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The planktonic community of Laguna Hule, Costa Rica

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Abstract: Laguna Hule is located in an explosion crater, north of Poas Volcano, Costa Rica, Central America, at an altitude of 740 m. It was sampled four times from August 1990 to June 1991. Steep crater walls surround much of the lake, protecting it from wind action. The hypolimnion was anoxic on all visits, and a steep conductivity curve was always observed. This could mean that the lake is meromictic or at least oligomictic, rarely mixing completely. A shift was observed in the most probable limiting nutrient, corresponding to the seasonality of precipitation. A total of 80 species of algae were observed, most of which were rare. This resulted in high diversity values. Chlorophyta and Cyanobacteria were the dominant groups, with 60% of the species belonging to Chlorophyta. Although chlorophyll *a* values were high, secchi transparencies were also relatively high. Zooplankton was composed of a few species of rotifers (3), cladocerans (5) and one cyclopoid copepod. Most species were small herbivores. *Chaoborus* larvae were extremely abundant. The horned form of *Ceriodaphnia cornuta* was the most abundant, presumably in response to the high abundance of the predatory *Chaoborus* larvae.

Key words: Plankton, lake, tropics, seasonality, community structure.

There are several studies on Costa Rican lakes (Umaña & Paaby 1990), however few, if any, deal with temporal or seasonal variation of their limnological characteristics (*e.g.* Umaña & Collado 1990). Even though seasonal changes in tropical regions are mild, specially in temperature, there is a cyclical fluctuation in climate affecting mainly precipitation and winds (Laporte 1980, Herrera 1985). Lewis (1973) argued that wind is one of the forces driving seasonal changes in tropical lakes. In Costa Rica the shift from the rainy to dry season generally occurs in coincidence with the time of stronger northeast winds and with the period of lower temperatures (Herrera 1985). These fluctuations result in a seasonal pattern of mixing and stratification (Lewis 1984). They may also produce a shift in the chemical environment and nutritional conditions of the lake, which in turn may induce changes in the planktonic community.

This work is a contribution to the limnology of Laguna Hule and to the general limnological knowledge in Costa Rica. The lake was sampled four times in a year to analyze the dynamics of its water column as well as its relationship with the composition of the planktonic community.

MATERIAL AND METHODS

Area description: Laguna Hule is located within a larger basin formed by a maar type explosion of a former crater (Soto & Alvarado 1990), north of Poas Volcano, Costa Rica, Central America (10°17'45" N., 84°12'56" W), 740 m above sea level (Fig. 1). It is part of the volcanic alignment associated to Poas Volcano, with its last piroclastic activity dated in 2730 ± 50 years (Malavassi, Gill & Trimble 1990). The steep walls around the lake are still covered by forest, but beyond the rim of the basin there are coffee plantations and cattle ranges.

The lake receives water from three streams draining northward from Congo Volcano. It has a surface outlet via the Río Hule. Water level

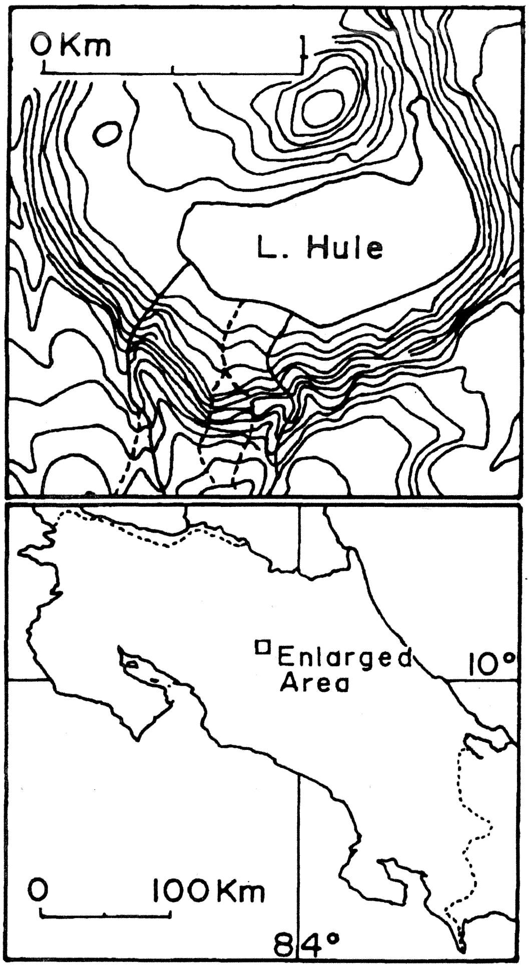

Fig. 1. Laguna Hule and surrounding topography with contours at 20 m intervals, and the lake's location in Costa Rica.

fluctuates annually, and part of the year the surface outflow dries up. The walls of the crater as well as the small subsidiary cone in its center (Bergoeing & Brenes 1978, Alvarado 1989) protect the lake from the northeast winds, which can only blow into the lake through the narrow ravine of the outflow.

The littoral zone is covered by a dense vegetation with the typical littoral zonation of emergents, floating leaved and submerged plants.

Sampling: The lake was visited four times in a year: August and November 1990 and February and June 1991. In 1989 the lake was visited to measure the depth in order to obtain the location of its deepest point and estimate its volume and mean depth.

Samples were always taken from the deepest point of the lake. Secchi depth readings were taken on each visit and depth profiles of temperature, dissolved oxygen (YSI model 57) and conductivity (YSI model 33M S-C-T) were measured. All measurements were performed near noon (10:00 to 13:00 hour). Samples for chlorophyll a, pH, phytoplankton counts and nutrients were taken from three depths, according to the observed water stratification.

Chlorophyll a was measured according to the phaeopigment correction method, after extraction in 90% acetone (Strickland & Parsons 1968). 500 ml of water were filtered for each analysis.

For the nutrient determinations, samples were brought in a cooler to the laboratory and filtered on Whatman GF/C glassfiber filters the same day of collection. They were then stored in a freezer until analyzed within no more than three days. Soluble Reactive Phosphorus was determined by the molibdate blue method (Golterman & Clymo 1969). Nitrite was determined with the sulphanilamide and N-(1-naphtil) etilen-diamine method (Golterman & Clymo 1969). Nitrate was reduced with Cd columns and measured as nitrite. Ammonium was measured with the nitroprussiate method (Strickland & Parsons 1968).

For phytoplankton analysis 100 ml were preserved with Lugol's acetic solution. Samples were taken in duplicate from each depth. Samples were allowed to settle for no less than 48 hours, and the excess water was removed with a 'U' shaped siphon. The remaining volume was further concentrated by centrifugation to a final volume of 1 ml. Aliquots of 0.1 ml were then observed in a Palmer-Malloney counting chamber under 400x magnification.

Algae were counted by units. Units consisted of cells, colonies or filaments, according to each species' morphology. For the counts a variation of the method described by Lewis (1978) was followed. No more the 100 units per species were counted for the more abundant forms. For the rare forms the count continued until 50 fields were reached in two diametral transects of 25 fields each. Results are reported as densities per liter.

Species were separated by morphotypes and a numerical code was assigned to each. Each morphotype was identified to the lowest level possible with the available keys (West & West

1971, Prescott 1962, Huber-Pestalozii 1968, Whitford & Schumacher 1973, Komárek 1983).

Zooplankton samples were taken by means of a 64 µm mesh net in vertical hauls from 20 m deep. Samples were preserved in 4% formalin and observed under the microscope in a Sedgwick-Rafter chamber.

RESULTS

The morphometric characteristics of the lake are listed in Table 1. Gocke (pers. comm.) has prepared a bathymetric map that shows two separate deep basins in the lake, but we were unable to detect two basins in our transects across the lake.

The temperature showed a marked difference between surface and bottom on all four sampling dates (Fig. 2). Surface temperature varied between 22.2 and 26.5 ^{o}C, while temperature at 25 m depth varied between 20.9 and 21.5 ^{o}C. This difference indicates a strong thermal stratification which may break only on rare occasions.

TABLE 1

Morphometric characteristics of lake Hule

Drainage Basin Area (ha)	320.2
Altitude (m a.s.l.)	740.0
Surface Area (ha)	46.0
Volume (x10^6 m^3)	6.8
Shore length (m)	3438.4
Shore Development	1.43
Max. Depth (m)	26.5
Mean Depth (m)	14.7

TABLE 2

A) pH values and B) ΣN/PSR ratios measured at several depths and dates from Laguna Hule

A) pH Values	8/90	11/90	2/91	6/91
0m	7.10	-	6.46	6.22
1m	6.26	-	-	5.90
>4m	6.16	-	-	6.96
B) ΣN/PSR ratios				
Ratio	64.7	5.87	1.06	11.96
Most probable limiting factor	P	N	N	P

The dissolved oxygen dropped sharply below 3 m of depth on three of the sampling dates (Fig. 2b). In the February 1991 (dry

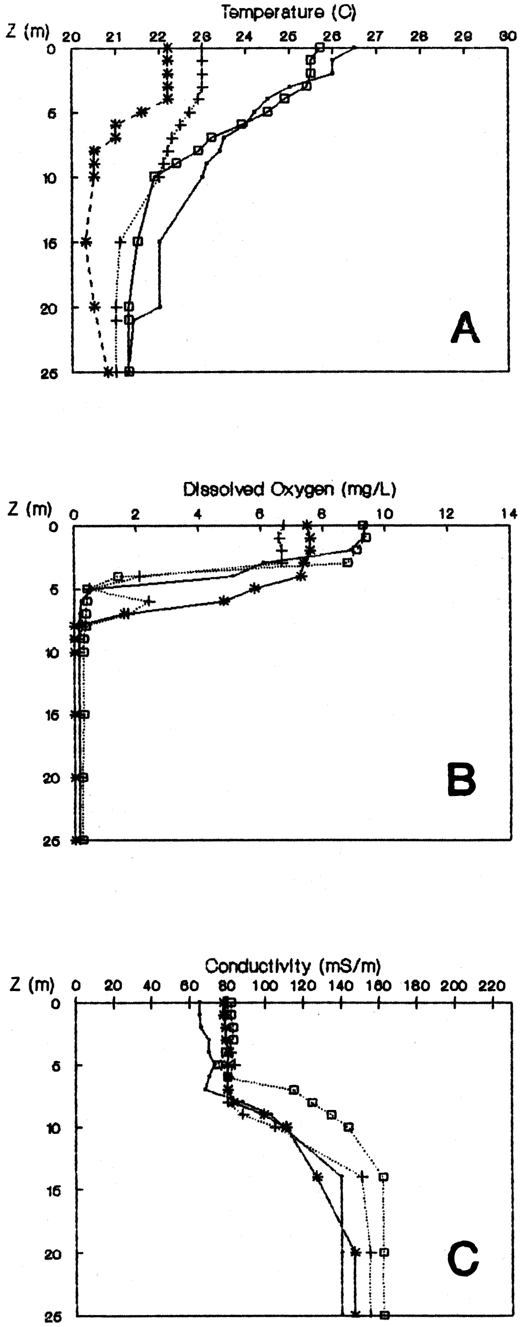

Fig. 2. Depth profiles in Laguna Hule: a) Temperature (°C). b) Dissolved Oxygen (mg O_2 l^{-1}). c) Conductivity (µS cm^{-1}); measured in each sampling date (–O– August 9.1990, –+–November 16.1990, –✱–February 7.1991, –□– June 14.1991).

season) oxygen profile the depth of rapid oxygen change was descended to 5 m, and the oxygen decline was more gradual. This indicates a deeper mixing during the dry and windier season. However the heterograde curve was maintained and the bottom waters were always anoxic.

Conductivity showed a drastic increase between 6 and 7 m of depth (Fig. 2c), producing a chemocline at this depth. In November 90 and February 91 the chemocline was deeper. There was a change in the difference in conductivity through the water column. In August 90 and June 91 the difference was 80 µS cm^{-1}, whereas in November 90 and February 91 it was 60 µS cm^{-1}.

The pH varied between 5.62 and 7.10, being slightly acid almost all the time, even at the surface (Table 2a). The low pH might be in part a result of the volcanic origin of the lake and its catchment area.

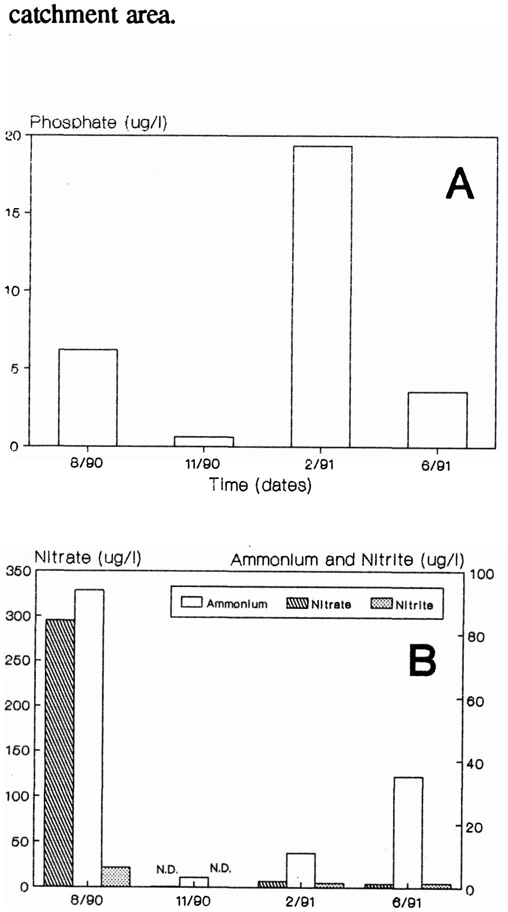

Fig. 3. Variation of the main nutrients in Laguna Hule: a) Phosphate (µg P-PO$_4$/l) . b) Inorganic Nitrogen compounds (µg/l of N-NO$_3$, N-NO$_2$ and N-NH$_4$).

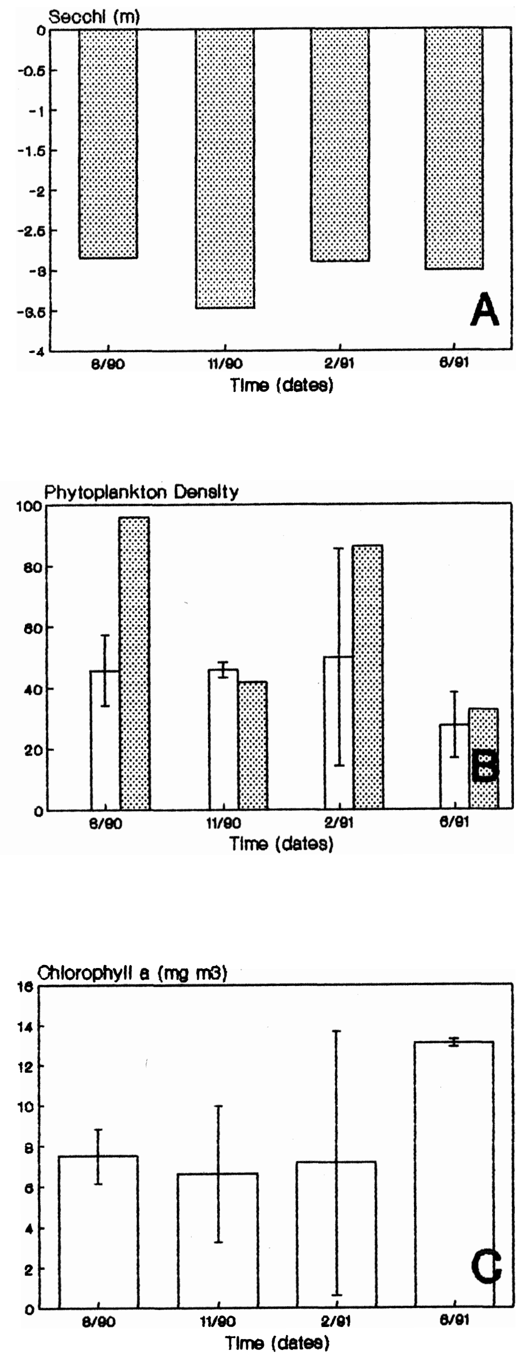

Fig. 4. Variation of the Secchi depth (A), total phytoplankton density (B) and Chlorophyll *a* in surface waters (C) in Laguna Hule. Clear bars are the mean phytoplankton abundance ± S.D. for the 0 to 1 m surface layer (n=4 in all cases except for June 1991, when n=3). Dotted bars are the density for depths greater than 4 m.

The surface Soluble Reactive Phosphate (SRP) decreased during the dry season (Fig. 3a) while the nitrogen compounds increased (Fig. 3b). The shift in the ratio ΣN/SRP indicates an alternation in the most likely limiting factor (Table 2b). During the rainy season P is most limiting and during the dry season it is N. Silica was determined once, in Jun 91 and it was found in moderate levels (10.2 to 14.6 mg SiO_2 l^{-1}) compared to the normal range in warm lake waters and waters draining igneous-rocks basins (Hutchinson 1957, Wetzel 1975).

The Secchi visibility varied between 2.8 and 3.5 m, and was greatest in November 90 (Fig. 4a). The increase in light penetration was not closely related to the density of phytoplankton (Fig. 4b), which showed a peak in February 91. Chlorophyll a in surface waters showed a peak in June 91 (Fig. 4c) which did not correspond to a similar shift in phytoplankton density or a substantial decrease in visibility.

Green algae dominated the phytoplankton of Laguna Hule (60-79%), followed by blue-greens (1.3 - 22.1 %). The rest of the groups were represented by few individuals. Most of the species (48) belonged to Chlorophyta, and the other groups were represented by a much lesser number of taxa (Table 3A). The number of species found per sample varied between 7 and 40 ($\bar{X}$= 29), for a total of 80 species. Due to the large number of rare species and low relative abundance of the dominant species, diversity values were high (Table 3B), with Shannon-Weaver index values ranging between 2.03 and 3.05 and equitability values always greater than 50%.

Twelve species appeared in at least 75% of the samples. These were the green algae: *Ankistrodesmus braunii; Arthrodesmus* cf. *phinus; Dictyosphaerium Ehrenbergianum; Mougeotia* sp.; *Oocystis* sp. 3; *Scenedesmus ecornis; Staurodesmus* sp. 1; *Staurastrum* sp.2; *Staurastrum muticum.* Also the Euglenophyta *Trachelomonas volvocina,* the Cyanobacteria *Coelosphaerium* sp., and a morphotype with spherical cells up to 10 µm in diameter, possibly a green alga.

Only *Arthrodesmus* cf. *phinus* reached percentages greater then 50% in surface waters.

TABLE 3

A) Number of species of algae by taxonomic group. B) Diversity (H') y equitability (J) values for the phytoplankton

Date	8/90			11/90			2/91			6/91			Total
Depth (m)	0	1	10	0	1	6	0	1	4	0	1	10	
Chlorophyta	22	21	3	28	25	26	27	24	20	21	17	15	48
Volvocales	1	1				1	1	1	1				2
Chlorococcales	9	8	1	14	12	12	14	10	7	8	9	6	22
Zignematales	12	12	2	14	13	13	12	13	12	13	8	9	24
Euglenophyta	1	1	1	2	1	1	2	1	1	1	1	1	3
Pyrrhophyta	2	2		2	1	1	1	2	1	2	1	1	6
Cryptophyta							2	3	2				3
Chrysophyta	2	1		2	1		2	1		1			3
Bacillariophyceae	1	1		2	1	2	1	1				1	3
Cyanophyceae	4	4	2	2	2	4	3	4	4	1	2	2	9
Not identified	3	4	2	3	2	3	3	4	4	3	1	3	5
Total	34	33	7	40	33	36	40	39	31	29	21	22	80

Diversity Values: H': Shannon's index; J:Equitability

Dates			8/90	11/90	2/91	6/91
Depth (m)	0	H'	2.03	2.86	3.05	2.47
		J	57.64	77.42	82.78	73.60
	1	H'	2.03	2.84	2.89	2.43
		J	58.08	81.10	78.82	79.90
	>4	H'	0.08	1.93	0.84	2.25
		J	4.32	53.73	24.59	72.75

TABLE 4

Relative abundance of selected algal species

		Species code									
Date	Depth	1007	1015	1059	1081	2096	7001	7011	7049	7050	8098
8/	0	**50.3**	0.0	2.2	0.0	0.7	12.5	2.0	0.4	0.0	1.1
'90	1	**53.2**	0.0	1.4	0.0	1.0	1.7	4.2	7.2	0.0	0.0
	10	>0.1	0.0	>0.1	0.0	0.5	0.0	0.0	0.0	**98.8>**	0.1
11/	0	6.9	0.0	5.8	**10.8**	8.4	0.2	1.1	0.0	0.0	**19.3**
'90	1	8.2	8.6	0.9	**13.0**	**11.7**	0.7	1.8	0.0	0.0	**17.0**
	6	1.1	10.6	0.2	1.8	**54.0**	0.2	0.9	0.0	0.0	9.2
2/	0	**13.2**	**10.5**	13.5	2.4	7.8	0.0	2.7	1.9	0.0	5.1
'91	1	**14.1**	**15.2**	10.2	1.0	**14.6**	0.3	2.6	1.3	0.0	4.4
	10	0.5	0.3	0.3	>0.1	1.6	0.0	0.2	**81.8**	0.0	0.2
6/	0	**23.8**	0.0	1.7	3.0	10.2	0.0	**22.2**	0.0	0.0	2.6
'91	1	**37.8**	0.0	1.6	2.6	3.2	0.0	3.2	0.0	0.0	0.0
	4	**18.0**	0.0	2.2	3.3	**22.4**	0.0	**19.8**	0.0	0.0	1.1

Chlorophyta: 1007: *Arthrodesmus* cf. *phinus*. 1015: *Closterium* sp.2. 1059: *Oocystis* dp.3. 1081: *Staurodesmus* sp.3. **Euglenophyta:** 2096: *Trachelomonas volvocina*. **Cyanobacteria:** 7001: *Anabaena variabilis*. 7011: *Coelosphaerium* sp. 7049: *Merismopedia tenuissima*. 7050: *Merismopedia* cf. *chondroidea*. **Not Determined:** 8098 Spherical cells 1 (10µm diameter).

In deeper water there were two types of *Merismopedia* (Cyanobacteria), which apparently belonged to different species (*M. tenuissima* y *M.* cf. *chondroidea*) and which represented a large portion of the algae counted (>80%). A total of ten species were dominating in at least one sample (Table 4). The number of species and total density were lower in Aug. 90 and June 91, and higher in February 91 and November 90 ($F= 7.337$, $\alpha<0.05$).

The zooplankton was composed of Rotifers (*Keratella* sp., *Polyarthra* sp. y *Ptygura* sp.), Cladocerans (*Bosmina hagmanni, B. longirostris, Ceriodaphnia cornuta* and *Daphnia laevis*), Cyclopoid copepods (*Microcyclops dubitabilis*) and *Chaoborus* sp. larvae. The horned form was the most abundant form of *C. cornuta*.

DISCUSSION

According to the seasonality of winds and temperature in Costa Rica (Laporte 1980, Barrantes *et al.* 1985), it is expected that lakes mix deeply between December to February. This pattern is also influenced by lake morphometry (Margalef 1983) and geographical location. A deeper mixing of the water column in Laguna Hule was observed in February 91, when a lowering of the layer of rapid oxygen decline was detected. A similar mixing pattern has been described for other lakes located roughly at the same latitude (Lewis 1973, 1984, Gliwicz 1980). However, as a result of the shelter provided by the surrounding topography circulation was not complete, and the bottom layer remained anoxic. The same conclusion arises from the drastic increase in conductivity below 5 to 8 m of depth. The occurrence of fish kills and a change in the color of the lake, reported by the local people to take place usually by December might indicate that the lake is oligomictic rather than meromictic. A similar phenomenon has been described also for Laguna Río Cuarto (Gocke *et al.* 1987) which is another lake protected from wind by the surrounding topography. The red coloration at Laguna Hule at the time of turn over is due to the presence of a purple colored *Merismopedia* cf. *chondroidea* which grow in the upper surface of the anoxic layer. These were observed floating in surface waters in February 91 as dense purple clumps or masses.

The composition of the phytoplankton is similar to other tropical lakes (Lewis 1978, Pollinger & Berman 1991), with Chlorophyta and Cyanobacteria dominating the community. Despite the poor representation of other groups, the diversity was high, with many abundant species and none reaching high percentages of the total abundance. Part of the high diversity is explained by the contribution of the tychoplankton detached from the well developed littoral vegetation. The stability of the water column might also contribute to this since it favors a greater degree of spatial heterogeneity (Reynolds 1984, Platt & Denham 1980). Another factor is the grazing pressure of filter feeders and raptorial feeders, which prevent the dominance either of the nannoplanktonic and of the larger algae.

The shift in the most probable limiting nutrient can be explained by climatic factors. During the rainy season there is an increased input of nitrogen (as nitrate) relative to phosphorus in runoff waters as nitrate is more mobile than phosphate in the soils (Payne 1986).

During the dry season N inputs decrease due to lower runoff. At the same time the deeper mixing that occurs in this period promotes the upwelling of phosphate trapped in the hypolimnion, making P more available than N during this season. Such changes in the limiting nutrient have been also proposed to explain part of the planktonic annual succession in temperate zone lakes and seem to be more common than normally thought (Sommer 1989).

The variation of the groups of algae did not correspond with the expected pattern if nutrient limitation was a key factor. A shift in dominance is expected from green algae at times when P is limiting to Cyanobacteria while N is limiting (Sommer 1989). But according to Tilman *et al.* (1986) bluegreens are expected to dominate at high temperatures (>20°C) unless the N:P ratio is greater than 20. In our case Chlorophyta was more abundant (in surface waters 0-1 m depth) in August and November 1990 (rainy and end of rainy season respectively) and the lowest value ocurred in June 1991 which is again rainy season. The variation was however not significant ($H=6.625$, $\alpha=0.0835$). Cyanobacteria showed lower values in November and February, although here again the differences were not significant ($H=4.3485$, $\alpha=0.2262$). The lack of significance is in part due to the high variability of the counts.

It can be speculated that the lower abundance of Cyanobacteria in November and February was a result of the stronger turbulence at that time. Diatoms showed a slight peak in November (variation was again not significant: $H=3.1420$, $\alpha=0.2078$) which could be also the result of the higher turbulence (Reynolds 1984). A deeper atelomixis (as defined by Lewis 1973) seems to be a more relevant factor explaining species shifts in Laguna Hule than nutrients. This may be so due to elevated turn over rates of nutrients within the mixed zone as predicted for tropical lakes by Kilham & Kilham (1990) and the effect of false bottom created by the steep thermocline, as has been proposed by Gliwicz (1976, 1980).

The depth of the photic zone, taken as 2.7 times the Secchi depth (Margalef 1983) is equal or even greater than the depth of efective mixing. Light does not seem to be a limiting factor in the lake. The increase in Secchi transparency during the deeper mixing period was modest in size and it remained virtually unchanged in all four visits, with a maximum variation of 10% around a mean value of 3.14 m.

There was a slight increase in surface (0-1 m depth) phytoplankton density in November and February, however the differences were not significant ($H=7.712$, $\alpha=0.052$) due to the high variability within dates. Chlorophyll a was also highly variable within dates (Fig. 4c) and the differences were not significant ($H=7.106$, $\alpha=0.069$) among dates. This high variation prevents a deeper analysis of their temporal variation. A more frequent sampling program would be necessary to get a better understanding of all these processes in the lake.

Another factor, not quantified here, is zooplankton grazing. There is evidence of selective feeding taking place by zooplankton, either by filter feeders (*D. laevis*, *C. cornuta*) and raptorial feeders (*Microcyclops dubitabilis*). However its influence in the temporal patterns observed seems to be small. No major trend in phytoplankton composition was found which could be attributed to a change of the grazing pressure with time. It is possible that zooplankton communities remain relatively constant along the year, as well as their pressure on the phytoplankton, however this needs to be studied further in more detail.

It is interesting to note that the horned form of *Ceriodaphnia cornuta* was the most abundant form of the species. This species develops its 'horns' in the presence of predators, and both morphs can be present in the same lake, if predators show an uneven distribution (Zaret 1972). In other lakes and reservoirs of Costa Rica *C. cornuta* has been found mostly without horns (Umaña & Collado 1990). The presence of high densities of the predaceous larvae of *Chaoborus* spp. might have induced the formation of a mostly horned *C. cornuta* population.

Chaoborus reaches high densities in Laguna Hule in part as a result of the presence of a permanent refuge in the anaerobic bottom layer. The probable absence of planktivorous fishes that could eliminate *Chaoborus* through predation and resource competition may also contribute to the abundance of this larvae in the lake. It will be interesting to study the fish community of this lake in detail to confirm its existence and composition.

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RESUMEN

La Laguna Hule se localiza en un cráter de explosión al norte del Volcán Poas, Costa Rica, América Central, a 740 m de altitud. Se tomaron muestras cuatro veces entre agosto 1990 y junio 1991. El lago está rodeado por las paredes casi verticales del cráter que lo protegen de la acción libre del viento. El hipolimnion permaneció anóxico en las cuatro visitas, y se observó una curva de conductividad con un aumento muy pronunciado en las capas profundas. Esto podría significar que el lago es meromíctico o al menos oligomíctico y rara vez se mezcla completamente. Se observó un cambio en el nutriente limitante más probable, en correspondencia con la estacionalidad de la precipitación. Se observaron un total de 80 especies de algas en el plancton, la mayoría de las cuales fueron escasas. Esto resultó en altos valores de los índices de diversidad. Chlorophyta y Cyanobacteria fueron los grupos dominantes. Un 60% de las especies pertenecían a Chlorophyta. Aunque los valores de clorofila *a* fueron altos, la transparencia de Secchi fue también relativamente alta. El zooplancton estaba compuesto por pocas especies de Rotifera (3), Cladocera (5) y un Copepodo Cyclopoide. La mayoría son herbívoros pequeños. Las larvas de *Chaoborus* fueron extremadamente abundantes. La forma con cuernos de *Ceriodaphnia cornuta* fue la más abundante, posiblemente en respuesta a la gran abundancia de las larvas depredadoras de *Chaoborus*.

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