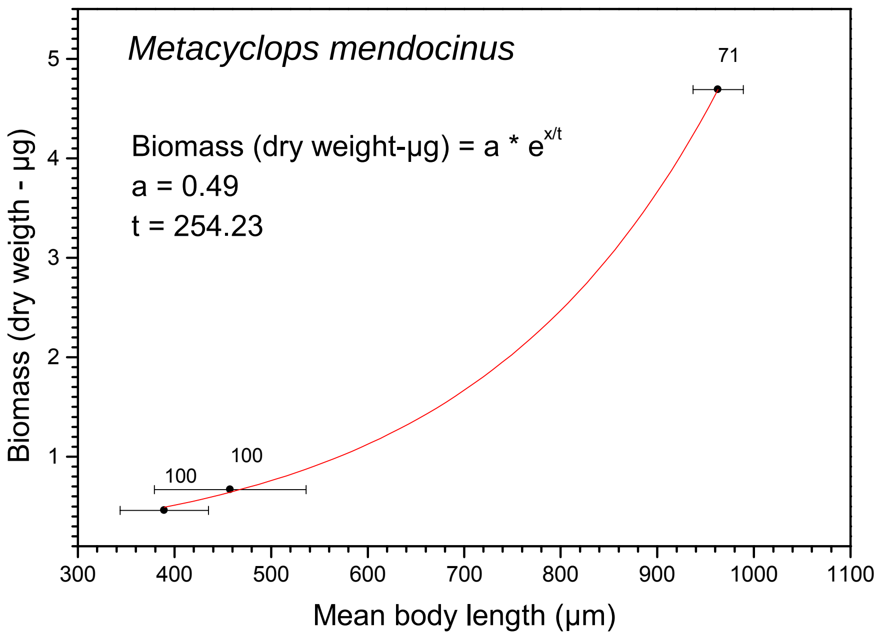
In this study, sedimentation chambers type Utermöhl of 10 and 25 ml of capacity from Hydro-Bios were used. The sample to be observed must be first mixed homogeneously by careful inversion of the sample's bottle. Then the chamber is filled with sufficient sample to permit overflow, and the chamber glass cover is slide over the top of the chamber to remove any excess water and to ensure that the exact volume of water -without any air bubbles- is enclosed. To ensure complete sedimentation of all organisms the chamber is placed on a vibration-free surface during 24-h before counting under microscope.

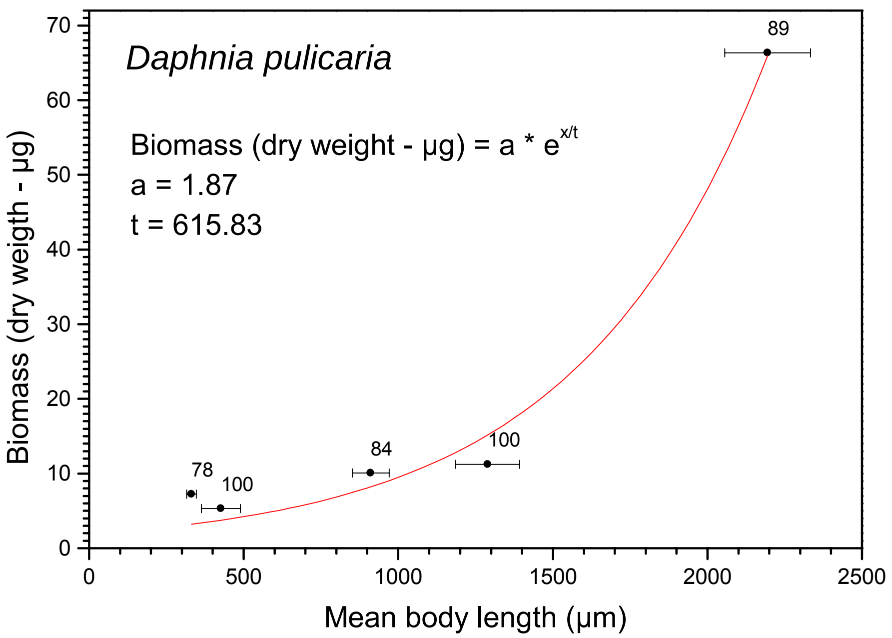
For each sample, as many optical fields as necessary for the count of at least 100 individuals of each important species must be observed in order to estimate the abundance to an accuracy of ±20 % at the 0.95 confidence limit. The surface of the counted area must be also determined. Relating this surface, the quantity of counted individuals, the chamber surface and the chamber volume a factor can be determined to estimate the abundance of each species in individuals per liter of water from a given depth. For cell volume determination, each species is represented by a geometrical body, which shape closely matches the form of the cells. Then, the cellular dimensions necessary to calculate the volume of the corresponding geometrical body are determined under microscope, and the biovolume is calculated by applying the corresponding volume formula of the geometrical solid. Here, ±20 cells of each species were measured.

Appendix F. Quantitative determination of zooplankton abundance

By the used method (McCauley, 1984), each zooplankton sample is filtered through an adequate filter (here a 55 µm-filter) and the organisms are rinsed with tap water. When the number of organisms in the sample is relatively low (subjectively established by simple inspection), the whole sample is settled and all organisms are counted by the inverted microscope technique. When the number of organisms in the sample is very large, it is necessary to take subsamples to make the counting feasible. In this case, and after rinsing, the zooplankton organisms presented in the sample are transferred into a volumetric flask, which is filled up to an exact volume (e.g. 50 ml, 100 ml, 200 ml). This volume is subjectively determined according to the density of organisms in the original sample. The new volumetric sample is thoroughly shaken to ensure a uniform distribution of the organisms and then one or more subsamples of 1 ml are quickly taken using an adjustable volume pipette with a 2 mm-diameter opening tip. The subsamples are placed in sedimentation chambers (in this work 5 ml-chambers type Utermöhl were used), which are filled to the top edge with tap water. To ensure the sedimentation of all organisms, the subsamples in the chambers are allowed to sediment for a sufficient period of time (here at least 10 minutes) and afterwards the chambers are closed with a glass coverslip and observed under the inverted microscope. At least five prepared chambers were observed and a minimum of 100 individuals of each species or each developmental stage were counted, when such quantity was available, in order to reduce the coefficient of variation to a maximum of 10% according to Cassie (1971).

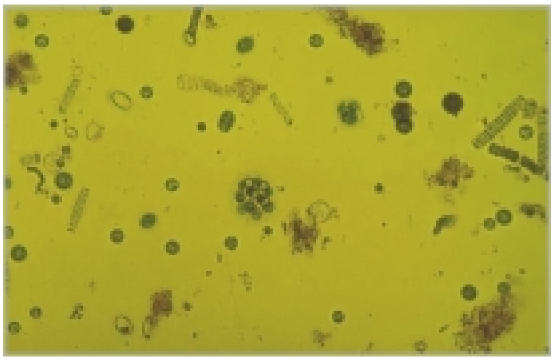
Appendix G. Biomass determination of *D. pulicaria* and *M. mendocinus*. Regression fitting between mean body size and biomass





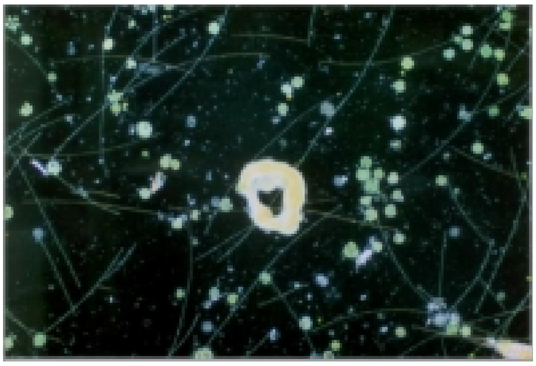
Biomass determination was carried out according to Masundire (1994) and McCauley (1984). Values indicate the number of measured organisms (body length) in each cohort.

Appendix H. Some phytoplankton species found in Lake San Pablo

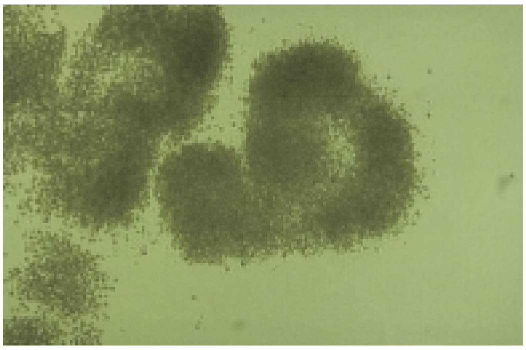


Microscopic general view of phytoplankton

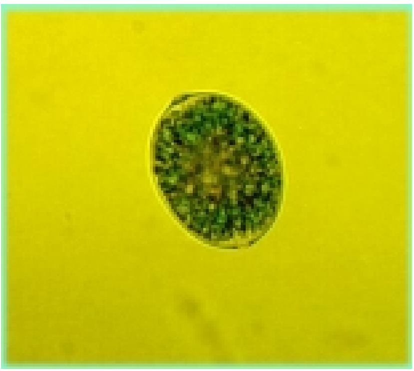
Aulacoseira granulata and *Pediastrum boryanum*



Microcystis aeruginosa, A.granulata and P.boryanum



Microcystis aeruginosa



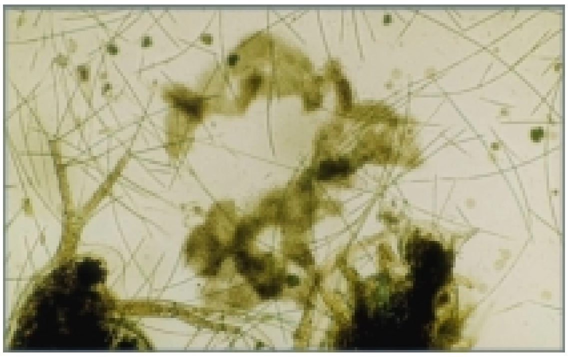
Neglectella sp

Planktosphaeria gelatinosa

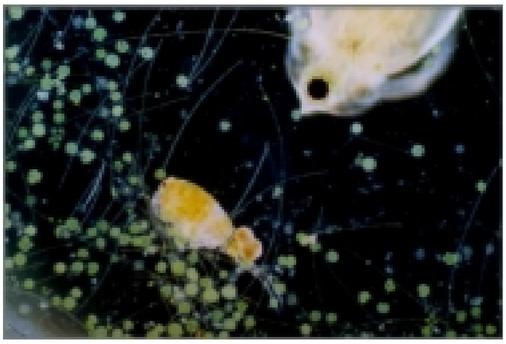
Scenedesmus linearis

Elakatothrix gelatinosa

Appendix I. Zooplankton and fish species in Lake San Pablo



Daphnia pulicaria



Metacyclops mendocinus

M. mendocinus, nauplius

Asplachna sp

Trichocerca similes

Keratella tropica

Micropterus salmoides

Carassius carassius x *C. auratus*

Appendix J. Macrophytes in Lake San Pablo

Ceratophyllum demersum

Eichhornia crassipes

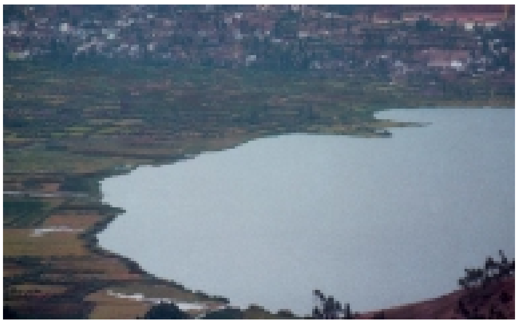
Myriophyllum quitense

Potamogeton illinoensis

Potamogeton striatus

Potamogeton pusillus

Appendix K. Eutrophication in Lake San Pablo: Causes and effects



Appendix L. Glossary

abiotic: refer to non-living components of the environment.

aerobic: (1) referring to an environment with molecular oxygen; (2) form of respiration that uses oxygen.

allochthonous: organic matter produced within an ecosystem and transferred to another, e.g. leaves falling into a stream.

altiplano: Anden region great extension localized to high altitude

anaerobic: (1) referring to an environment without molecular oxygen (2) form of respiration that does not require oxygen.

anoxic: environment in which free oxygen is absent.

aphotic zone: deep-water zone where light penetration is not enough for photosynthesis.

atelomixis: incomplete vertical mixing of a stratified lake resulting in transfer of nutrients from deeper waters into the euphotic zone, often stimulating phytoplankton production.

benthic: referring to the bottom area of lakes and the organisms that inhabit it.

biodiversity: diversity of living organisms that inhabit an ecosystem.

biological oxygen demand (BOD): measure of organic pollution through the reduction in the oxygen content of a water sample due to bacterial decomposition of the organic matter present in the sample.

biomass: total mass of living organisms (vegetal and animal) in a given area or volume, and expressed as dry weight per unit area or volume. It is also known as standing crop.

biotic: referring to living beings.

catchment area: area drained by a river or stream.

cline: gradual change in some environmental feature.

cohort: group of individuals of a similar age within a population

community: group of interacting species in a given area

copepodid: second larval stage of copepods (cohort), which resembles the adult except that the abdomen is not segmented and there may be only three pairs of thoracic appendages.

epilimnion: the upper, well-mixed zone of a stratified lake.

euphotic zone: the upper, illuminate zone of a water body.

eutrophication: nutrient enrichment of a lake often from the disposal of sewage effluent within its cathment area, resulting in high primary production in the epilimnion and oxygen depletion on the hypolimnion.

heat budget: the difference in heat content over some time interval.

hypolimnion: the cooler, often oxygen-depleted layer in a stratified lake that lies beneath the metalimnion and epilimnion.

life-form: biological forms of phytoplankton related with the environment where they live, that is functional morphology.

limiting factor: environmental factor which limits the growth of an individual or population.

maximum Depth (z_m): The greatest depth of a water body.

mean depth ($\bar{z}$): The volume of a lake divided by its surface area at zero depth.

metalimnion: water stratum with the greatest thermal discontinuity demarcated by the intersections of the nearby homoiothermal epilimnion and the hypolimnion. The terms "Sprungschicht" and "discontinuity layer" are used as functional synonyms in German and in the United Kingdom respectively.

mixed layer: water layer recently mixed by wind or convection currents

monomictic: referring to a lake that has one mixing event each year.

naupli: first larval stage of copepods, with three pairs of limbs and a single eye and subsequent moults take it through four or five more naupliar phases or instars until it enters a second larval estage, the copepodid.

niche: functional position of an organism in a community.

oligomictic: referring to a lake in which stratification breakdown occurs rarely and irregularly

oligotrophic: referring to a nutrient-poor lake with low primary production.

overturn: Vertical mixing process that occurs with the breakdown of thermal stratification in lakes.

PAR: photosynthetically active radiation

Paramo: Region above 3,000 m a.s.l. in the tropical Andes with characteristic weather and vegetation.

pelagic: referring to the open water of a lake or the sea.

primary production: biomass produced by photosynthetic and chemosynthetic organisms.

relative depth (Z_r): Maximum depth as a percentage of the mean diameter

$$Zr = \frac{50 z_m \sqrt{\pi}}{\sqrt{A_0}}$$

secondary forest: forest re-establishing on an area cleared of primary forest and usually containing a high proportion of pioneer species.

stability: Stability of a lake (S) is the inertial resistance to complete mixing caused by vertical density differences, measuring in g-cm cm^{-2}.

taxonomy: science of naming, describing and classifying organisms.

thermal resistance to mixing: this concept developed by Birge (1910; 1916) is a function of the density difference between the top and bottom of a defined thickness of water, expressed as the amount of work required to mix completely such column of water. $W(ergs) = \frac{AC^2}{12}(\rho_2 - \rho_1)$, where A = area and C = height of water column. To make comparisons it is assumed that A and C are constants; A=1 cm^2 and C= 100 cm. Comparisons are made against the density difference of water at 4° C and 5° C, that is $8x10^{-6}$ g/cm^3

thermocline: it refers to the plane of maximum rate of decrease of temperature with respect to depth. Usually it is accepted as a change of >1 °C per meter. In tropical lakes > 0.3 °C per meter.

trophic level: position of an organism in a food chain, determined by the number of energy transfer steps to that level.

trophogenic zone: upper, illuminated strata in a water body, where photosynthesis occurs.

tropholytic zone: lower strata in a water body, where decomposition and mineralisation take place.

7 References

APHA (1989). Standard Methods for the Examination of Water and Wastewater. Washington D.C.: American Public Health Association. 1550 pp.

Arai, T. (1981). Climatic and geomorphological influences on lake temperature. *Verh.Internat.Verein.Limnol*, **21:** 130-134.

Armengol, X. & Miracle, M. R. (2000). Dial vertical movements of zooplankton in lake La Cruz (Cuenca, Spain). *Journal of Plankton Research*, **22:** 1683-1703.

Baigún, C. & Marinone, C. (1995). Cold-temperate lakes of South America: do they fit northen hemisphere models? *Arch.Hydrobiol.*, **135:** 23-51.

Banderas Tarabay, A., Gonzáles V., R. & De la Lanza, E. G. (1991). Limnological aspects of a high-mountain lake in Mexico. *Hydrobiologia*, **224:** 1-19.

Barros, Z. (1999). Estudio limnológico en la laguna Toreadora. Unpublished Work

Birge, E. A. (1910). An unregarded factor in lake temperatures. *Trans. Wis . Acad. Sci. Arts. Lett.*, **16:** 989-1004.

Birge, E. A. (1916). The work of the wind in warming a lake. *Trans. Wis. Acad.Sci. Arts. Lett.*, **18:** 341-391.

Bohrer, R. N. (1980). Experimental studies on diel vertical migration. In: Kerfoot,W.C. (Ed.), *Evolution and Ecology of Zooplankton Communities*, pp. 111-121. New Hampshire: University Press of New England. 121 pp.

Boström, B., Andersen, J. M., Fleischer, S. & Jansson, M. (1988). Exchange of phosphorus across the sediment-water interface. *Hydrobiologia*, **170:** 229-244.

Boström, B., Jansson, M. & Forsberg, C. (1982). Phosphorus release from lake sediments. *Arch.Hydrobiol.Beih.*, **18:** 5-59.

Brooks, J. L. & Dodson, S. I. (1965). Predation, body size and the composition of plankton. *Science*, **150:** 26-35.

Cabrera, S., Lopez, M. & Tartarotti, B. (1997). Phytoplankton and zooplankton response to ultraviolet radiation in a high-altitude Andean lake: short- versus long-term effects. *Journal of Plankton Research*, **19:** 1565-1582.

Carney, H. J., Richerson, P. J. & Eloranta, P. (1987). Lake Titicaca (Peru/Bolivia) phytoplankton: Species composition and structural comparison with other tropical and temperate lakes. *Arch.Hydrobiol.*, **110:** 365-385.

Carpenter, S. R. (1993). Statistical analysis of the ecosystem experiments. In: Carpenter, S. R. & Kitchell, J. F. (Eds.), *The trophic cascade in lakes*, pp. 26-42. Cambridge: Cambridge University Press. 42 pp.

Carpenter, S. R., Morrice, J. A., Elser, J. J., Amand, A. S. & Mackay, N. A. (1993). Phytoplankton community dynamics. In: Carpenter,S.R. & Kitchell,J.F. (Eds.), *The trophic cascade in lakes*, pp. 116-152. Cambridge: Cambridge University Press. 152 pp.

Carpenter, S. R. & Kitchell, J. F. (1996). *The trophic cascade in lakes*. Cambridge: Cambridge University Press. 385 pp.

Carrera, P. (2002). Beschreibung und Klassifizierun eines kleinen Flißgewässers der Hochandenregion (Río Itambi) in Hinblick auf Einzugsgebiet, Gewässerstruktur und Dynamic. 1-129. Technische Universitäat Berlin. Dissertation.

Carrera, P. & Gunkel, G. (2003). Ecology of an high Andean stream, Rio Itambi, Otavalo, Ecuador. *Limnologica*, **33:** 29-43.

Casallas, J. & Gunkel, G. (2002). Algunos aspectos limnológicos de un lago altoandino: El Lago San Pablo, Ecuador. *Limnetica*, **20:** 29-46.

Cassie, R. M. (1971). Sampling and statistics.*A handbook on methods of assessment of secondary productivity in fresh waters*, pp. 174-209. Oxford: Blackwell. 209 pp.

Castro, S. & Peñafiel, J. (2002). Historia de la lobina negra (*Micropterus salmoides*), que habita en el lago "Imbakucha" otavalo-Ecuador y estimación de la producción. Primer encuentro intercultural para la gestión integral de cuencas y asentamientos humanos "Imbacucha" 2002. Otavalo-Ecuador. Conference Proceeding.

CEPIS (1990). Metodologías simplificadas para la evaluación de la eutroficación en lagos cálidos tropicales. Centro Panamericano de Ingeniería Sanitaria y ciencias del Ambiente - Organización Mundial de la Salud and Organización Panamericana de la Salud. 74 pp.

Cisneros, R. O. & Mangas, I. (1991). Zooplankton studies in a tropical lake (Lake Xolotlán, Nicaragua). *Verh.Internat.Verein.Limnol*, **24:** 1167-1170.

Cole, G. A. (1988). *Manual de Limnología*. Buenos Aires: Editorial Hemisferio Sur S.A. 405 pp.

Collado, D., Fernando, C.yH. & Stephan, D. (1984). The freshwater zooplankton of Central America and the Caribbean. *Hydrobiologia*, **113:** 105-119.

Cruz-Pizarro, L., Reche, I. & Carrillo, P. (1994). Plankton dynamics in a high mountain lake (Las Yeguas, Sierra Nevada, Spain). Indirect evidence of ciliates as food source for zooplankton. *Hydrobiologia*, **274:** 29-35.

Davidson, A. T., Marchant, H. J. & De la mare, W. K. (1996). Natural UVB exposure changes the species composition of Antartic phytoplankton in mixed culture. *Aquat.Microb.Ecol.*, **10:** 299-305.

Dejaoux, C. & Iltis, A. (1992). *Lake Titicaca, A Synthesis of Limnological Knowledge*. Dordrecht, The Netherlands: Kluwer Academci Publishers.

De Lange, H. J. & Van Donk, E. (1997). Effects of UVB irradiated algae on life history traits of *Daphnia pulex*. *Freshwater Biology*, **38:** 711-720.

Donato, R. J. Ch. (1991a). Fitoplancton del embalse de Chuza (Parque Nacional Natural Chingaza). *Cuad.Divulg.*, 1-25.

Donato, R. J. Ch. (1991b). Fitoplancton y aspectos físicos y químicos de la laguna de Chingaza (Una laguna tropical de alta montaña). *Cuad.Divulg.*, 1-18.

Dos Santos, U. L. & De Andrade,yC. F. (1997). Levantamento de ciclopídeos (Crustacea, Copepoda) no Brasil e avaliaçâo preliminar de seu potencial como predadores dos vetores da dengue. *Revista de Saúde Pública*, **31:** 221-226.

Dumont, H. (1994). Rehabilitación ambiental y aprovechamiento sustentable de los lagos de Imbabura. Report.

Escuela Politécnica Nacional, U. d. I. A. (1995). Batimetría del Lago San Pablo. Mapa 1:5000

Esteves, F. A. (1988). *Fundamentos de Limnología*. Rio de Janeiro: Editora Interciencia Ltda.

Fernandez, A. (1982). *Guia para el estudio de las algas*. Trujillo, Perú: Departamento de Ciencias Biológicas, Universidad Nacional de Trujillo.

Fernando, C. H. (1980a). The freshwater zooplankton of Sri Lanka, with a discussion of tropical freshwater zooplankton composition. *Int.Revue ges.Hydrobiol.*, **65:** 85-125.

Fernando, C. H. (1980b). The species and size composition of tropical freshwater zooplankton with special reference to the Oriental Region (South East Asia). *Int.Revue ges.Hydrobiol.*, **65:** 411-426.

Fernando, C. H. (1994). Zooplankton, fish and fisheries in tropical freshwaters. *Hydrobiologia*, **272:** 105-123.

Galárraga, E., Zevallos, O., Toledo, P., Criollo, C., Robelly, N. & Ruales, J. (1992). Estudio para la Recuperación y Protección de la Zona Turística de los Lagos de la Provincia de Imbabura con fines de Equilibrio Ecológico y Promoción Turística. República del Ecuador - Ministerio de Relaciones Exteriores. Report.

Gasiunaite, Z. R. & Olenina, I. (1998). Zooplankton-phytoplankton interactions: a possible explanation of the seasonal succession in the Kursiu Marios Lagoon. *Hydrobiologia*, **363:** 333-339.

Gaviria, S. (1994). Los copépodos (Arthropoda, Crustacea) de vida libre de las aguas continentales de Colombia. *Rev.Acad.Col.Cien.Ex.,Fís.& Nat.*, **19:** 361-385.

Gieskes, W. W. C. & Buma, A. G. J. (1997). UV damage to plant in a photobiologically dynamic environmental: the case of marine phytoplankton. *Plant Ecology*, **128:** 16-25.

Gliwicz, A. M. (1994). Relative significance of direct and indirect effects of predation by planktivorous fish on zooplankton. *Hydrobiologia*, **272:** 201-210.

Gonzáles de Infante, A. (1988). El Plancton de las Aguas Continentales.. Washington, D.C., Organización de los Estados Americanos OEA. Serie de Biología. 130pp.

Green, J. (1994). The temperate-tropical gradient of planktonic Protozoa and Rotifera. *Hydrobiologia*, **272:** 13-26.

Guderian, R. & Gunkel, G. (2000). *Handbuch der Umweltveränderungen und Ökkotoxicologie Band 3A: Aquatische Systeme: Grundlagen - Physicalische Belastungsfaktoren - Anorganische Stoffeinträge*. Berlin: Springer - Verlag.

Gunkel, G. (2000). Limnology of an equatorial high mountain lake in Ecuador, Lago San Pablo. *Limnologica*, **30:** 113-120.

Gunkel, G. .(2003). Limnología de un lago tropical de alta montaña, Lago San Pablo Ecuador: Características de los sedimentos y tasa de sedimentación. *Revista de Biología Tropical*, **51:** 381-390.

Gunkel, G. & Casallas, J. (2001). Limnology of an Equatorial High Mountain Lake, Lago San Pablo, Ecuador: Limitation of lake productivity by Deep Diurnal Mixing. *Proceedings of the International Association of Theoretical and Applied Limnology*, **28**: 1818-1823.

Gunkel, G. & Casallas, J. (2002). El lago San Pablo (Imbacucha)-Un lago eutrófico? Primer encuentro intercultural para la gestión integral de cuencas y asentamientos humanos "Imbacucha" 2002. Otavalo-Ecuador. Conference Proceeding.

Gunkel, G. & Casallas, J. (2002b). Limnology of an Equatorial High Mountain Lake - Lago San Pablo, Ecuador: The significance of deep diurnal mixing for lake productivity. *Limnologica*, **32:** 33-43.

Halac, S., Felip, M., Camarero, L., Sommaruga-Wograth, S., Psenner, R., Catalan, J. & Sommaruga, R. (1997). An *in situ* enclosure experiment to test the solar UVB impact on plankton in a high-altitude mountain lake. I. Lack of effect on phytoplankton species composition and growth. *Journal of Plankton Research*, **19:** 1671-1686.

Haney, J. F., Craggy, A., Kimball, K. & Weeks, F. (1990). Ligth control of evening vertical migrations by *Chaoborus punctipennis* larvae. *Limnology and Oceanography*, **35:** 1068-1078.

Haney, J. F. & Hall, D. J. (1973). A preservation technique for Cladocera. *Limnology and Oceanography*, **18:** 331-333.

Häder, D.-P. (1995). Influence of ultraviolet radiation on phytoplankton ecosystems. In: Wiessner, W., Schnepf, E. & Starr, R. C. (Eds.), *Algae, Environment and Human Affairs*, pp. 41-55. Bristol: Biopress Ltd. 55 pp.

Häder, D. P. (1997). Penetration and effects of solar UV-B on phytoplankton and macroalgae. *Plant Ecology*, **128:** 4-13.

Häder, D. P. (1999). Effects of solar UV-B radiation on aquatic ecosystems. *Verhandlungen der Gesellschaft für Ökologie*, **29:** 463-471.

Henry, R., Pellegrini Caramashi, E. M. & Tundisi, J. G. (1978). Survey of ecological factors in a shallow tropical reservoir. *Revista brasileira de biología*, **38:** 171-175.

Hessen, D. O., De Lange, H. J. & Van Donk, E. (1997). UV-induced changes in phytoplankton cells and its effects on grazers. *Freshwater Biology*, **38:** 513-524.

Holdridge, L. (1978). *Ecología basada en las zonas de vida*. San José, Costa Rica: Instituto Iberoamericano de Ciencias Agrícolas.

Hrbacek, J., Dvorakova, M., Korinelk, V. & Prohazkova, L. (1961). Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. *Verh.Internat.Verein.Limnol*, **14:** 192-195.

Huber-Pestalozzi, G. (1938). *Das Phytoplankton des Süsswassers. Die Binnengewässer*. Stuttgart: E. Schweizebartische Verlagsbuchhandlung.

Hutchinson, G. E. & Löffler,H. (1956). The thermal classification of lakes. *Proc.Nat.Acad.Sci.*, **42:** 84-86.

Idso, S. B. (1973). On the concept of lake stability. *Limnology and Oceanography*, **18:** 681-683.

Iltis, A. (1992). Phytoplancton. Algae:General floristic study. In: Dejaoux,C. & Iltis,A. (Eds.), *Lake Titicaca. A Synthesis of Limnological Knowledge*, pp. 176-181. Dordrecht, The Netherlands: Kluwer Academic Publishers. 181 pp.

INAMHI . Boletines Metereológicos. (1999). Instito Nacional de Meteorología e Hidrología. Centro Nacional de Análisis y Pronóstico.

Infante, A. G. (1982). Annual variation in abundance of zooplankton in Lake Valencia (Venezuela). *Hydrobiologia*, **93:** 194-208.

Jokiel, P. L. & York, R. H. (1984). Importance of ultraviolet radiation in photoinhibition of microalgal growth. *Limnology and Oceanography*, **29:** 192-199.

Kiersch, B., Mühleck, R. & Gunkel, G. (2003). Las macrófitas de algunos lagos altoandinos del Ecuador y su posible utilización como bioindicadores de eutrofización. *Revista de Biología Tropical*.

Kinzie III, R. A., Banaszak, A. A. & Lesser, M. P. (1998). Effects of ultraviolet radiation on primary productivity in a high altitude tropical lake. *Hydrobiologia*, **385:** 23-32.

Knoechel, R. & Kalff, J. (1975). Algal sedimentation: The cause of a Diatom-blue-green succession. *Verh.Internat.Verein.Limnol* , **19:** 745-754.

Koste, W. & Böttger, C. (1992). Rotatorien aus Gewässern Ecuadors II. *Amazoniana*, **XII:** 263-303.

Koste, W. & Böttger, K. (1989). Rotatorien aus Gewässern Ecuadors. *Amazoniana*, **X:** 407-438.

Lampert, W. (1989). The adaptative significance of of diel vertical migration in zooplankton. *Ecology*, **66:** 68-82.

Lazzaro, X. (1987). A review of planktivorous fishes, their evolution, feeding behaviours, selectivities and impacts. *Hydrobiologia*, **146:** 97-167.

Leibold, M. A. (1990). Resources and predators can affect the vertical distributions of zooplankton. *Limnology and Oceanography*, **35:** 938-944.

Lewis, S. M. & Weibezahn, H. F. (1987). Chemistry, energy flow, and community structure in some Venezuelan fresh-waters. *Verh.Internat.Verein.Limnol*, **2/3:** 145-207.

Lewis, W. M. Jr. (1973). The thermal regime of the lake Lanao (Philippines) and its theoretical implications for tropical lakes. *Limnology and Oceanography*, **18:** 200-217.

Lewis, W. M. Jr. (1983). A revised classification of lakes based on mixing. *J.Fisch.Aquat.Sci.*, **40:** 1779-1787.

Lewis, W. M. Jr. (1987). Tropical limnology. *Ann.Rev.Ecol.Syst.*, **18:** 159-184.

Lewis, W. M. Jr. (1995). Tropical lakes: How latitude make a difference. In: Timotius,K.H. & Göltenboth,F. (Eds.), *Tropical Limnology*, pp. 29-44. Salatiga, Indonesia: Satya Wacana Christian University. 44 pp.

Lewis, W. M. Jr. (1996). Tropical lakes: How latitude makes a difference. In: Schiemer, F. & Boland, K. T. (Eds.), *Perspectives in Tropical Limnology*, pp. 43-64. Amsterdam: SPB Academic Publishers. 64 pp.

Lewis, W. M. Jr. (2000). Basis for the protection and management of tropical lakes. *Lakes & Reservoirs: Research and Management* , **5:** 35-48.

Lorenzen, C. J. (1967). Determination of chlorophyll and pheo-pigments: Spectrophotometric equations. *Limnology and Oceanography*, **12:** 343-346.

Löffler, H. (1963). Zur Ostrakoden- und Copepodenfauna Ekuadors. *Arch.Hydrobiol.*, **59:** 196-234.

Löffler, H. (1964). The limnology of tropical high-mountain lakes. *Verh.Internat.Verein.Limnol*, **XV:** 176-193.

Lund, J. W. G., Kipling, C. & Le Cren, E. D. (1958). The Inverted Microscope Method of Estimating Algal Numbers and the statistical Basis of Estimations by Counting. *Hidrología*, **2:** 143-170.

Lundgren, A. (1985). Model ecosystems as a tool in frehwater and marine research. *Arch.Hydrobiol.*, **2:** 157-196.

Lürling, M. & Van Donk, E. (1997). Life history consequences for *Daphnia pulex* feeding on nutrient limited phytoplankton. *Freshwater Biology*, **38:** 693-709.

Lütz, C., Seidlitz, H, K. & Meindl, U. (1997). Physiological and structural changes in the chloroplast of the green alga *Micrasterias denticulata* induced by UV-B simulation. *Plant Ecology*, **128:** 54-64.

Mackereth, F, J, H., Heron, J. & Talling, J, F. (1989). *Water Analysis: Some revised methods for Limnologists*. Cumbria: Freshwater Biological Association. 121 pp.

Makarewicz, J, C. (1993). Phytoplankton as indicators of environmental health. *Verh.Internat.Verein.Limnol*, **25:** 363-365.

Margalef, R. (1978). Life forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol.Acta*, **1:** 493-509.

Margalef, R. (1983). *Limnología*. Barcelona: Ediciones Omega, S.A.

Margalef, R. (1994). *Limnology now. A paradigm of planetary problems*. Amsterdam: Elsevier Science B.V.

Masundire, H., M. (1994a). Mean individual dry weight and leght-weight regressions of some zooplankton of Lake Kariba. *Hydrobiologia*, **272:** 231-238.

Masundire, H., M. (1994b). Seasonal trends in zooplankton densities in Sanyati basin, Lake Kariba: multivariate analysis. *Hydrobiologia*, **272:** 211-230.

McCauley, E. (1984). The estimation of the abundance and biomass of zooplankton in samples. In: Downing,J.A. & Rigler,F. (Eds.), *A manual on methods for the assesment of secondary productivity in fresh water*, pp. 228-265. London: Blackwell. 265 pp.

Melack J M. (1979). Temporal variability of phytoplankton in tropical lakes. *Oecologia*, **44:** 1-7.

Melack, J, M. (1996). Recent developments in tropical limnology. *Verh.Internat.Verein. Limnol*, **26:** 211-217.

Michel, J. (2000). Enhancing efficiency in limnological analysis with the new dual channel FIAstar 5012 System. 1-4. Report.

Miller, M, C., Kannan, M. & Colinvaux, P, A. (1984). Limnology and primary productivity of Andean and Amazonian tropical lakes of ecuador. *Verh.Internat.Verein.Limnol*, **22:** 1264-1270.

Molina, J. (1983). Estudios del fitoplancton de aguas tropicales frias y continentales. Embalse del Sisga (Colombia). Universidad Javeriana, Bogotá. Thesis.

Mora M., G. & Téllez B., L, S. (1991). Estudio limnológico del lago de Tota (Boyacá - Colombia). 1-105. Universidad Nacional de Colombia, depto. de Biología. Thesis.

Mortimer, C, H. (1981). The oxygen content of air-saturated fresh waters over ranges of temperature and atmospheric pressure of limnological interest. *Mitt.Internat.Verein.Limnol,* **22**: 1-23.

Munawar, M. & Talling, J, F. (1986). Seasonality of freshwater phytoplankton. *Hydrobiologia*, **33**.

Murphy, G, C. (1962). Effect of mixing depth and turbidity on the productivity of fresh water impoundments. *Trans.Am.Fish.Soc.* , **61:** 69-75.

Nilssen, J, P. (1984). Tropical Lakes - Functional ecology and future development: The need for a process oriented approach. *Hydrobiologia*, **113:** 231-242.

Nusch, E, A. (1980). Comparison of different methods for chlorophyll and phaepigment determination. *Arch.Hydrobiol.*, **14:** 14-36.

O'Brien, W. J. (1974). The dynamics of nutrient limitation of phytoplankton algae: a model reconsidered. *Ecology*, **55:** 135-141.

OECD (1982). *Eutrophication of waters - monitoring, assessment and control*. Paris:, Organisation for Economic Cooperation and Development. 154 pp.

Olesen, B. & Maberly, C. (2001). The effect of high levels of visible and ultra-violet radiation on the photosynthesis of phytoplankton from a freshwater lake. *Arch.Hydrobiol.*, **151:** 301-315.

Orstom-Pronareg. (1983a). Cartas de suelos del Lago San Pablo, Mojanda, Cubilche y Cusín (1:60,000). Quito, Ecuador, DINAREN.

Orstom-Pronareg (1983b). Cartas geológicas del Lago San Pablo, Mojanda, Cubilche y Cusín (1:60,000). Quito, Ecuador, DINAREN.

Osborne, P. L. (2000). *Tropical Ecosystems and Ecological Concepts*. Cambridge: Cambridge Universuty Press. 464 pp.

Page, L. M. & Burr, B. M. (2001). Species summary for *Micropterus salmoides* (Lacepède, 1802). Internet page. www.fishbase.org/Summary/SpeciesSummary.cfm? ID: 3385

Paredes Castillo, D. (1994). Rehabilitación ambiental y aprovechamiento sustentable de los lagos de San Pablo, Yaguarcocha y Cuicocha en la provincia de Imbabura. primer borrador, 1-25.. Quito, Consultoria Socio-económica y Planificación. Report.

Payne, A. I. (1986). *The Ecology of Tropical Lakes and Rivers*. Chichester: JOHN WILEY & SONS. 301 pp.

Pennak, R. W. (1957). Species composition of limnetic zooplankton communities. *Limnology and Oceanography*, **2:** 222-232.

Powell, T., Kirkish, M. H., Neale, P. J. & Richerson, P. J. (1984). The diurnal cycle of stratification in Lake Titicaca: Eddy diffusion. *Verh.Internat.Verein.Limnol*, **22:** 1237-1243.

Ravera, O. (1989). The "enclosure" method: Concepts, technology, and some examples of experiments with trace metals. In: Boudou,A. & Ribeyre,F. (Eds.), *Aquatic*

Ecotoxicology: Fundamental Concepts and Methodologies, pp. 249-272. Boca Ratón, Florida: CRC Press. 272 pp.

Reid, J. W. (1985). Chave de identificaçao e lista e referencias bibliograficas para as especies continentales sulamericanas de vida libre da orden Cyclopoida (Crustacea, Copepoda). *Bolm.Zool.Univ.S.Paulo*, **9:** 17-143.

Reid, J. W., Molina A.,J.A. & Fukuschima,M.M. (1990). *Metacyclops leptopus totensis*, new subspecies (Crustacea, Copepoda) from Lago de Tota, Colombia. *Proc.Biol.Soc.Washington*, **103:** 674-680.

Rey, J. (1992). VI.3. Zooplankton VI.3a. The Cladocera. In: Dejaoux,C. & Iltis,A. (Eds.), *Lake TiticacaA Synthesis of Limnological Knowledge*, pp. 254-267. Dordrecht, The Netherlands: Kluwer Academic Publishers. 267 pp.

Reynolds, C. S. (1982). Phytoplankton periodicity: its motivation, mechanisms and manipulation. *Rep.Freshwat.Biol.Assoc.*, **50:** 60-75.

Reynolds, C. S., Wiseman,S.W. & Clarke,M.J.O. (1984). Growth- and loss-rate responses of phytoplankton to intermittent artificial mixing and their potential application to the control of planktonic algal blooms. *J.Appl.Ecol.*, **21:** 11-39.

Reynolds, C. S., Wiseman,S.W., Godfrey,B.M. & Butterwick,C. (1983). Some effects of artificial mixing on the dynamics of phytoplankton in large limnetic enclosures. *Journal of Plankton Research*, **5:** 203-234.

Richerson, P. J., Neale, P. J., Wurtsbaugh, W. A., Alfaro T., R. & Vincent, W. (1986). Patters of temporal variation in lake Titicaca. A high altitude tropical lake. I. Background, physical and chemical processes, and primary production. *Hydrobiologia*, **138:** 205-220.

Roldán, G. (1992). *Fundamentos de Limnología Neotropical*. Medellín: Editorial Universidad de Antioquia. 529 pp.

Roldán, G. & Ruiz, E. (2001). Development of Limnology in Colombia. In: Wetzel, R. G. & Gopal, B. (Eds.), *Limnology in Developing Countries*, pp. 69-119. New Delhi: International Association for Limnology (SIL). 119 pp.

Rott, E. (1981a). Ein Beitrag zur Algenflora andiner hochlandseen Ecuadors (Sudamerika). *Ber.nat.-med.Ver.Innsbruck*, **68:** 13-29.

Rott, E. (1981b). Some results from phytoplankton intercalibrations. *Schweiz.Z.Hydrol.*, **43:** 34-62.

Schwoerbel, J. (1986). *Methoden der Hydrobiologie - Susswasserbiologie*. Stuttgart: Gustav Fisher Verlag. 369 pp.

Scott,J.T. (1964). A comparison of the heat balance of lakes in winter. Tech. Rep. 13, 1-138.. Madison, Dept. of Meteorol.,Univ. of Wisconsin. Report

Sommer, U. (1993). The scientific basis of eutrophication management: reconciling basis physiology and empirical biomass models. 5th International Conference of the Conservation and Management of Lakes. . Istituto Italiano di Idrobiologia, Stresa, Italy. Conference Proceeding.

Steinitz-Kannan, M. (1997). Diatom species in ecuadorian lakes. Report.

Steinitz-Kannan, M., Colinvaux, P. A. & Kannan, R. (1983). Limnological studies in Ecuador: 1. A survey of chemical and physical properties of Ecuadorian lakes. *Arch.Hydrobiol.*, **1:** 61-105.

Talling, J. F. (1965). The photosynthetic activity of phytoplankton in East African lakes. *Int.Revue ges.Hydrobiol.*, **50:** 1-32.

Tilzer, M. M. (1973). Diurnal periodicity on the phytoplankton assemblage of a High-mountain lake. *Limnology and Oceanography*, **18:** 15-30.

Titman, D. & Kilham, P. (1976). Sinking in freshwater phytoplankton: Some ecological implications of cell nutrient satatus and physical mixing processes. *Limnology and Oceanography*, **21:** 409-417.

Utermöhl, H. (1958). Zur Vervollkommnung der quantitativen Erfasung des Planktons. *Mitt.Internat.Verein.Limnol*, **9:** 1-38.

Valdivia Villar, R. S. (1988). Lista de Cladóderos dulceacuícolas del Perú. *Amazoniana*, **X:** 283-297.

Veen, A., Reuvers, M. & Ronçak, P. (1997). Effects of acute and chronic UV-B exposure on a green alga: a continuous culture study using a computer-controlled dynamic light regime. *Plant Ecology*, **128:** 28-40.

Villalobos, L. (1994). Distribution of *Daphnia* in high mountain and temperate lakes of South America. *Verh.Internat.Verein.Limnol*, **25:** 2400-2404.

Vincent, W. F., Neale, P. J. & Richerson, P. J. (1984). Photoinhibition: algal responses to bright light during dial stratification and mixing in a tropical alpine lake. *J.Phycol.*, **20:** 201-211.

Vollenweider, R. A. (1968). Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors of eutrophication. OECD. DA 5/SCI/68.27, 1-250. Paris.

Von Sperling, E. (1997). The process of biomass formation as the key point in the restoration of tropical eutrophic lakes. *Hydrobiologia*, **342/343:** 351-354.

Wetzel, R. G. (1983). *Limnology*. Philadelphia: Saunders College Publishing. 767 pp.

Wetzel, R. G. & Likens, G. E. (1991). *Limnological Analyses*. New York: Springer Verlag. 391 pp.

Whitton, B. A. (1968). Phytoplankton from Ecuadorian Lakes. *Nova Hidrologia*, **16:** 267-268.

Wright, S. (1927). A revision of the South American species of *Diaptomus*. *Trans.Amer.Micr.Soc.*, **46:** 73-121.

Wurtsbaugh, W. A. & Vincent, W. F. (1985). Nutrient limitation of algal growth and nitrogen fixation in a tropical alpine lake, lake Titicaca (Perú- Bolivia). *Freshwater Biology*, **15:** 185-195.

Wurtsbaugh, W. A., Vincent, W. F., Vincent, C. L., Carney, H. J., Richerson, P. J. & Alfaro T., R. (1992). V.6. Nutrients and nutrient limitation of phytoplankton. In: Dejoux, C. & Iltis, A. (Eds.), *Lake Titicaca A Synthesis of Limnological Knowledge*, pp. 147-160. Kluwer Academic Publischers. 160 pp.

Zauke. G. P., Niemeyer, R. G. & Gilles, K. P. (1992). Limnologie der Tropen und Subtropen: Grundlagen und Prognoseverfahren der limnologischen Entwicklung von Stauseen. 1-174.. Lech, ecomed Fachverlag. Angewandter Umweltschutz. Serial (Book,Monograph)

Acknowledgments

I would like to express my gratitude to everyone who has contributed to the elaboration of the present work. It would be impossible to name here everyone who helped me but, the following people deserve a special mention here.

I would like to thank Professor Dr. Martin Jekel for the gentle welcome in the Water Protection Department and for being one of the juries of this work.

I am very grateful to Dr. Günter Gunkel for giving me the opportunity to participate in the project on mountain lakes in Ecuador. I thank him for his permanent support during the years that we worked together in this project; for his advices and recommendations and for the time we spend together during the field work in Ecuador.

A special recognition to Professor Dr. Brigitte Nixdorf, not only because she accepted to be jury of my dissertation work, but also for her constant help and support from the start, when I first wanted to come to Germany.

I am very grateful to all those persons who collaborated to collect the data during field and laboratory work: Fabian Tapia, David Neira and Helman Maldonado, students from the National Polytechnical University of Ecuador, who made possible the regular sampling at Lake San Pablo and assisted me during my work in Ecuador. Anke Kitzmann , Helge Nordmann and Frank Zetzsche, students from the Technical University of Berlin, who collaborated with field work in August 1999 during the realization of their study project. The staff from the Secretary of Environmental Sanitation (Quito, Ecuador) for its collaboration with the chemical analysis of water samples; and to Dr. Gabriele Gunkel and Dr. Camilla Beulker for their assistance with analysis of phytoplankton in Berlin.

Special thanks to the Echavarria family, who lives at the shore of the lake, for its immense assistance in so many occasions, and to Cristina Padilla for her friendship and help during field work at Lake San Pablo.

I also thank the German Research Council (DFG) and the Ministry of Economic Cooperation and Development (BMZ) for financial support and the National Polytechnical University of Ecuador for the logistic support.

I am also grateful to my sister Clara van Lanschot and her husband Robbert for the corrections of the first version of the manuscript. A Special thanks to Mr. Charles Hooper, who made the final corrections of it.

Finally, I owe a very special thank to my wife Lorena Martínez , who has not only accompanied me for the last 14 years, but also had greatly contributed to the realization of this work with her affection, patience, tolerance and good advices. She has also helped me with the corrections and the final edition of the manuscript. I would like to add, that without her help it would not have been possible the realization of this work.