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Limnology of an equatorial high mountain lake – Lago San Pablo, Ecuador: The significance of deep diurnal mixing for lake productivity

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Abstract

Equatorial high mountain lakes are a special type of lake occurring mainly in the South American Andes as well as in Central Africa and Asia. They occur at altitudes of a few thousand meters above sea level and are cold-water lakes (<20 °C). Relatively little is known about them. A long-term limnological study was therefore undertaken at Lake Lago San Pablo, Ecuador to analyze the basic limnological processes of this lake, which has a tendency for eutrophication. Lago San Pablo is spread over an area of 668 hectares, has a maximum depth of 35 m, and is located 2660 m above sea level. Its thermal stratification is a monomictic one, with only 1–2 °C difference between the epi- and hypolimnion; overturn is achieved by strong winds during the dry summer period. The stratification phase is characterized by an oxygen deficit in the lower part of the hypolimnion. Besides, strong convective currents occur due to nocturnal cooling, and partial lake mixing was observed during the nocturnal period. This type of lake mixing is called atelomixis, which is characterized by the partial mixing of isolated layers (difference in temperature or ionic content) during stratification.
The nutrient level of the lake is quite high: mean P_{total} concentration = 0.22 mg/l, mean N_{total} = 1.05 mg/l, soluble reactive phosphorus (SRP) > 0.01 mg/l, and soluble inorganic nitrogen > 0.2 mg/l. Nitrogen and phosphorus are available in the epilimnion all year round ($N_{sol. inorg.}$ = 0.3 to 1.7 mg/l N, SRP = 0.04 to 0.63 mg/l P). The N/P ratio is sometimes > 14, sometimes < 10, indicating a variability of the limiting nutrient factor. Considering the nutrient level, the phytoplankton biomass is quite low (about 4,000 cells per ml on average; maximum cell number: 13,000 in 1998 and 10,000 in 1999). The mean epilimnic chlorophyll content (Chl *a*) was 10 μg/l in 1998 and 11 μg/l in 1999, and the maximum Chl *a* content was 16 and 22 μg/l in 1998 and 1999, respectively.
Phytoplankton production can be limited by nutrients, mainly nitrogen, but convective currents can also cause a significant loss of biomass. The lake's euphotic zone is smaller than its epilimnic zone, indicating that light radiation is limiting in the deeper water body, this is caused by a weak thermocline due to destratification by nocturnal cooling, the atelomixis.

Key words: Lago San Pablo – Andes – high mountain lakes – eutrophication – primary production – stratification – atelomixis – UV radiation

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Introduction

The limnology of tropical lakes is a main field of contemporary research worldwide due to the lack of knowledge of the subject (GOPAL & WETZEL 1995; WETZEL & GOPAL 1999). Available results point out that the chemical and physical properties as well as the biological processes of tropical lakes differ significantly to those of the well investigated temperate lakes of the northern hemisphere (LEWIS 1987, 2000; ROLDÁN 1992). Tropical lake processes are mainly determined by a high solar radiation, water heating with an intensification of microbiological processes, and a low oxygen concentration in water. The seasonal variation of the climate is not very significant and is mainly determined by rain intensity. Solar radiation input and water temperature do not change significantly throughout the year. Besides in tropical regions the output from the catchment area cannot be compared with exportations in temperate zones, due to the differences in vegetation, soils and nutrient recycling processes.

Considering the fact that the morphometric parameters and chemical composition of the water of tropical lakes exhibit great variance, more intensive development of tropical lake ecosystem studies is required. High mountain lakes are a special type of tropical lake. They are situated near the equator at an altitude of about 2,000 to 4,000 m above sea level, mainly in the Andes of South America (Ecuador, Columbia, Mexico, northern Peru), in Africa (Ethiopia Kenya, Uganda, Tanganyika) and in Asia (Indonesia, Papua New Guinea). Only a few researchers have investigated these lakes so far, though LÖFFLER (1964) recognized their unique nature decades ago. The well-investigated Lake Titicaca cannot be used as a model lake because of its latitude (14–17° south) and size (8,448 km^2 surface area, 284 m depth).

Tropical high mountain lakes are cold-water lakes with a consistently high solar radiation input throughout the year. Due to their high altitude, they are exposed to intense UV radiation (KINZIE et al. 1998). The heat balance of the water body is determined by the day/night cycle. Heating occurs during the daytime due to solar radiation input, and intensive cooling occurs during the night due to the transfer of heat to the atmosphere and to temporary wind mixing, leading to convective nocturnal mixing, which is also known to occur in tropical lowland lakes, the atelomixis (TALLING 1969; LEWIS 1973; IMBERGER 1985). The term atelomixis is used for lakes in which partial mixing processes during the stratification period lead to complex stratification and multiple thermoclines.

The recycling of nutrients is determined by lake mixing processes, and the annual wet/dry season cycle may lead to a corresponding cyclic variation of physical and chemical parameters. The scanty amount of data available on atelomixis was obtained from studies in Ethiopian crater lakes (TALLING 1969; WOOD et al. 1976).

Little is known about nutrient cycle in tropical high mountain lakes, but nitrogen is a production-limiting factor. Intensive nitrogen metabolism occurs in warm tropical areas, whereas the nitrogen output from high mountain lake catchments may be decreased due to the low air temperatures. In addition, the biodiversity of tropical high mountain lakes has not yet been characterized, but we must assume that the more or less remote cold water lakes in hot tropical zones have relatively little biodiversity and maybe endemic species occur.

Intensive studies of Lago San Pablo, a high mountain lake in Ecuador, were carried out to describe the limnological processes characteristic of this ecosystem. The main objective of the study was to obtain a better understanding of tropical cold water lakes and to develop a basis for lake management including existing or future tropical high mountain reservoirs used to supply drinking water in many countries.

Some limnological aspects of Lago San Pablo are already known from the above-mentioned investigation program as well as from other studies carried out in recent years, e.g., on the overall lake system (GUNKEL 2000), its physical and chemical conditions (CASALLAS & GUNKEL 2002), sediment chemistry and sedimentation rate (GUNKEL 2002), thermal stratification (GUNKEL & CASALLAS 2002), the biodiversity and abundance of algae (ROTT 1981; CASALLAS & GUNKEL 2002), the occurrence of macrophytes (KIERSCH et al. 2002), and the biodiversity of Rotatoria (KOSTE & BÖTTGER 1982, 1992), Ostradoca and Copepoda (LÖFFLER 1963).

Material and Methods

From December 1997 to January 2000, Lago San Pablo was regularly monitored once or twice monthly. Measurements were taken at the deepest point of the lake, and special monitoring procedures were carried out (inflow, outflow, 24-hour vertical profiles and lake crossing profiles). Water temperature and conductivity were measured on-site using field electrodes (WTW) on a 40 m cable. Oxygen, NO_2 and pH levels in the water samples were determined directly on the boat using WTW electrodes respectively NO_2-indicator strips. The water samples were filtered on shore, and chemical analyses were carried out on the same day in Quito at the Subsecretaria Saneamiento de Quito (NO_3^-, NH_4^+, N_{total}, SRP, $P_{soluble}$, P_{total}, BSB_5, SiO_2) and the Escuela Politecnica Nacional de Quito (DOC). The chemical analyses were performed in accordance with the US Standard Methods for Water Chemical Analyses (APHA 1989).

Water samples for plankton analyses were collected using a water sampler and a plankton net with a trapping mechanism. The quantitative analyses were carried out at the Technical University of Berlin as well as by Dr. G. HEISIG-GUNKEL, Berlin. Living plankton samples were analyzed at the Escuela Politecnica Nacional de Quito.

An automatic water temperature measurement station was set up near the shoreline at a depth of 24 m (ecoTech multilogger with PT 100 sensors, Mirkomec-Multisens and MM-grafix software). The sensor chain was equipped with sensors at depths of 0.5, 2, 3, 6, 9, 15 and 20 m, and the measured temperatures were stored every 5 minutes. The PT 100 sensors achieve an accuracy of 0.1 °C, and a high level of precision was ensured using by sensors of a single production series. A meteorological station was set up at the shoreline to measure temperature, rainfall, wind intensity and wind direction (ecoTech multilogger).

Enclosure experiments were carried out using bags consisting of a polyethylene tube 0.9 m in diameter and 7 m in length. Four of these enclosures were mounted on a platform near the shoreline at a water depth of 24 m. The lake was used as a control, one enclosure was used as a closed epilimnic system, two were enriched with nutrients (NO_3^- and PO_4^{3-}, resp.), and one was protected against UV radiation (using a Secafur membrane).

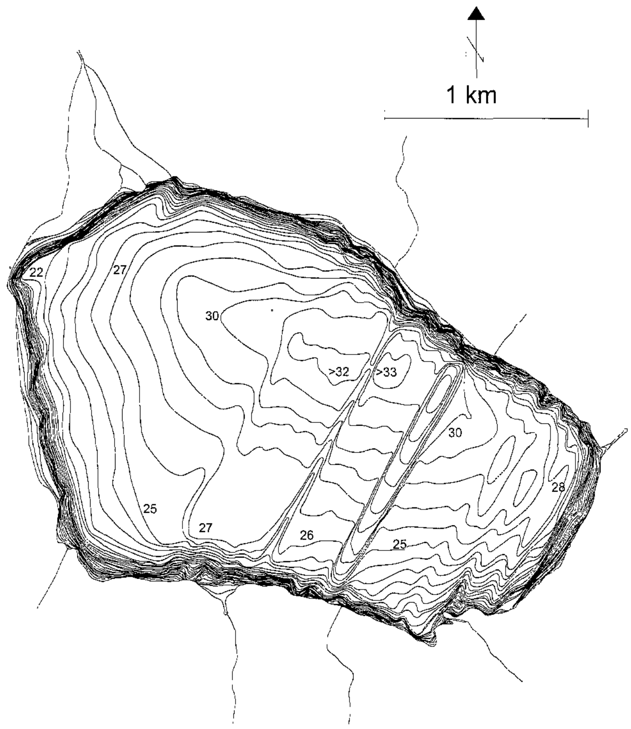

Fig. 1. Morphometric map of Lago San Pablo, Ecuador, water depth in m (EPA 1995).

Study Area

Lago San Pablo is a high mountain lake situated 2,660 m a.s.l. in the northern part of the Andes Mountains in Ecuador/South America. The lake is located near Otavalo, latitude 0° 12′ north and longitude 78° 13′ east. It is a natural lake situated in a valley between the volcanoes Imbabura (4,609 m), Cusin (3,889 m) and Mojanda (4,263 m). The lake has a maximum depth of 35.2 m (mean depth 26 m). It is nearly circular, with a steeply sloping shoreline (Fig. 1). The main characteristics of the lake are listed in Table 1.

The lake's main water inlet is a small mountain creek, the Rio Itambi, with a catchment area of 14,700 hectares that extends to 4,000 m a.s.l. The lake's water outlet consists of a Totora swamp and two small man-made ditches that form the Desaguadera creek. The catchment area is intensively used for agriculture up to about 3,600 m a.s.l. Due to the steep slope (32% of the catchment area has a slope of >70%), a high erosion rate can be expected. The catchment area and lake use were already described in a previous article (GUNKEL 2000).

The regional climate is determined by regular and intense air temperature oscillation. The mean daytime temperature is 13.6 °C, with a mean maximum daytime air temperature of 22.4 °C and a mean nighttime minimum air temperature of 8.3 °C (1999 to 2000). The average rain intensity is 985 mm/year, with about 86 mm/3 months during the dry season from June to August

Table 1. Morphometric parameters of Lago San Pablo, lake morphometric data from EPA (1995), water balance data from ZEVALLOS (1992).

Altitude	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
Watershed area	147.9 km^2
Form of the watershed area	nearly circled
Mean altitude of watershed area	3,100 m
Factor watershed/lake surface	26
Maximum depth	35.2 m
Mean depth	24.6 m
Volume	140×10^6 m^3
Hypolimnion/Epilimnion	0.87
Inflow Rio Itambi,	43.8×10^6 m^3/a
Small rivers	
Precipitation	5.0×10^6 m^3/a
Inflow total	48.8×10^6 m^3/a
Unknown inflow (springs), calc.	1.5×10^6 m^3/a
Evaporation	6.9×10^6 m^3/a
Outflow	36.5×10^6 m^3/a
Rio Desaguadero	26.2×10^6 m^3/a
Channel	10.4×10^6 m^3/a
Irrigation	6.9×10^6 m^3/a
Outflow total	43.4×10^6 m^3/a
Water residence time	3.2 years

(mean of 20-year data registration) and a mean monthly rain intensity of 100 mm/month during the rainy season. The wind is very irregular, and brief gusts of wind (fall winds) with mean wind velocities of 1.2 m/sec can be observed mainly in the afternoon.

Results

Thermal stratification and lake stability

The thermal stratification of the lake is determined by a high solar radiation input throughout the year as well as by strong winds in the dry season extending from June to August. This produces a typical monomictic mixing system with an overturn period occurring from June to August (Fig. 2). During the stratification period in September to May, the epilimnic temperature at the surface is 19–20 °C with a short-term maximum of 20.5 °C. The epilimnion, which extends to a depth of about 15 m, has a mean temperature of 18 °C, but the thermal gradient is not very sharp. The hypolimnion temperature is about 17.5 °C; hence, the temperature difference between the epi- and hypolimnion is very small. An analysis of lake stability according to Idso (1973) indicates that the stability is about

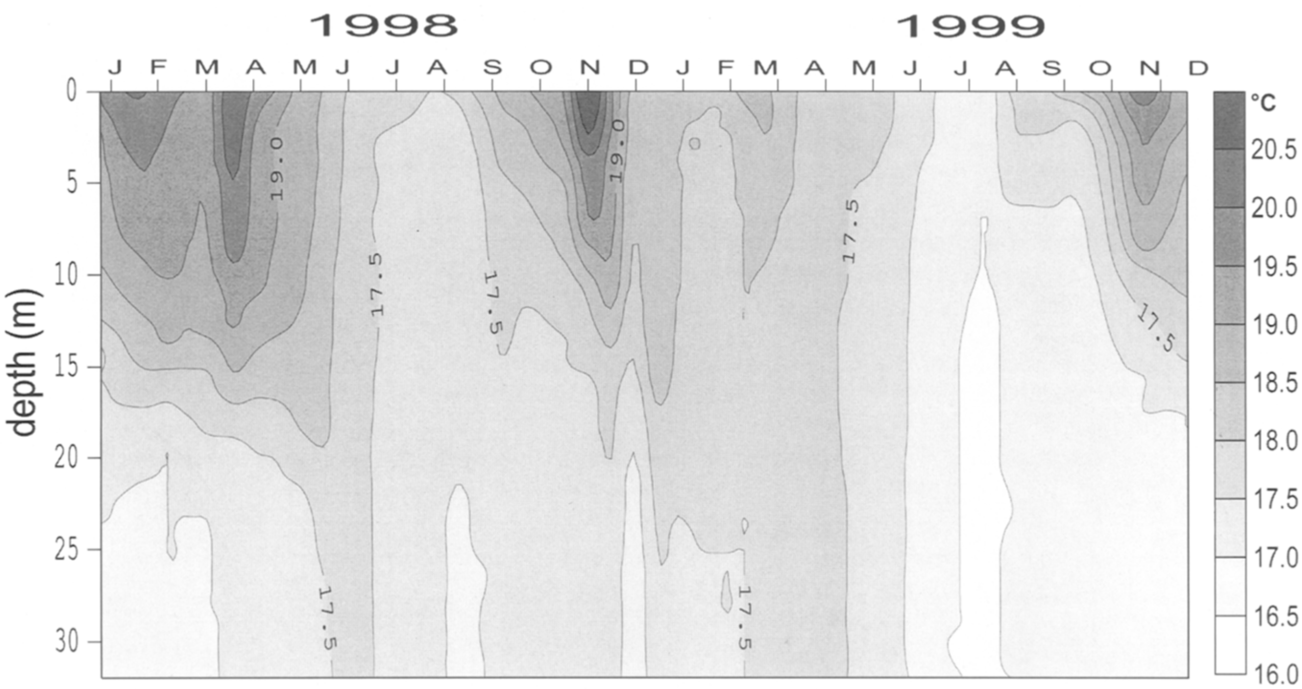

Fig. 2. Thermal stratification of Lago San Pablo, data were collected once or twice a month at about 10:00 a.m. using an electrode-equipped water-proof cable, the calculation of the isopleths was done with Surfer.

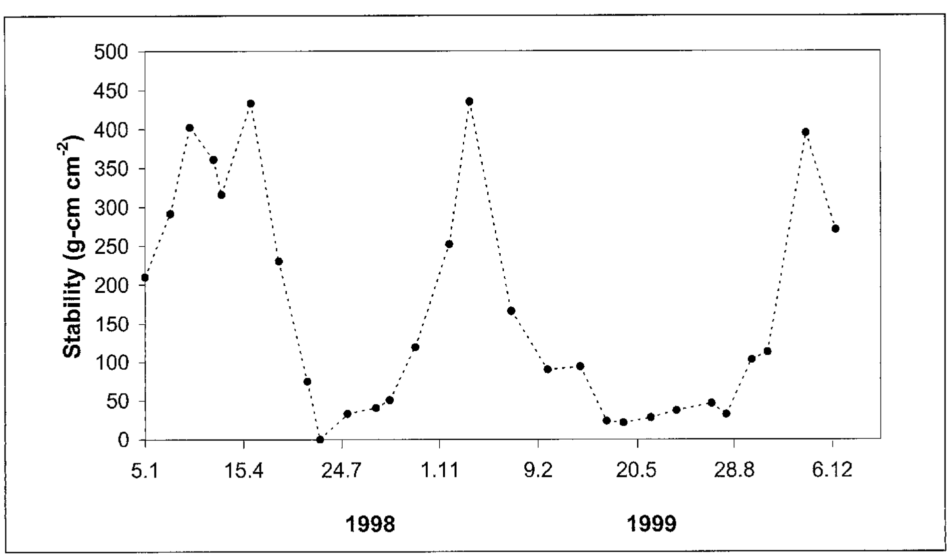

Fig. 3. Stability of lake stratification calculated as the amount of energy needed for whole-lake mixing, according to Idso (1973).

800 g-cm cm^{-2} during the stratification period and nearly zero during overturn (Fig. 3). The stratification of the water body was also confirmed by chemical analyses, e. g., of oxygen concentration (Fig. 4). The epilimnion is saturated with oxygen (about 6 to 8 mg/l O_2), but the hypolimnion below 15 m exhibits an oxygen deficit (O_2 < 1 mg/l) during the stratification period (from November/December to April/May). This oxygen deficit is caused by the high productivity of the lake, which is meso- to eutrophic in nature. This stratification of the water body was also confirmed by the increase in nitrogen and phosphorus concentrations in the hypolimnic water.

Using a sensor chain for continuous temperature measurement, thermal effects were registered with high temporal resolution. Short-term, far-reaching temperature oscillations occur during stratification periods. The typical thermal stratification of the lake is shown in Fig. 5. Solar radiation input leads to daytime heating extending to a depth of 5 m. Homothermic of the water body down to levels of > 20 m can be observed for a few hours during the night. The temperature difference between the epilimnion at 0.5 m and the hypolimnion at 20 m is 1 to 2 °C during the day, but decreases to 0.8 to 0.05 °C during the night (Fig. 5).

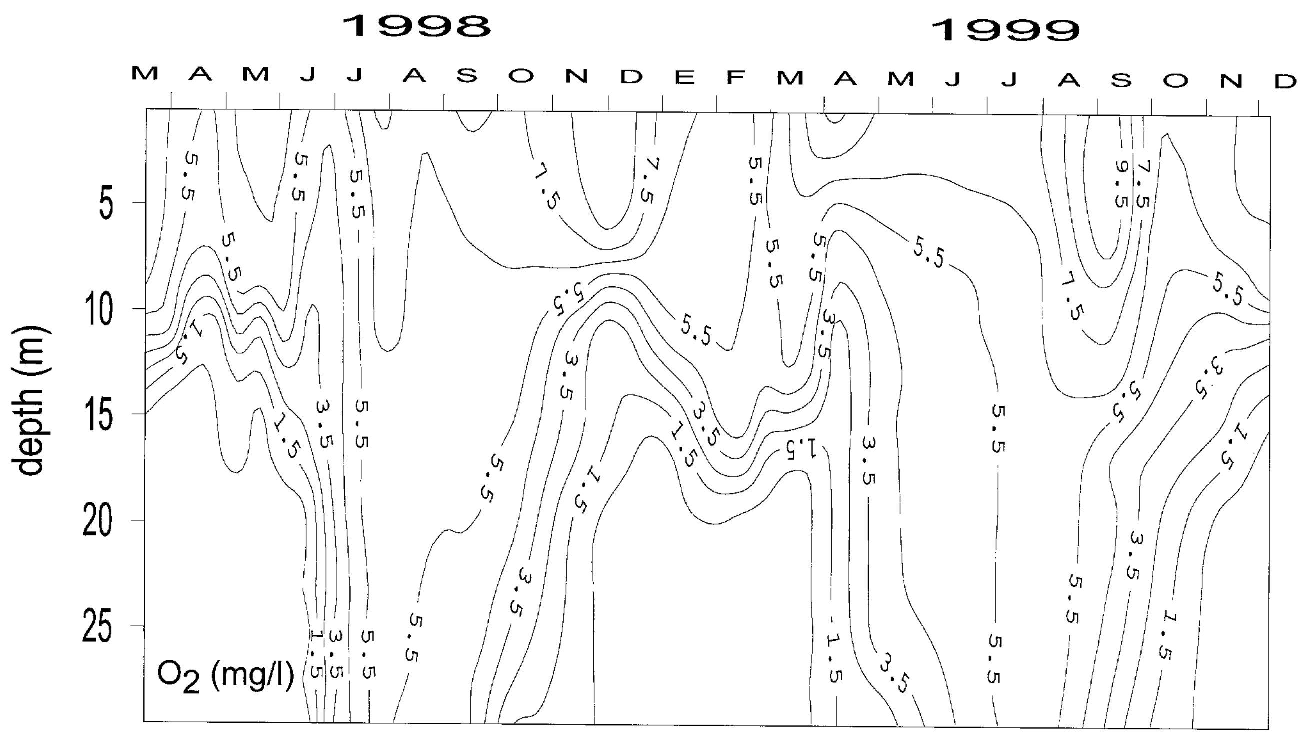

Fig. 4. Isopleths of oxygen in Lago San Pablo, the calculation of the isopleths was done with Surfer.

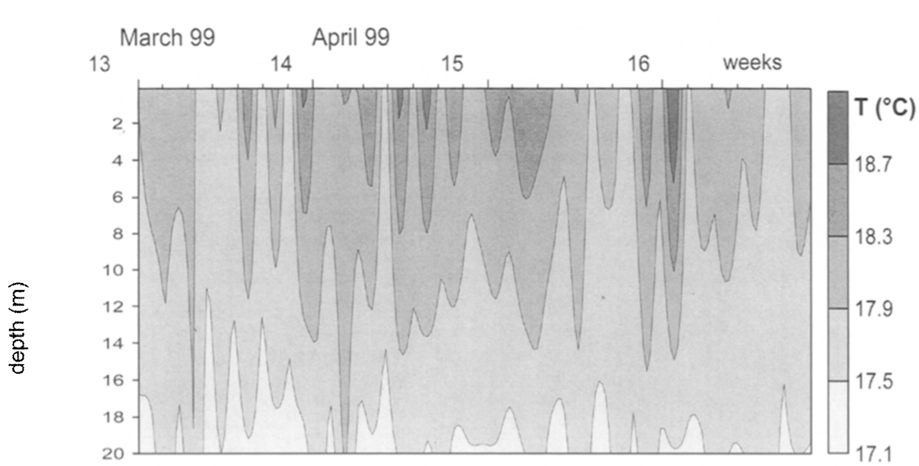

Fig. 5. High resolution of thermal stratification of Lago San Pablo measured using a PT100 sensor chain with a data logger, the calculation of the isopleths was done with Surfer.

This oscillation of the temperature difference between the surface (0.5 m) and the upper hypolimnion (20 m) indicates a periodic heating process due to solar radiation input, and a periodic cooling process due to intensive daily wind fall, evaporation and the transfer of heat to the atmosphere. An inverse thermal stratification pattern can be observed regularly during the night (Fig. 6).

The temperature difference between the 0.5 m and 20 m levels is 0.8 to 1.3 °C in the daytime and 0.0 to 0.6 °C at night (Fig. 5). Consequently, significant thermal stratification can be observed during the day, with maximum stratification occurring around noon. During the night, however, this stratification is more or less abolished due to convective mixing processes. The

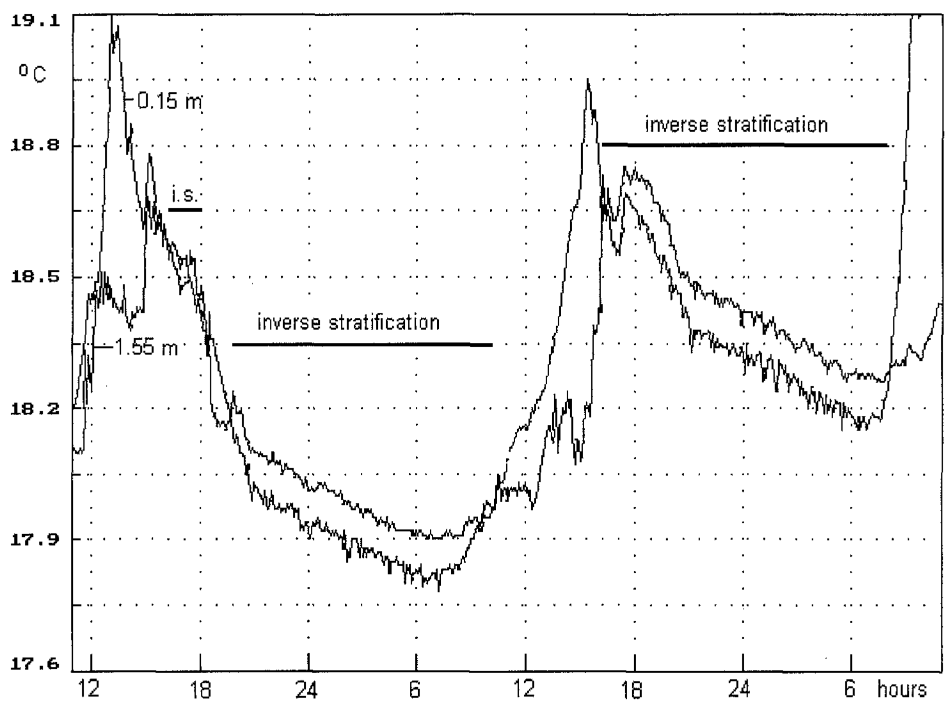

Fig. 6. Inverse stratification of Lago San Pablo due to nocturnal cooling, detected using temperature sensors positioned at depths of 0.15 and 1.55 m (25.10.–27.10.98).

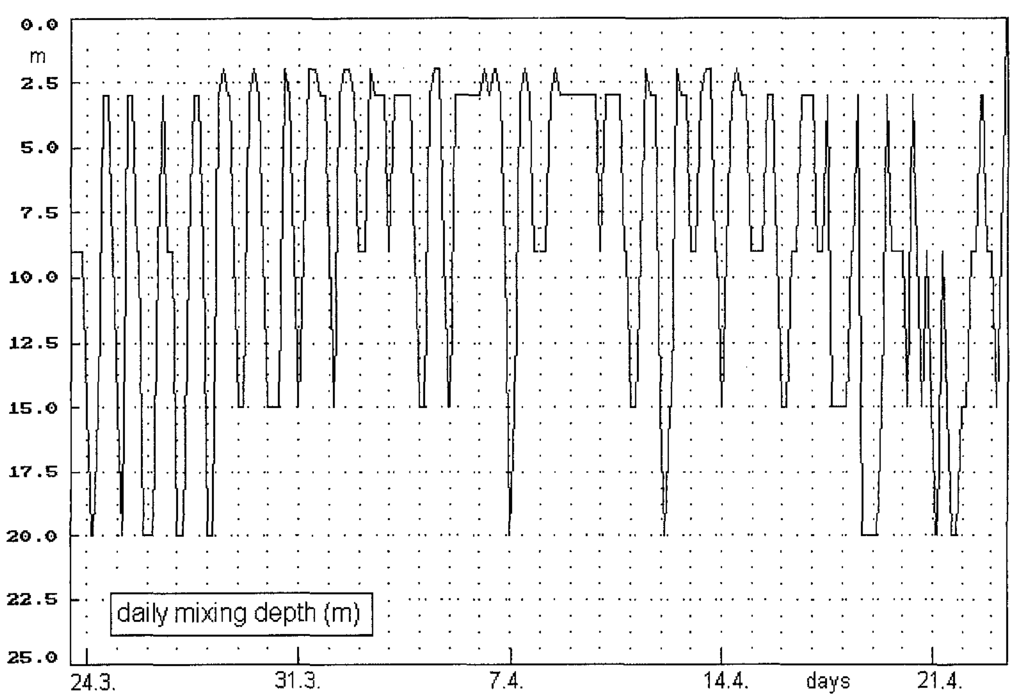

Fig. 7. Water mixing depth of Lago San Pablo due to nocturnal cooling. The mixing depth was calculated using the PT100 sensor chain data; the water depths for $\Delta t < 0.1$ °C are given, data of March/April 1999.

intensity of water mixing between the epi- and hypolimnion depends on the daily climate, daytime heating, nighttime cooling and wind intensity.

Our calculation of the water mixing depth at $\Delta t < 0.1$ °C indicates that some deep mixing occurs (> 20 m) in addition to other insignificant mixing processes (at about 9 m, Fig. 7).

Phytoplankton development in Lago San Pablo

The Lago San Pablo is a weak eutrophic lake with a high phosphorus concentration and a moderate nitrogen concentration (Table 2). The biodiversity of its phytoplankton is described in Table 3, with the most dominant species being *Scenedesmus linearis*, followed by *Pediastrum boryanum*, *Aulacoseira granulata* and *Trachelomonas volvocina* .

The transparency (Secchi disc) of Lago San Pablo is observed at 2.1 to 4.2 m (mean 3.1 m), corresponding to a compensation depth of 6.4 to 8.1 m (mean 7.3 m) according to TILZER (1988). The epilimnic zone usually extends to a depth of 15 m during the lake stratification period, so the euphotic zone is smaller than the epilimnic zone. The reason for this is diurnal cooling and the water mixing processes.

The intensive diurnal water mixing influences the development of the phytoplankton population, because a significant part of the population is transported during the mixing period from the euphotic zone to the aphotic zone. Moreover, population losses occur due to limited light input and sedimentation.

This is confirmed by the phytoplankton abundance and the vertical distribution in the lake, given are the data of the two dominant species *Scenedesmus linearis* (Fig. 8) and *Pediastrum boryanum* (Fig. 9). During stratification period (up to 13th week) *Scenedesmus linearis* has a maximum of cell number below the euphotic zone, and a significant biomass is found in the deep hypolimnion down to 25 m. During circulation period (after 22nd week) algae cells are found in a high number in the hypolimnion as was to be expected. *Pediastrum boryanum* reaches a high density after the beginning of stratification in September (35th week), and a high portion of the population is found in the aphotic zone with a population maximum at 14 m and still a cell number of 2,014 per ml in 29.5 m depth.

Table 2. Water chemistry of Lago San Pablo (data from 1998 and 1999).

Parameter	Depth	Mean	Extreme (min/max)
P_{total} (mg/l)	Epilimnion	0.19	0.06–0.63
	Hypolimnion	0.24	0.06–0.60
SRP (mg/l)	Epilimnion	0.09	0.04–0.25
	Hypolimnion	0.14	0.01–0.29
N_{total} (mg/l)	Epilimnion	0.92	0.31–1.74
	Hypolimnion	1.15	0.27–3.25
NO_3^--N (mg/l)	Epilimnion	0.044	0.002–0.237
	Hypolimnion	0.066	0.002–0.312
NO_2^--N (mg/l)	Epilimnion	0.009	0.003–0.055
	Hypolimnion	0.037	0.003–0.155
NH_4^+-N (mg/l)	Epilimnion	0.141	0.008–1.000
	Hypolimnion	0.382	0.008–1.190
SiO_2 (mg/l) *)	Whole lake	50.2	31.7–82.5
TOC (mg/l)	Whole lake	3.8	0.03–35.2
BSB_5 (mg/l)	Whole lake	3.9	0.3 –10.0
O_2 (mg/l)	Epilimnion	6.6	2.6–10.6
	Hypolimnion	4.2	< 0.9–7.4
O_2 saturation (%)	Epilimnion	97.8	38–157
	Hypolimnion	61.6	< 12–107

*) Data of 1998.

Limiting factors of bioproduction

Experiments were carried out in four epilimnic enclosures to determine the limiting factors of primary bioproduction by analyzing the impact of deep diurnal mixing, UV radiation, and increased P and N concentrations. The lake's natural phytoplankton development was used as a control. Enclosure A (Fig. 10) was not manipulated, but was closed off like the ones at 7 m to exclude deep diurnal mixing processes and sedimentation losses. The number of phytoplankton cells in this enclosure was significantly higher than observed during the lake's natural phytoplankton development. The species composition did not differ significantly. During the first 9 days of exposure, dominate species were *Pediastrun boryanum*, *Trachelomonas volvocina* and *Aulacoseira granulata*. In Lago San Pablo cell density amounted about 720–1,230 cells per ml, while in the enclosure A, cell number increased to 14,450 n/ml. Additional a population of *Chlamydomonas* spec. occurred after 9 days in the enclosure A with a high biomass (68,000 cells/ml).

No inhibitory effect of UV radiation was observed (Fig. 10, enclosure B), and phytoplankton development was similar to that in enclosure A. The addition of P and N (enclosures C and D, respectively) also did not stimulate an increase in phytoplankton biomass during the first 7 days of exposure compared to enclosure A. Later an increase of the Chl *a* was registered in the enclosure D (supplemented to 0.17 mg/l NO_3-N), which demonstrates the supplemental limiting effect of N. Consequently diurnal mixing processes are the main limiting factor, and nitrogen serves as a second factor. These results were confirmed in a second run of experiments.

Changes in the limiting process were observed in further enclosure experiments carried out under different climate conditions. In April, no nitrogen was detectable in the epilimnic zone, and an enclosure experiment demonstrated that nitrogen was the main limiting factor. These results were also confirmed by a second run of experiments. Thus, primary bioproduction at Lago San Pablo is subject to multifactorial regulation. It is limited by light on account of deep diurnal mixing as well as by nutrients, i.e., nitrogen. It seems that the light deficit is more significant because nutrients are normally available in the epilimnic zone, and the occurrence of cyanobacteria is subdominant.

Discussion

Limnological processes in tropical high mountain lakes differ from the well-known processes that occur in lakes of temperate zones (LÖFFLER 1964; LEWIS 1987). Only few tropical high mountain lakes have been investigated so far, and many of those studied were shallow lakes. To the authors' knowledge, no comprehensive, long-time ecosystem study of a deep tropical high mountain lake

Table 3. Phytoplankton of Lago San Pablo (data from 1998 and 1999, mass classification: isolated < 5 n/ml; little = 5–50 n/ml; moderate = 50–500 n/ml; frequent = 500 –5,000 n/ml; masses = > 5,000 n/ml).

Species	Constancy	Abundance
Cyanophyceae		
Microcystis aeruginosa KÜTZING 1833	discontinuous	moderate
Cryptophyceae		
Cryptomonas ovata EHRENBERG	discontinuous	moderate
Cryptomonas sp. EHRENBERG 1838	discontinuous	little
Chroomonas acuta HANSGIRG 1895	discontinuous	little
Euglenophyceae		
Euglena sp. EHRENBERG 1830		isolated
Trachelomonas volvocina EHRENBERG 1833	discontinuous	frequent
Chlorococcales		
Scenedesmus linearis KOM. 1974	continuous	masses
Ankyra judayi (G. M. SMITH) FOTT 1957		little
Pediastrum boryanum var. *boryanum* (TURP.) MENEGH.	discontinuous	frequent
Lagerheimia sp. CHODAT 1895	discontinuous	little
Oocystis marssonii LEMM. 1898	discontinuous	little
Oocystis naegelii A. BR. 1855		isolated
Nephrocytium schilleri (KAMM.) COMAS 1980		isolated
Neglectella sp. VODENICAROV & BENDERLIEV 1971	discontinuous	little
Planktosphaeria gelatinosa G. M. SMITH 1918	discontinuous	little
Sphaerocystis schroeteri CHOD. 1897	discontinuous	little
Golenkinia radiata CHOD. 1894		isolated
Monoraphidium komarkovae KOMARKOVA-LEGNEROVA 1969		isolated
Lagerheimia sp. CHOD. 1895	discontinuous	little
Elakatothrix gelatinosa (SNOW) PRINTZ sensu SKUJA 1948	discontinuous	little
Coelastrum microporum NÄG. in A. BR. 1855	discontinuous	isolated
C. pseudomicroporum	discontinuous	isolated
Peridiniales		
Peridinium sp. EHRENBERG 1838		isolated
Gymnodinium sp. STEIN 1878		isolated
Conjugatophyceae		
Cosmarium sp. CORDA ex RALFS 1848		isolated
Diatomeae		
Aulacoseira granulata (EHRENBERG) SIMONSEN 1979	continuous	frequent
Fragilaria ulna (NITZSCH) LANGE-BERTALOT 1980		isolated
Nitzschia sp. HASSALL 1845 nom. cons.		isolated
Cocconeis sp. EHRENBERG 1838		isolated
Cymbella sp. AGARDH 1830		isolated
Gyrosigma sp. HASSAL 1843		isolated

has been performed before now (OSBORNE 1995; TUDORANCEA et al. 1999; LEHMUSLUOTO et al. 1999; ROLDÁN & RUIZ 2001).

Deep tropical lakes may exhibit a stable thermal stratification, as was observed at Lago San Pablo and in other types of lakes. Stratification stability is determined by the altitude and local climate (mainly wind intensity, air temperature and solar radiation). The general circulation pattern (mono-, di- or polymictic) cannot be predicted. Nonetheless, a small vertical temperature gradient of

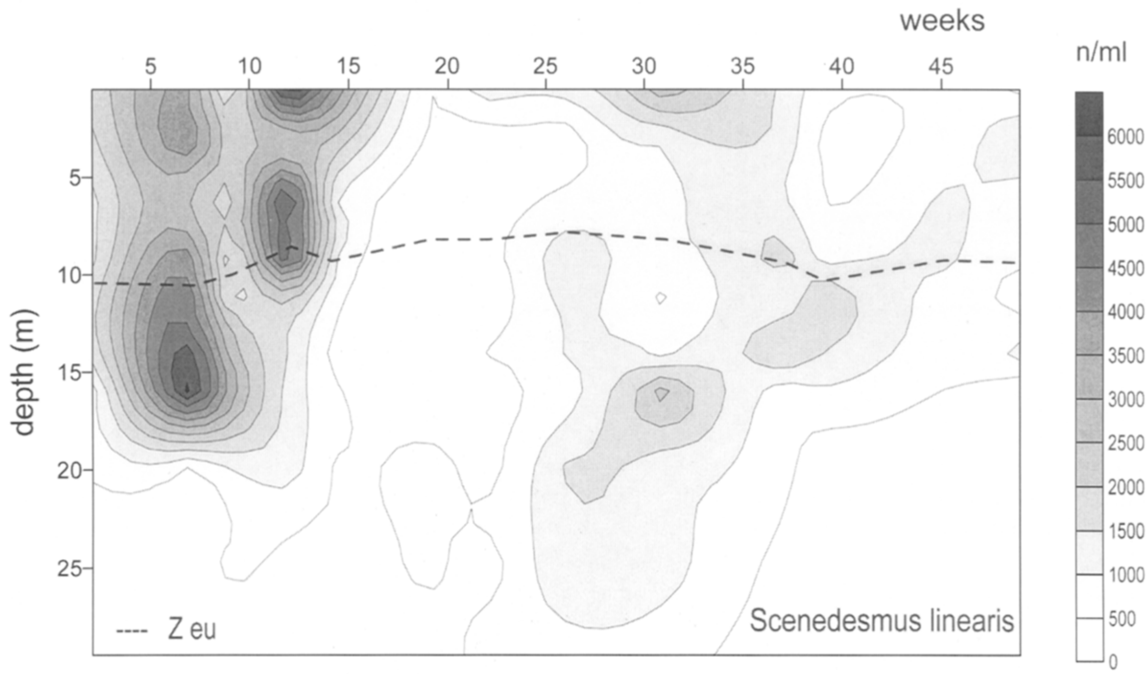

Fig. 8. Abundance of *Scenedesmus linearis* in Lago San Pablo, given is the compensation depth Z_{eu} calculated by 5 $\sqrt{Z_{sd}}$ according to TILZER (1988). Phytoplankton sampling was done in 1999 every month at 0.5, 3, 6, 9, 11, 14, 16, 20, 25 and 29.5 m depth, the calculation of the isopleths was done with Surfer.

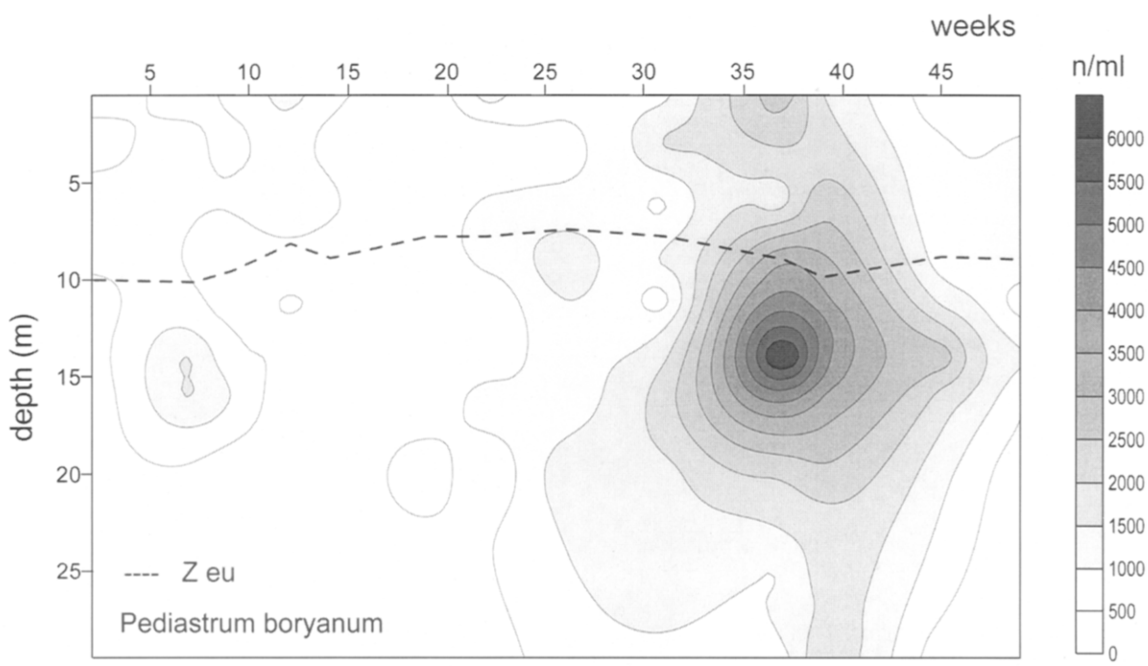

Fig. 9. Abundance of *Pediastrum boryanum* in Lago San Pablo, given is the compensation depth Z_{eu} calculated by 5 $\sqrt{Z_{sd}}$ according to TILZER (1988). Phytoplankton sampling was done in 1999 every month at 0.5, 3, 6, 9, 11, 14, 16, 20, 25 and 29.5 m depth, the calculation of the isopleths was done with Surfer.

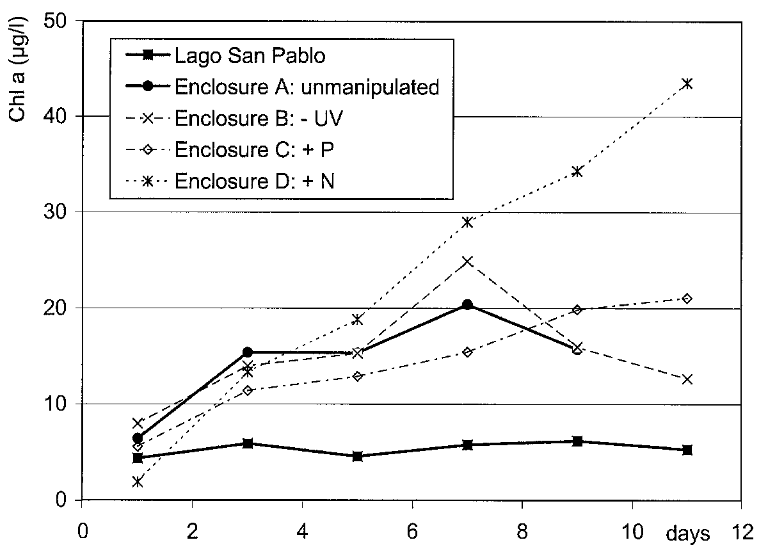

Fig. 10. Enclosure experiments at Lago San Pablo performed in August/September 2000 to determine limiting factors of phytoplankton development. The enclosure was 0.9 m in diameter and 7.0 m in height. A = Lago San Pablo as a control, B: unmanipulated enclosure, C = enclosure with UV protection, D = enclosure supplemented to 0.12 mg/l SRP, E: enclosure supplemented to 0.17 mg/l NO_3-N.

only a few degrees can cause a stable thermal stratification (LEWIS 1983). The persistence and dynamics of the thermal stratification must be monitored continuously 24 hours a day in order to recognize short-term mixing processes during the night. Diurnal mixing due to wind effects and to heat transfer to the atmosphere is a well-known process (IMBERGER 1985) that is typical of tropical lakes because the water temperature often raises the air temperature during the night. Convective currents create polymictic conditions in shallow tropical lakes, but in deep thermal stratified lakes like Lago San Pablo, the mixing process is short-term and extends down into the hypolimnic zone. After a few days of mixing, the epilimnic zone becomes deeper than the euphotic zone.

This process was first observed in Ethiopian crater lakes (TALLING 1969; WOOD et al. 1976, 1984) and described as *atelomixis* but, unfortunately, no investigations on water chemistry or plankton development were carried out. A similar stratification pattern was observed at some tropical lakes (LEWIS 1983; GÖCKE 1997) as well as at Lago San Pablo, which generally exhibits a monomictic circulation period, while atelomixis occurs during stratification periods, depending on the weather conditions.

Atelomixis is of great significance for primary production: A light deficit occurs because the epilimnic zone extends to the euphotic zone. Apart from inhibition of algae development due to the light deficit, increased losses of phytoplankton cells through sedimentation must also be assumed. During the daytime, algae cells develop in the euphotic zone and are transported by convective currents to the aphotic zone. There, they are subjected to sedimentation processes, and only some of the cells return to the euphotic zone during the next partial mixing period.

At Lago San Pablo, the consequence of this limitation principle is clearly recognizable: The high nutrient level leads to only moderate phytoplankton development. Nonetheless, the lake exhibits intensive macrophyte development in the littoral zone (KIERSCH et al. 2002), demonstrating a high production potential. The lack of oxygen in the hypolimnion as well as the high sedimentation rate of 0.6 cm/year (GUNKEL 2002) confirms that there is a high production level with increased sedimentation of plankton algae and/or macrophytes. Without a doubt, atelomixis cannot gain significance as a limiting factor of primary production unless sufficient supplies of nutrients (i.e., P and N) are available.

We did not observe an effect of high UV radiation input on primary production, and self-protecting mechanisms like MAA's (mycosporine-like amino acids) and PPC (photoprotective carotinoids) seem to be adequately effective. However, some researchers obtained contradictory results (KINZIE et al. 1998).

Further investigations seem necessary to verify the present findings based on data obtained in other high Andean lakes as well as in tropical high mountain lakes in Africa and Asia.

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References

CASALLAS, J. & GUNKEL, G. (2002): Algunos aspectos limnologicos de un lago altoandino: El Lago San Pablo, Ecuador. Limnetica (accepted).

EPA (1995): Batimetria del Lago San Pablo. Mapa 1 : 5000. Escuela Politecnica Nacional, Unidad de Ingenierria Ambiental. Quito, Ecuador.

GOECKE, K. (1997): Basic morphometric and limnological properties of Laguna Hule, a caldera lake in Costa Rica. Revista de Biologia Tropical **44–45**: 537–548.

GOPAL, B. & WETZEL, R. G. (eds.) (1995): Limnology in developing countries. Vol. 1. Internat. Association for Limnology, Intern. Scientific Publ., New Delhi.

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

– (2002): Limnología de un Lago Tropical de Alta Montaña, Lago San Pablo-Ecuador: Caraterísticas de los sedimentos y tasa de sedimentatción. Revista de Biología Tropical (accepted).

– & CASALLAS, J. (2002): Limnology of an equatorial high mountain lake, Lago San Pablo, Ecuador: Limitation of lake productivity by deep diurnal mixing. Proc. Int. Ass. Theoret. Applied Limnol. **28** (accepted).

IDSO, S. B. (1973): On the concept of lake stability. Limnol. Oceanogr. **18**: 681–683.

IMBERGER, J. (1985): The diurnal mixed layer. Limnol. Oceanogr. **30**: 737–770.

KIERSCH, D., MÜHLECK, R. & GUNKEL, G. (2002): Las macrofitas de algunos lagos altoandinos del Ecuador y su posible utilizazion como bioindicatores de eutrofizacion. Revista de Biologia Tropical (accepted).

KINZIE, R. A. III, BANASZAK, A. T. & LESSER, M. P. (1998): Effects of ultraviolet radiation on primary productivity in a high altitude tropical lake. Hydrobiologia **385**: 23–32.

KOSTE, W. & BÖTTGER, K. (1989): Rotatorien aus Gewässern Ecuadors. Amazoniana **10**: 407–438.

– & BÖTTGER, K. (1992): Rotatorien aus Gewässern Ecuadors II. Amazoniana **12**: 263 – 303.

LEHMUSLUOTO, P., MACHBUB, B., TERANGNA, N., ACHMAD, F. BOER, L., BRAHMANA, S. S., SETIADJI, B., PRIADIE, B.TIMOTIUS, K. H. & GOELTENBOTH, F. (1999): Limnology in Indonesia – From the legacy of the past to the prospects for the future. In: R. G. WETZEL & B. GOPAL (eds.), Limnology in developing countries. Vol. **2**, pp. 119–234. Internat. Association for Limnology, Intern. Scientific Publ., New Dehli.

LEWIS, W. M. (1973): The thermal regime of Lake Lanao and its theoretical implications for tropical lakes. Limnol. Oceanography **18**: 200–217.

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

– (2000): Basis for the protection and management of tropical lakes. Lakes & Reservoirs: Research and Management **5**, pp. 35–48.

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

– (1964): The limnology of tropical high-mountain lakes. Verh. Internat. Verein. Limnol. **15**: 176–193.

OSBORNE, P. L. (1995): Limnology in the wet tropics: Papua New Guinea. In: B. GOPAL & R. G. WETZEL (eds.), Limnology in developing countries. Vol. 1, pp. 121–160. Internat. Association for Limnology, Intern. Scientific Publ., New Dehli.

ROLDÁN, G. (1992): Fundamentos de limnología neotropical. Universidad de Antioquia. 529 pp.

– & RUIZ, E. (2001): Development of limnology in Colombia. In: R. G. WETZEL & B. GOPAL (eds.), Limnology in developing countries. Vol. 3, pp. 69 - 119. Internat. Association for Limnology, Intern. Scientific Publ., New Dehli.

ROTT, E. (1981): Ein Beitrag zur Algenflora andiner Hochlandseen Ecuadors (Südamerika). Ber. nat.-med. Ver. Innsbruck **68**: 13–29.

TALLING, J. F. (1969): The incidence of vertical mixing, and some biological and chemical consequences, in tropical African lakes. Verh. Internat. Verein. Limnol. **17**: 998–1012.

TILZER, M. M. (1988): Secchi disk – chlorophyll relationships in a lake with highly variable phytoplankton biomass. Hydrobiologia **162**: 163–171.

TUDORANCEA, C., MARIAM, Z. G. & DADEBO, E. (1999): Limnology in Ethiopia. In: R. G. WETZEL & B. GOPAL (eds.), Limnology in developing countries. Vol. 2, pp. 63–118. Internat. Association for Limnology, Intern. Scientific Publ., New Dehli.

WETZEL, R. G. & GOPAL, B. (eds.) (1999): Limnology in developing Countries. Vol. 2. Internat. Association for Limnology, Intern. Scientific Publ., New Delhi.

WOOD, R. B., BAXTER, R. M. & PROSSER, M. V. (1984): Seasonal and comparative aspects of chemical stratification in some tropical crater lakes in Ethiopia. Freshwater Biology **14**: 551–574.

– PROSSER, M. V. & BAXTER, R. M. (1976): The seasonal pattern of thermal characteristics of four of the Bishoftu crater lakes, Ethiopia. Freshwater Biology **6**: 519–530.

ZEVALLOS, O. (1992): Situacion ambiental de Lago San Pablo, principales factores que la determinan. Report al ministerio, Quito, Ecuador.