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Limnology of Botos Lake, a tropical crater lake in Costa Rica

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Abstract: Botos Lake, located at the Poas Volcano complex (Costa Rica) was sampled eight times from 1994 to 1996 for physicochemical conditions of the water column and phytoplanktonic community composition. Depth was measured at fixed intervals in several transects across the lake to determine its main morphometric characteristics. The lake has an outlet to the north. It is located 2580 m above sea level and is shallow, with a mean depth of 1.8 m and a relative depth of 2.42 (surface area 10.33 ha, estimated volume 47.3 hm^3). The lake showed an isothermal water column in all occasions, but it heats and cools completely according to weather fluctuations. Water transparency reached the bottom on most occasions (> 9 m). The results support the idea that the lake is polymictic and oligotrophic. The lake has at least 23 species of planktonic algae, but it was always dominated by dinoflagellates, especially *Peridinium inconspicuum*. The shore line is populated by a sparse population of *Isoetes* sp. and *Eleocharis* sp. mainly in the northern shore where the bottom has a gentle slope and the forest does not reach the shore.

Key words: Crater lake, limnology, neotropics, temporal variation, plankton, *Peridinium inconspicuum.*

There is little information for tropical crater lakes in the neotropics. These lakes are usually at high elevation, with low temperatures and diluted soft waters as a result of their small watersheds that comprise only the crater itself (Löffler 1972). Among their limnological characteristics of interest is their mixing pattern, which affects the rest of the parameters of the lake, such as its oxygenation and water chemistry and the phytoplanktonic community composition among others (Roldán 1992).

Tropical lakes are thought as permanently stratified due to low seasonal variation in temperature. Nevertheless Hutchinson and Löffler (1957) had already put forward a model that considered altitude as another important factor in tropical lakes, and proposed that high elevation lakes were polymictic. Most reports (e.g. Banderas *et al.* 1991) on the circulation pattern of high altitude tropical lakes conclude that such lakes are polymictic. However, considerable variation due to differences in depth, shape (Baxter *et al.* 1965) and location of the lake (Zutshi 1991) have been observed. Recently Lewis (1987) has proposed a modification of their model and included lake morphometry as another important factor, specially depth. For Lewis lakes less than 10 m deep are polymictic regardless of their altitude. In other lakes in Costa Rica it has been observed that although morphometry as well as altitude are important in determining a lake's mixing pattern, the actual influence of both factors is not as simple as proposed in the models mentioned above (Gocke *et al.* 1981, Umaña *et al.* 1999).

Botos Lake is located within Poas Volcano

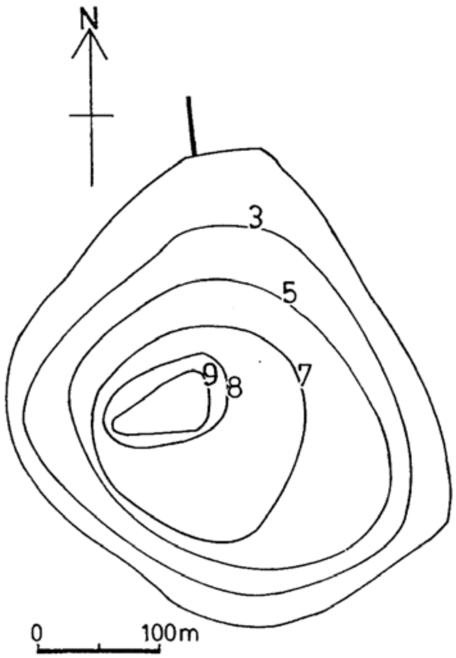

Fig. 1. Botos Lake, depth contours in meters.

complex, at 10º11'18" lat. N and 84º13'30" long. W. It occupies an extinct wide crater named "Cono Botos" (Alvarado 2000) at an altitude of 2580 m above sea level, and it is approximately 7 540 years old (Prosser 1986). It has a surface area of 10.33 ha, and drains through Angel River. The forest around the lake is classified as Tropical/Subtropical Rainy-Cloud Forest with paramo vegetation according to Gómez (1986). The climate is characterized as very wet and cold, with a short dry season (Herrera 1986).

According to previous studies, the temperature fluctuates between 7 and 14ºC (Pittier 1890, Brenes 1932, Vargas 1979). The lake is acidic, with pH values ranging between 4.39 (Horn & Haberyan 1993) and 6.5 (Hargraves & Víquez 1981). It has a low alkalinity (<0.4 meq/l) mainly as a result of free carbon dioxide in the water. Hardness is also low (9.16 meq/l). Löffler (1972) reported high visibility values (>8m) and Horn & Haberyan (1993) measured Secchi values of 6.3 m, which makes of this lake one of the clearest lakes in Costa Rica.

The phytoplankton has been studied by Hargraves & Víquez (1981), who reported a high predominance by the dinoflagellate *Peridinium incospicuum* (86%) and *P. volzii* (10%), their list of eleven species includes mostly benthic species detached from the shores. The limnology of Botos Lake is examined here as a contribution to the knowledge of the limnology of small neotropical lakes.

MATERIALS AND METHODS

The lake was visited on eight occasions within a two year period, between 1994 and 1996 (Listed in Table 1). During each visit measurements of temperature and dissolved oxygen profiles were made with an YSI (model 57) oxygen meter. Water transparency was determined with a Secchi disk. Water samples from different depths were taken for measurements of pH and alkalinity at the site and for nutrient analysis (Nitrate, Nitrite, Phosphate and Silica) at CIMAR's laboratories according to standard methodologies (Strickland & Parsons 1972). Depth soundings were carried using a weighted line following several transects across the lake in order to determine its volume and morphometric characteristics.

For the phytoplankton two aliquots of 100 ml were taken in each visit and fixed with Lugol's solution for later counting according to Ütermohl technique (Lund *et al.* 1959). Identification of the planktonic algae were made to the lowest level possible with the literature available (West & West 1904, West & West 1905, West & West 1908, West & West 1912, West & West 1923, Prescott 1962, Huber-Pestalozzi 1968, Whitford & Schumacher 1973 Ková ik 1975, Comas González & Permán 1978, Comas González 1980, Parra *et al.* 1981, Komárek 1983, Komárek & Anagnostidis 1986, Krammer & Lange-Bertalot 1986, Anagnostidis & Komárek 1988, Krammer & Lange-Bertalot 1988, Komárek & Anagnostidis 1989, Anagnostidis & Komárek 1990, Krammer & Lange-Bertalot 1991a, Krammer & Lange-Bertalot 1991b, González González & Mora-Osejo 1996). Individual cells, filaments or colonies were counted following four transects close to the main diameter of the counting chamber. Most frequent species were counted until a count of 100 units were recorded, at this point the length of the transects needed to complete the count were recorded and less abundant species were further counted until the four transects were finished. All counts were transformed to densities in units per milliliter.

Samples for chlorophyll determinations were also taken, filtered through glass fiber filters and extracted in 90% acetone. Chlorophyll *a* was determined using the SCOR/UNESCO's tri-chromatic method (Strickland & Parsons 1972).

RESULTS

Botos Lake has a maximum depth of 9 m. It has a shallow character (Z_r=2.42) occupying a wide depression with gentle sloping shores (Fig. 1). Its volume is estimated as 4.73×10^5 m^3, which gives a mean depth of 1.80 m.

The water column was isothermal in all our visits to the lake, however the temperature was higher in July and August samplings, and lower in the other dates (Fig. 2A). In a few cases a small temperature gradient was observed near the surface. As a result of this homeothermal conditions, the lake was well-oxygenated down to the bottom in all visits (Fig. 2B).

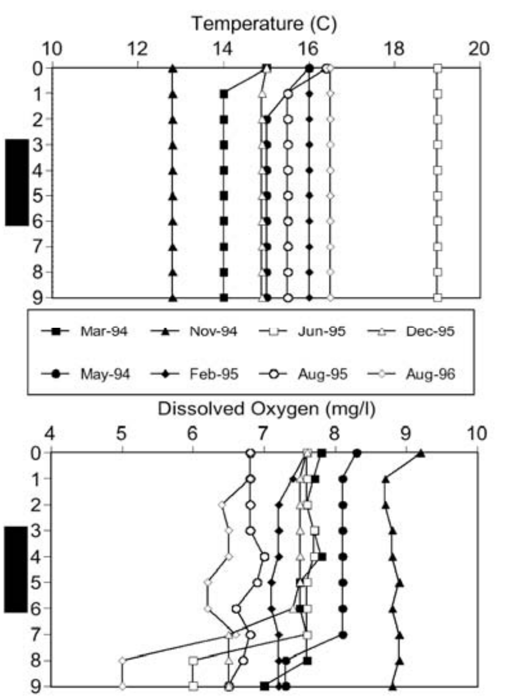

Fig. 2. A) Temperature B) Dissolved oxygen isoclines at Botos Lake.

The pH remained in a narrow range between 4.5 and 6 (Fig. 3A), although changes involved the whole water column. The lake had a high transparency, with Secchi depth

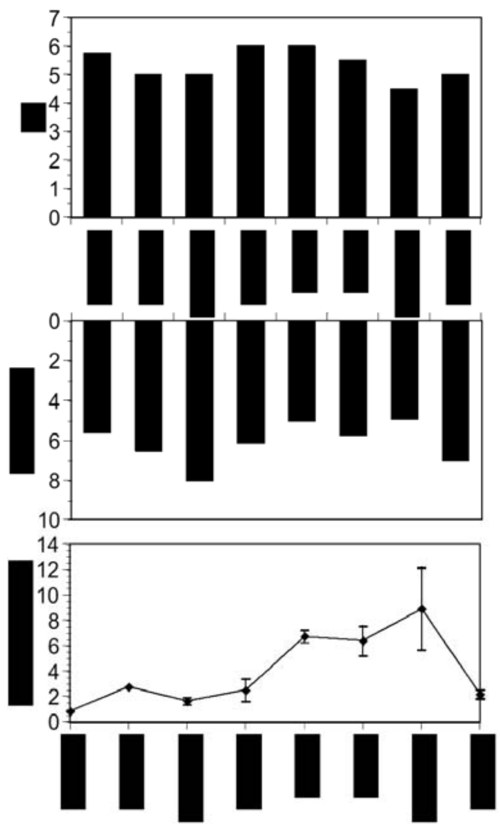

Fig. 3. Variation of: A) pH B) Secchi depths C) Chlorophyll a, with time at Botos Lake.

ranging between 5 and 8 m (Fig 3B) and with low chlorophyll values all the year round (Fig. 3C). The chlorophyll variation among dates was significant ($F_{7,8}$= 0.80, α<0.01), with values being higher in 1995 samples than in the rest of the sampling dates.

Soluble Reactive Phosphorus (SRP) reached values of 23.25 µg $P\text{-}PO_4 \cdot l^{-1}$, however it also showed values below the detection limit, with a mean of 13.75 ± 6.38 µg $P\text{-}PO_4 \cdot l^{-1}$. SRP was

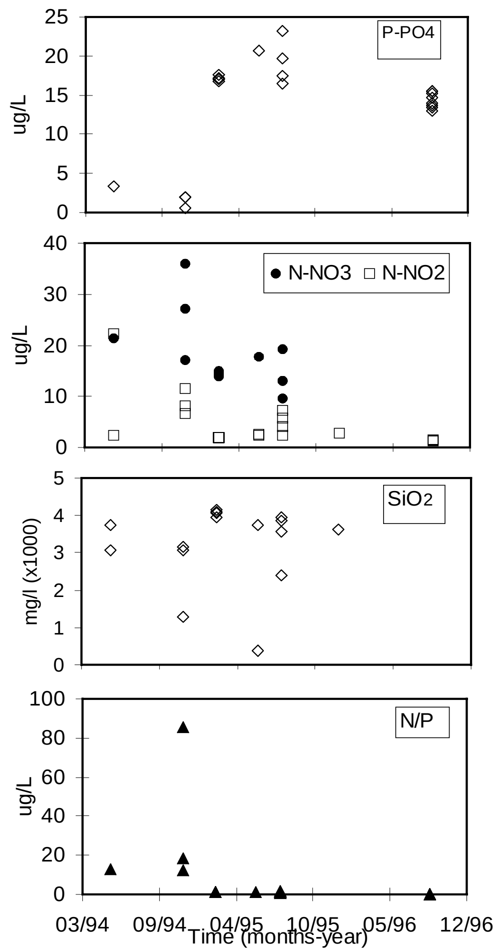

Fig. 4. Variation of the nutrients: A) Phosphate B) Nitrate and Nitrite C) Silicate D) N/P ratios, at Botos Lake.

higher in 1995 and 1996 samples ($F_{5,15}$= 64.68, α<0.01) (Fig. 4A). Nitrate-nitrogen varied between 9.65 and 35.95 µg $N\text{-}NO_3 \cdot l^{-1}$, with a mean of 17.86 ± 7.02 µg $N\text{-}NO_3 \cdot l^{-1}$; differences among sampling dates were not significant ($F_{4,8}$= 3.29, α>0.05). Nitrites were low, between 1.27 and 22.35 µg $N\text{-}NO_2 \cdot l^{-1}$ with a mean of 4.09 ± 4.71 µg $N\text{-}NO_2 \cdot l^{-1}$, but showed significant differences among sampling dates ($F_{6,17}$= 3.60, α<0.05). Nitrogen species were lower in 1995 than in 1994 (Fig 4B). Silica was enriched with values varying between 389.9 and 4138 mg $Si\text{-}SiO_2 \cdot l^{-1}$, with a mean of 3258.8 ± 1069 mg $Si\text{-}SiO_2 \cdot l^{-1}$. This element did not show any pattern of variation among dates ($F_{5,15}$= 1.53, α>0.05) (Fig. 4C). The N/P ratio (as the sum of NO_3+NO_2 divided by the SRP) was above the theoretical Redfield Ratio of 7 in 1994, but remained below the Redfield Ratio in 1995 (Fig. 4D), the differences among dates were significant ($F_{5,15}$= 3.49, α<0.05). Although ammonia was not measured as a result of technical problems at the laboratory, it should be scarce due to high oxygenation of the water.

A total of 23 species of microalgae were observed (Table 1), but only a few species were ever dominant, with more than 90% of the abundance in most cases. The dominant groups were Dinophyceae (between 49.7 to 81.7%) and Cyanophyta (from 15.5 to 42.9%) (Fig.5). Dominant species were the same in all sampling dates, these include the dinoflagellate *Peridinium incospicuum* which was always the most abundant species with a mean density of 4.0x10^5 cells/l. It almost had

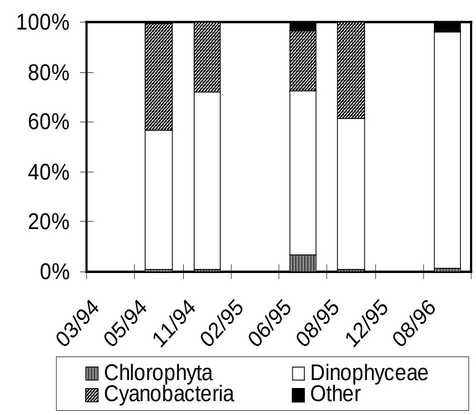

Fig. 5. Temporal variation of relative abundance of the phytoplankton in Botos Lake.

significant differences among dates ($F_{4,4}$= 6.00, α= 0.0554) with the highest values in November 94 and the lowest in August 1995. The second most abundant species was the blue-green algae *Limnothrix* sp. It attained a mean density of 1.6x10^5 cells/l and showed significant differ-ences among dates ($F_{4,4}$= 8.81, α<0.05) with lower values in August 1995 and August 1996. The green alga *Arthrodesmus octocornis* also reached high percentages in November 1994 (Fig. 6).

TABLE 1

List of phytoplanktonic species in the samples from Botos Lake

Taxonomic Group	**Species name**	**Average**	**Maximum**	**Minimum**	**Frequency**
Chlorophyta	*Arthrodesmus incus*	495,1	3709,2	0,0	2
	Arthrodesmus octocornis	13375,4	101031,3	0,0	7
	Chlamydomonas sp. 2	165,3	1487,8	0,0	1
	Closterium sp.	82,5	742,9	0,0	1
	Cosmarium moniliforme	330,2	1487,8	0,0	2
	Cosmarium sp. 1	1158,9	6704,6	0,0	3
	Cylindrocystis crassa	82,7	743,9	0,0	1
	Penium sp.*	0,0	0,0	0,0	0
	Scenedesmus sp.	332,0	2988,2	0,0	1
Euglenophyta	cf. *Colacium* sp.	246,9	2222,4	0,0	1
Dinophyceae	*Cystodinium* sp.	164,7	741,8	0,0	2
	Peridinium volzii	329,6	1483,7	0,0	3
	Peridinium inconspicuum	403155,0	665986,2	189003,8	9
	Glenodinium sp.*	0,0	0,0	0,0	0
Cryptophyta	*Cryptomonas* sp.	329,9	1483,7	0,0	3
Bacillariophyceae	*Aulacoseira* cf. *islandica*	164,9	1483,7	0,0	1
	Cyclotella sp.	1488,0	9657,4	0,0	3
	Frustulia sp.*	0,0	0,0	0,0	0
	Navicula sp.	248,8	1494,1	0,0	2
Cyanobacteria	*Anabaena* sp.	166,0	1494,1	0,0	1
	Limnothrix sp.	165617,0	308916,9	0,0	8
Unidentified	Undetermined No.1	2563,0	14114,7	0,0	2
	Undetermined No. 2	4372,7	22255,2	0,0	5

Average, maximum and minimum abundance expressed as number of units per liter, and frequency of appearance in the samples for each species. (*) These species were seen during previous scanning of the settled samples but did not appear in the actual counts.

Total abundance fluctuated between $3x10^5$ and $10x10^5$ individuals per liter (Fig. 7A), with a mean of $5.9x10^5 \pm 2.1x10^5$. The higher values occurred by the end of 1994, but the differences were not significant ($F_{4,4}$= 3.79, α>0.05).The Shannon-Weaver index of diversity varied between 0.2 and 1.2, with a mean of 0.66 ± 0.28, being lower in 1996 than in the previous years (Fig. 7B), but the differences among dates were not significant ($F_{4,4}$= 2.11, α>0.05).The number of species per sampling remained constant between 5 and 8 species (Fig. 7C) although there were significant differences among dates ($F_{4,4}$= 7.15, α<0.05) due to low variability within samples of the same date.

The vertical distribution of the nutrients was examined on two different dates. It showed some differences between February and August 1995 (Fig. 8). During February the vertical distribution was quite uniform; however, there were small variations which show that even though the water column was isothermal, the lake was actually not mixing actively at the moment of sampling, as can be observed from the temperature and dissolved oxygen profiles (Fig. 2). This layering, although weak, combined with the differing metabolism of plankton (due

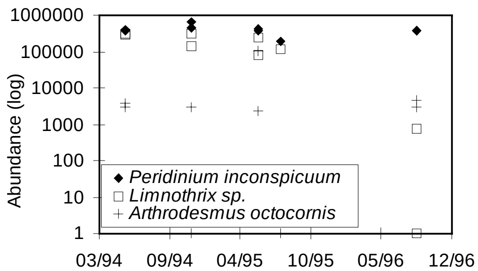

Fig. 6. Temporal variation in the abundance of selected species in Botos Lake.

to the light gradient) produce the observed vertical variations. Most nutrients declined at the surface in August 1995 except for phosphate, whose surface maximum is difficult to explain. Depth distribution of chlorophyll *a* was examined in three occasions. It also showed differences among dates, even between samplings at the same month one year later (Fig. 9). In August 1996 the differences in chlorophyll *a* among depths were significant ($F_{3,4}$= 7.5181, α<0.05).

DISCUSSION

Although the lake's water column remained isothermal in all visits, there was a temperature shift. Temperature variation however involved the whole water column, and the lake did not develop a thermocline, apart from a few cases where a small thermal gradient was observed in the top two meters. The reason for this lies in its shallowness and wide open basin where it is located, which allows its exposure to the winds, that can mix the whole lake easily. As a result, the water column was well-oxygenated in all our visits, with a couple of cases when there was a sharp decline of ca. 2 mg $O_2 \cdot l^{-1}$ in dissolved oxygen near the bottom. The lake should be classified as polymictic lake, which corresponds to what is expected from high altitude lakes (Löffler 1972, Haberyan *et al.* 1995). Lewis (1987) proposed a classification of the lakes according to the frequency of their mixing, which depends more on the lake morphology than in its geographical location. According to Lewis, lakes that are 3 to 10 m deep should be discontinuously polymictic. Botos Lake falls in this category. The few instances when a small decline in temperature was observed close to the surface were probably sporadic and were easily eroded away at night. The vertical distribution of the nutrients examined on two different dates showed that there can be some differences down the water column at certain dates. The profiles in February were quite homogeneous, but in August 1995 there were differences between samples taken at different depths even though the water column was isothermal. This is an indication that the lake was actually not mixing actively at the moment of sampling. This layering, although weak, can be the result of differences in plankton metabolism at different depth due

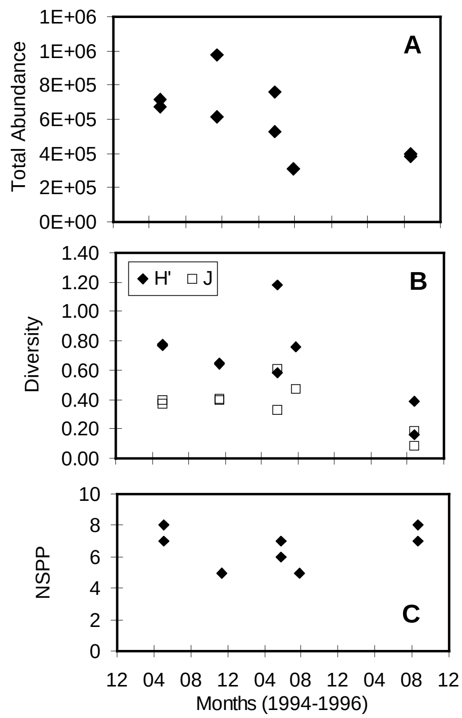

Fig. 7. Temporal variation in the total abundance (A), diversity indices (B) and number of species (C) in Botos Lake.

to the light gradient that are omnipresent in all lakes (Wetzel 1975). It is possible that this kind of vertical variation in the organism's activity in the lake, produces small gradients in the water column during less windy periods. These vertical gradients should erode during

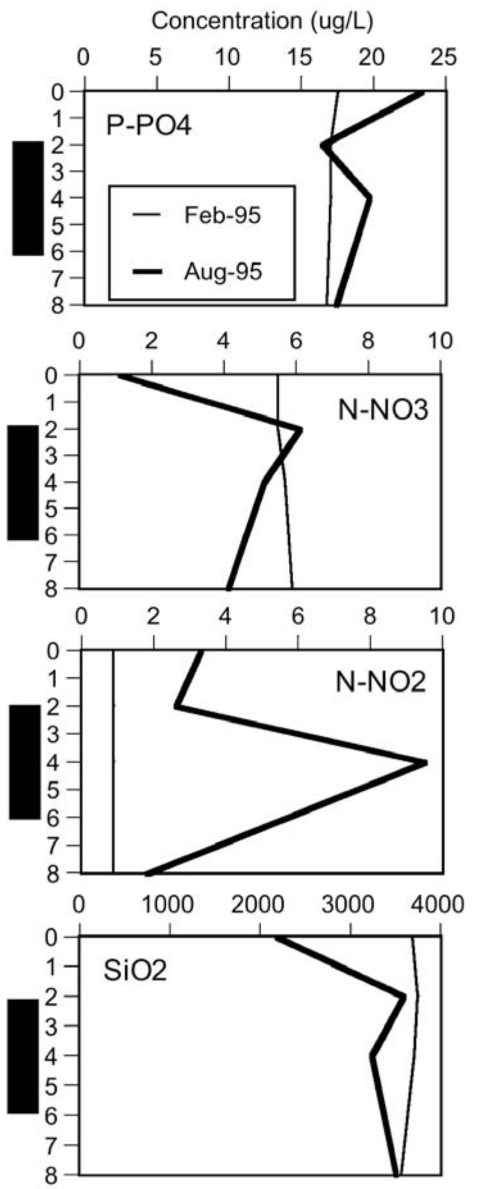

Fig. 8. Nutrient vertical profiles at two different dates (Feb. 1995 and August 1995) in Botos lake.

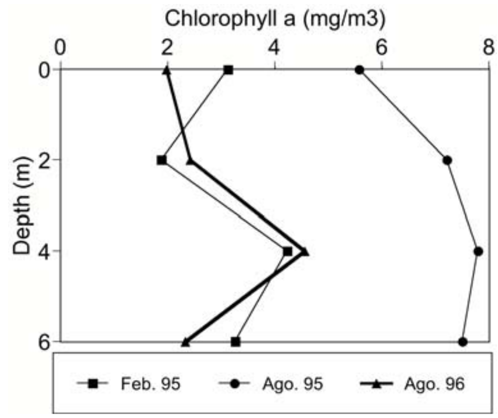

Fig. 9. Depth distribution of chlorophyll a at different dates in Botos Lake.

the night since only frequent mixing events can explain the distribution of heat in the water column.

Nutrient levels were low in the lake, specially the nitrates. The low levels of nutrients are in agreement with other results from high mountain lakes, specially those located within a crater (Löffler 1972) which are supposed to have diluted waters. Nevertheless, orthophosphate levels were not equally low, and the low values of the N/P ratio can be interpreted as an indication that nitrogen is more acutely scarce in the lake than phosphorus is. Although ammonia was not measured, its level should be low due to the oxygenation of the water column, as has been reported in the literature (Wetzel 1975). This needs to be addressed with more specific studies on the subject in the future. Some studies on ground waters that surface at sites on the down slopes of the volcanoes at the Cordillera Volcánica Central show high phosphorus levels associated to the volcanic activity in the zone (Pringle *et al.* 1990, 1993). This fact supports the relatively high concentration of phosphate in Botos Lake.

The lake can be classified as oligotrophic. The levels of nutrients fall below or at the limit between oligotrophic and mesotrophic lakes (Lampert & Sommer 1997). Its high water transparency and low chlorophyll values also indicate oligotrophic conditions, although the total density of the phytoplankton, on the order of 10^5 cells per milliliter, is in the range of eutrophic lakes according to Margalef (1980). This apparent contradiction can be explained by the composition of the phytoplankton, which is dominated by a dinoflagellate. This species is a slow growing species classified as a K strategist in the literature (Reynolds 1984) and may have low chlorophyll concentrations, but accumulates in the water due to slow growth and metabolism. The low values of chlorophyll and nutrients in the water as well as its high water transparency are indicative of low productivity, which agrees with the low temperatures, high acidity, and the predominance of a dinoflagellate in the phyto-plankton.

Even though the data do not allow a detailed analysis of the monthly variability of the nutrient concentration, it is evident that there are periods of higher nutrient concentration. An example of this is the higher phosphate levels in 1995 than in 1994. The nitrate and nitrite showed a reverse pattern of variation between both years, indicating that the inter-annual variation can be higher than seasonal differences. This behavior is common among tropical lakes (Rhode 1974, Richerson *et al.* 1984) and other high mountain lakes (Zutshi 1991), and can be explained by the uniformity of the climate in the location, which has a short dry season (Herrera 1986) and the fact that the lake does not develop a stratification during the year.

The dominance of *P. inconspicuum* has been a constant feature of Botos Lake throughout the study and even before (Hargraves & Víquez 1981). This is a common species in many other lakes that are not as acid as Botos (Haberyan *et al.* 1995). An examination of this and other unpublished data show that the species' abundance increases with altitude. This increase with altitude is more likely influenced by a decrease that has been documented in conductivity and hardness with altitude of the lake. Reynolds (1984) classifies the genus *Peridinium* as a late invader in the seasonal succession in temperate lakes, becoming abundant by late summer when stratification is stronger and nutrient availability is lowest due to uptake by algae during summer. It is also referred to as the dominant tropical dinoflagellate. The stability of environmental conditions in Botos Lake, which does not stratify, but has a mixing depth well within the euphotic zone due to its shallowness and high water transparency, seems to favor these slow-growing species, which has also been classified as a K-strategist (Reynolds 1984). Sommer (1989) indicates that *Peridinium* is usually limited by phosphorus, and includes it with the species that dominate at the climax of phytoplankton succession in lakes. The abundance of phosphorus relative to nitrogen also aids in explaining the dominance of this species in Botos Lake.

Given that the lake did not show any degree of stratification at any sampling date, but it warmed and cooled uniformly, major changes in the phytoplankton composition are not expected. Interannual variations may be more important than the variation along any given year. For instance, along with climatic changes, Poas Volcano was active during the sampling period (1994-1996) which affected the acid rain and sulfur vapors reaching the lake. This phenomenon does not repeat every year, but its magnitude seems to outweigh interannual variations.

RESUMEN

Se visitó regularmente la laguna Botos situada en el macizo volcánico del Poas por un periodo de dos años. Se examinó la variación de las condiciones físico químicas y de las poblaciones del fitoplancton. El lago tuvo una columna de agua isoterma en cada visita, sin embargo se calentó y se enfrío por completo de acuerdo a los cambios climáticos. Los resultados apoyan la idea de que el lago es polimíctico y oligotrófico. En el lago habitan 23 especies de algas planctónicas, pero fue siempre dominado por dinoflagelados, en especial por *Peridinium inconspicuum*.

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