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Basic morphometric and limnological properties of Laguna Hule, a caldera lake in Costa Rica

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Abstract: Laguna Hule, a caldera lake at 740 m above sea level, is situated on the Atlantic slope of the Cordillera Volcanica Central in Costa Rica. The lake area is 56.9 ha, the volume 7.8 x $10^6 m^3$ and the maximum depth 22.5 m. At the time of the study (January/February 1989) the boundary between the oxic and anoxic layer was at 10 m, i.e. 33 % of the lake's volume was anoxic. Relatively low concentrations of H_2S (up to 4.1 µmol l^{-1}) were present in the hypolimnion simultaneously with large amounts of Fe and Mn (114 and 21.5 µmol l^{-1} resp.). The thermocline was very weakly developed (total temperature difference between surface and bottom water layer amounted to only 1.3°C). This small difference, the relatively high concentrations of ammonia and iron in the epilimnion and the low O_2 saturation (81 %) of the surface layer indicate that, during or shortly before the study time, a partial circulation of the lake had occurred causing a substantial entrainment of hypolimnetical water into the epilimnion. The mixing process did not produce a total circulation but was probably the reason for the intrusion of small amounts of O_2 into layers below the chemocline, which enabled the production of nitrite by nitrifying bacteria within the hypolimnion. On Feb 7 the gross primary productivity was 2.74 g C $m^{-2}d^{-1}$ and the community respiration between surface and 6 m amounted to 1.98 g $Cm^{-2}d^{-1}$ It is concluded from the results of the present as well as from an earlier study (May 1979) and from comparisons with the nearby located Laguna de Río Cuarto, that the productivity pattern of Laguna Hule is very much governed by its mixing behavior.

Key words: Tropical lake, chemical limnology, primary productivity.

In Costa Rica, a large variety of mostly small lakes exists, many of them - as would be anticipated from the geological nature of the country - are associated with volcanism in different ways. Most of the lakes are not yet described, however, a small yet steadily growing number of publications exist already about several of them. Umaña & Paaby (1991) gave a short account on the state of knowledge in limnology of the country. The first limnological study, that should be mentioned, was performed by Kohkemper (1954), who should be regarded as the pioneer of Costa Rican limnology. Kohkemper studied the Laguna de Río Cuarto, a maar at the Atlantic slope of the Cordillera Volcánica de Costa Rica. Recently Horn and Haberyan (1992) published a quite comprehensive study on Costa Rican lakes. The authors visited 30 lakes and report several important morphometric and chemical parameters as e.g. size, maximum depth and concentration of several major ionic constituents. The work gives an excellent overview and allows an interesting comparison of some of the lakes of Costa Rica.

For detailed further investigations, however, additional precise morphometric studies are necessary. It is obvious that a variety of limnological properties, *e.g.* species composition of the flora and fauna, can be studied without having any knowledge of morphometric characteristics of a lake. A deeper insight in productivity, however, is only possible when the morphometry of the lake's basin is known. Until now this is the case with only very few Costa Rican lakes. The present paper tries to fill this gap with respect to Laguna Hule, which occupies a caldera on the Atlantic side of the Cordillera Volcánica de Costa Rica together with two other smaller lakes (Figs. 1 and 2).

This paper is based on field studies, which were performed in January and February 1989. Morphometric measurements were among the main aims of our work. We also studied the oxygen/hydrogen sulfide distribution and its relation to E_h sensitive compounds (especially Fe and Mn). Additionally, primary productivity and community respiration of the plankton were measured.

Results of an earlier study made in May 1979 (Gocke, Bussing and Cortés, not published) are included in the discussion. Recently an interesting paper dealing mainly with species composition and seasonal variation of the phytoplankton was published by Umaña (1993). It shows from a more biological viewpoint that Laguna Hule is a very interesting lake.

MATERIALS AND METHODS

Morphometric Survey An enlarged aereal photograph (Instituto Geográfico Nacional de Costa Rica) was used to draw an exact map of the lake. This photograph served also to determine the positions of 9 transects, which were more or less equally spaced over the whole lake. The depth sounding was performed with a portable echosounder (Furuno FE 4200). To obtain precise near shore depths values, additional measurements were made by hand at 10 m intervals up to 50 m distance from the shore.

Fig. 1. Location of the Laguna Hule.

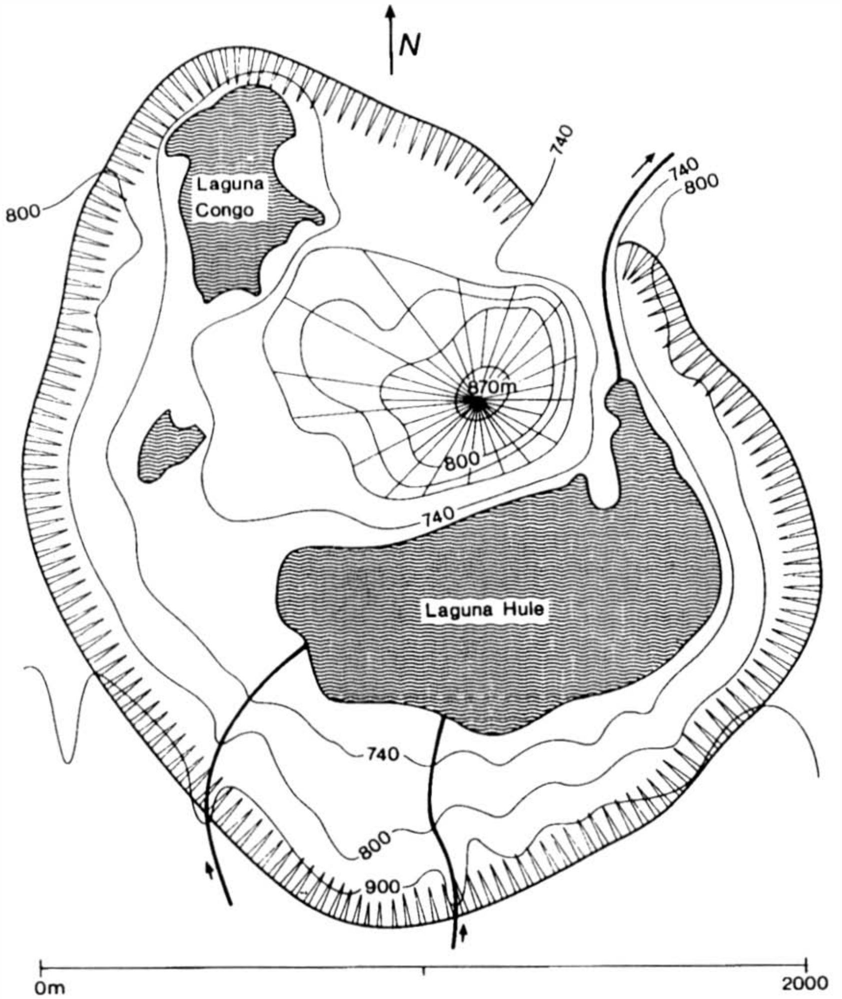

Fig. 2. Caldera Bosque Alegre with its three lakes and the secondary cone. Contours in meters.

This was done with a weighted disc connected to a marked cable. The cable was also used to check the reliability of the echosounder. The survey in the rather flat bay near the lake's outflow was made with a marked bar, at the tip of which a disc was fixed. The water volume and related parameters were calculated according to Hutchinson (1957).

Physico-chemical Survey Water samples were taken from the eastern deep part of the lake (Fig. 3). Sampling was performed between 9:00 and 10:00 in the morning with a 5 l plastic Niskin bottle. Temperature, conductivity (at 25°C), pH and oxygen concentration were measured with automatic probes (WTW, Weilheim, Germany). Alkalinity was measured by titration with 0.1 n HCl up to a final pH of 4.3, calcium and magnesium were determined with the EDTA titrimetric method and complexometric endpoint detection, chloride was titrated with $HgNO_3$ and diphenylcarbazone as indicator, sulfate was determined turbidimetrically after addition of $BaCl_2$ (APHA 1980). Cl^- and SO_4^{2-} measurements were repeated in Germany using ion chromatography (Small *et al.* 1975). Iron and manganese concentrations were obtained photometrically with 2,2'bipyridine and formaldoxim, resp. The Merck spectroquant reagent kits (Merck 1987) were used and the reagents were added directly after sampling. The accuracy of the determinations was

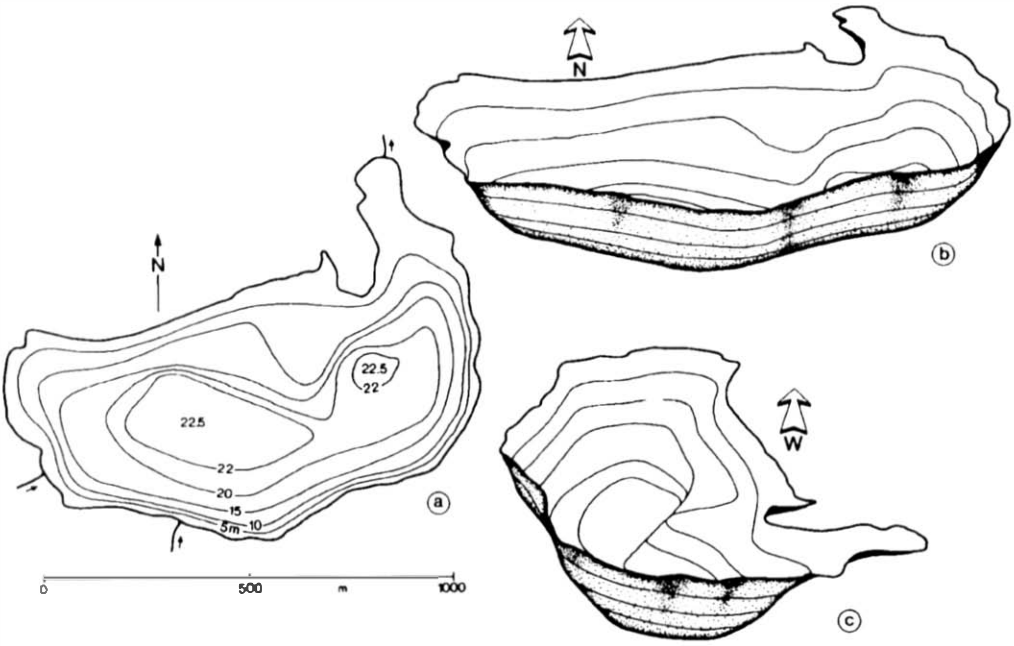

Fig. 3 a. Bathymetric map of the Laguna Hule. b. Three-dimensional view of the lake from south to north. Projection angle 33°. Vertical exageration 10 times. c. View from east to west. Projection angle 75°. Vertical exageration 10 times. The scale applies only to part a.

checked with internal standards of Fe and Mn. Oxygen concentrations for primary productivity measurements were obtained with the Winkler technique. This technique was also used occasionally to check the accuracy of the O_2 probe. Hydrogen sulfide was determined photometrically after formation of the methylene blue compound (Grasshoff 1983). Nitrite and ammonium were measured photometrically after formation of the azo dye and the indophenol blue dye resp. (Grasshoff 1983).

Biological Survey Chlorophyll **a** and phaeophytins were measured according to the procedure of Lorenzen (1967); 90 % acetone was used to extract the pigments from the algae, which were filtered onto glass fiber filters.

The primary productivity was measured with the aid of the "light and dark bottle method" first introduced by Gaarder and Gran (1927). The technique uses the O_2 concentration changes as a measure of photosynthetic activity. Sets of 2 light and 1 dark bottle (100 ml nominal volume) were incubated at 0, 1, 2, 4 and. 6 m depth for 6 h (9:30-15:30). A PQ value of 1.2 and an RQ value of 0.83 were employed to convert O_2 units into mg of organic carbon produced or respired (Vollenweider 1974). Values are given on a 24 h basis, which means that net primary productivity is the difference between the gross primary productivity of the total daily light hours and the respiration of the whole day (for details see Vollenweider 1974 & Gocke *et al.* 1990).

RESULTS AND DISCUSSION

Morphometric Properties From the active Poas volcano a fracture line runs north down the Atlantic slope of the Cordillera Volcanica, in which two lake systems are located. The first one, at about 11 km distance from Poas, lies within a caldera, which represents the remants of a former twin volcano, of which only the southern one, the inactive Cerro Congo, still exists (Bergoeing & Brenes 1978). According to Alvarado (1984) the caldera came into existence during the period between the Late Upper Pleistocene and the Early Holocence, which means that it is about 20.000 years old. Horn

& Haberyan (1983), however, conclude that the caldera was formed only about 3000 to 4000 years ago, based on radiocarbon data.

The caldera forms a steep hole with roughly 2 km of diameter and 333 ha of area (Fig. 2). The steepest and highest walls are located at the south and rise to 160 m above the caldera's bottom. The rim gradually slopes downward to the north. Somewhat eccentric inside the caldera a small secondary cone rises up to 130 m above lake level. This cone probably was built up shortly after the forming of the caldera, separating an originally circular lake into 3 smaller ones (Bergoeing & Brenes 1978) The rims of the caldera, especially the steep ones in the south are covered with dense primary forest belonging to the premontane rain forest life zone according to Holdridge (1978). The vegetation of the caldera's floor, however, is greatly altered by human activity. Now mostly secondary forest and pasture exist.

Three lakes are situated within the caldera at 740 m above sea level, the largest one is named "Laguna Hule", the second one "Laguna Congo" and a third one of only small size and reduced depth is called "Laguna Bosque Alegre" (Fig. 2). Laguna Hule is of about half-moon shape, its topography is influenced by screes of the secondary cone so that a somewhat narrow passage results in the deepest parts of the lake (Fig. 3). Relatively steep shores exist in the south, whereas the northern part is gently sloped. A flat bay of less than 5 m depth exists in the northeast, densely covered with higher aquatic vegetation. This is the part from where the lake's outlet, the Río Hule, originates.

During the time of our visit (Jan/Feb 1989) the outlet was dried up since the lake's water level was about 0.5 m lower than during the rainy season. No permanent water connection between the 3 lakes exists, but during the rainy season occasionally Laguna Congo might overflow into Laguna Bosque Alegre. From there water apparently can only seep into Laguna Hule. During the time of our visit Laguna Hule received water from 2 small brooklets which originate from the slopes of Cerro Congo. According to the Climatological Atlas of Costa Rica (Instituto Meteorologico Nacional) the mean annual precipitation of the area is 4500 to 5500 mm, lowest precipitation generally occurs in March and highest in July.

TABLE I

Morphometric properties of Laguna Hule and Laguna de Río Cuarto

	Laguna Hule	**Laguna de Río Cuarto**
Location	84°12’W, 10°17’NI’W	84°13’W, 10°21’W
Vegetation life zone	Premontane rain forest	Tropical wet forest (a)
Altitude (m)	740	360
Geomorphology (lake origin)	Caldera lake	Maar
Area (ha	56.9	33.2
Maximum length (m)	1160	760
Maximum width (m)	620	610
Length of shoreline (m)	3920	2260
Shoreline development index	1.47	1.11
Basin slope between surface and 10 m isobath (degree)	7.1°	45°
Maximum depth (m)	22.5	66
Mean depth (m)	13.1	45.5
Depth of chemocline (m)	10 (b)	25 (c)
Volume, total (m^3)	$7.46 \times 10^6 = 100\%$	$15.1 \times 10^6 = 100\%$
Volume of oxic layer (m^3)	$5.00 \times 10^6 = 67\%$ (d)	$7.66 \times 10^6 = 51\%$ (e)

(a) transition to premontane rain forest
(b) and (d) February 1989
(c) and (e) February 1979

The calculated area of Laguna Hule is 56.9 ha. This value coincides quite well with that given by Horn & Haberyan (54.7 ha) but differs somewhat from the 46.0 ha stated by Umaña (1993). Our 9 transects with an echosounder revealed a maximum depth of 22.5 m contrasting to those of Horn & Haberyan (19.5 m) and Umaña (26 m). The water volume amounted to 7.76 x $10^6 m^3$. In February 1989 about 33.5 % of the lake's water was anoxic. During our first visit (May 20, 1979) 44 % was completely anoxic and an additional 12 % suboxic with an O_2 saturation of less than 5 %.

It is quite interesting to compare the morphological properties of Laguna Hule (LH) with those of Laguna de Río Cuarto (LRC), which is the second lake system within the above mentioned fracture line at about 6 km distance north of Laguna Hule (Table). Laguna de Río Cuarto is a maar with an area much smaller than that of Laguna Hule (33.2 versus 56.9 ha). Due to its much greater maximum depth, however, (66 versus 22.5 m) and its much steeper mean shore inclination (45° versus 7° between the surface and the 10 m isobath), the volume of LRC is about twice that of LH (15.12 versus 7.76 x $10^6 m^3$). The smaller shore inclination and the greater value for the shore line development (1.47 versus 1.11) result in a relatively and absolutely much larger lake floor of moderate depth in Laguna Hule than in Laguna de Río Cuarto. This is the reason for the much better developed benthic vegetation in the first lake. Whereas in LRC only a small belt was populated by phytobenthos, which consisted mainly of *Chara* sp., quite extensive areas of LH, especially the shallow bay near the outlet, were covered by *Nymphea* and *Potamogeton* species.

Chemical Properties Calcium and magnesium concentrations in the epilimnion of Laguna Hule amounted to 9.3 mg l^{-1} and 3.5 mg l^{-1} respectively. A small vertical scattering was observed which, however, was probably due to methodological uncertainties. The concentrations in the anoxic hypolimnion could not be measured due to interferences by several chemical constituents in the water of this layer. Judging from the vertical distribution of conductivity and alkalinity we assume that the hypolimnetic concentrations of Ca and Mg were about the same as in the epilimnion. An increase of these ions in the deep layers, which is often observed and attributed to biological precipitation of carbonates from the epi- into the hypolimnion, is most unlikely in Laguna Hule due to its "low" pH (around 7 in the upper layers). The increase in conductivity (at 25°C) and alkalinity (from around 80 to 100 µmhos and from around 0.82 to 1.04 meq l^{-1} resp.) is probably due to the relatively high iron and ammonium concentrations of the hypolimnion (Cole 1975). At the moment we do not have an explanation for the decrease of conductivity and alkalinity in the lowest water layer (Fig. 4). In February 1991 Umaña (1993) observed a much more pronounced vertical increase of conductivity (from 80 to 140 µmhos).

Chloride concentrations obtained by titration were between 1.3 and 2.5 mg l^{-1}. This concentration range is near the detection limit of the method. Vertical variations apparently were absent or smaller than the error range of the method. Ion chromatography made with a sample from the epilimnion only resulted in a concentration of 2.3 mg l^{-1}. This value is about an order of magnitude lower than that observed by Horn & Haberyan (1993), who found 32.1 mg l^{-1} of Cl^- in the epi- and 9.5 mg in the hypolimnion. These authors cite the study of Bumby (1982), who obtained 2.4 mg l^{-1} of Cl^- in 1973, a value very close to ours. Chloride concentrations usually are very little affected by metabolic processes and hence the vertical Cl^- distribution tends to be uniform. Therefore the pronounced stratification found by Horn & Haberyan (ibid.) as well as the much higher concentrations reported by them compared to our values must have had a physical cause. Perhaps inputs of juvenile chloride from the surrounding drainage area due to reported increased volcanic activity of the Poas volcano were the reason for the discrepancies.

The sulfate concentration was also re-determined with ion chromatography and resulted in 0.83 mg l^{-1} = 8.6 µmol l^{-1}. Our preliminary turbidimetric determinations gave 1 mg l^{-1} (about the detection limit). Since this is also much lower than the values of Horn & Haberyan (1993), who found 2.19 mg l^{-1} in the epilimnion, this might be another indication for recent volcanic input.

The vertical distribution of temperature is shown in Fig. 4. The total temperature difference

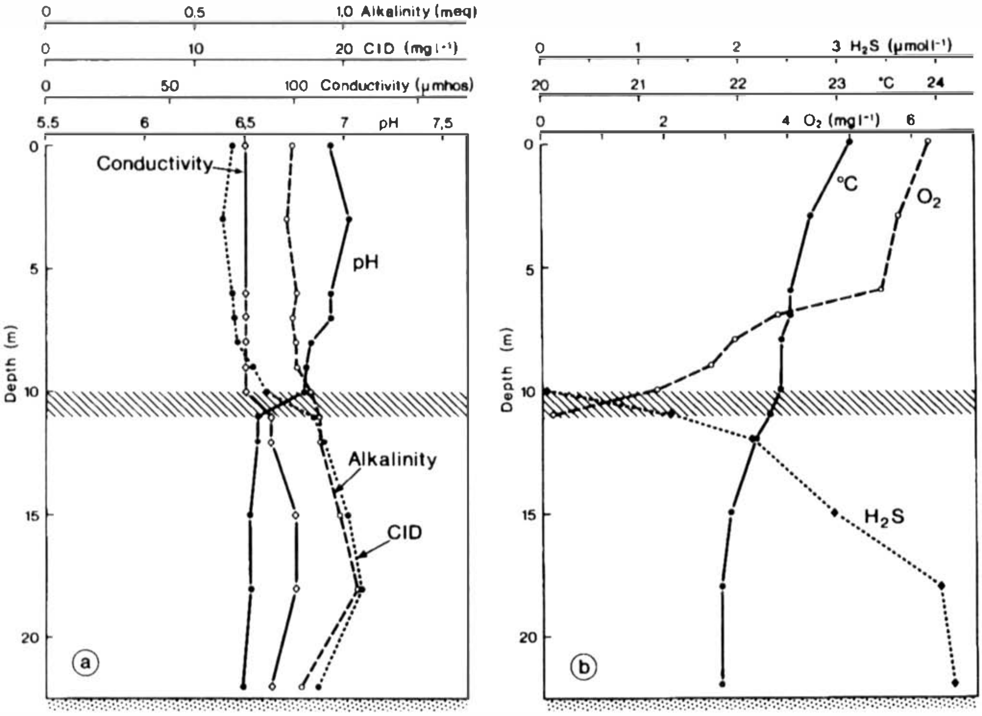

Fig. 4 a. Vertical distribution of conductivity, pH, alkalinity and inorganic carbon (CID). b. Vertical distribution of temperature, oxygen and hydrogen sulfide. Shaded area indicates depth of chemocline.

betweenS lake surface and bottom was only 1.3°C. A very feeble thermocline existed between 10 and 12 m. The distribution of O_2, H_2S as well as several chemical constituents, however, indicates clearly, that this layer was the border between epi- and hypolimnion. Oxygen decreased from 6.23 mg l^{-1} (= 81 %) saturation) at the surface of the lake to almost nil at 11 m. When Umaña (1993) performed his studies in February 1991, he observed that O_2 dropped to zero already at 8 m. Hydrogen sulfide started at 10 m and increased to 4.1 μmol l^{-1} at 22 m. An overlapping of O_2 and H_2S occurred between 10 and 11 m (Fig. 4). Even though H_2S is not stable in the presence of O_2, such an overlapping is often found in limnic and marine environments. It indicates that the velocity of mixing of H_2S into the layer of the thermocline due to diffusion or turbulence is greater than the velocity of its oxidation to higher oxidation states (Kremling 1982).

In May 1979 the stratification was completely different. A double thermocline existed, the upper one lying between 2 and 4 m and the lower more gradual one between 6 and 10 m. That this twofold stratification did not represent only a short-time phenomenon during the daylight hours was shown by the O_2 curve, which had a saturation of 120 % between 0 and 2 m followed by a rapid decrease to 53 % at 4 m and to 6 % at 5 m. Below 10 m no oxygen was detected.

The above mentioned findings show, that a partial circulation of Laguna Hule occurred probably in January and February, which apparently is the period of less thermal stability. During this time the upper part of the hypolimnion is mixed into the epilimnion. This process results in a deeper reaching oxic zone. However, the O_2 concentration of the entire epilimnion is reduced below the saturation due to the entrainment of anoxic deep water containing H_2S. As in Laguna de Río Cuarto (Gocke *et al.* 1987), this mixing did not reach the deepest layers of Laguna Hule as revealed by the H_2S concentration in the hypolimnion (Fig. 4). Wood *et al.* (1984) report similar observations from East-African crater lakes.

The distribution of iron and manganese in lakes is affected by oxic/anoxic conditions. In Laguna Hule around 1 mg of Fe was found in the epilimnion (Fig. 5). Due to the low solubility of the Fe $(OH)_3$ almost no iron should be present in true ionic form. Instead, it probably occurs partially as a complex of Fe and natural organic chelators, the bulk, however, should exist as finely dispersed and colloidal ferric hydroxide. When we sampled the small brooklets, which enter the lake from the south, we observed that their beds were completely filled with huge masses of yellow/brownish Fe $(OH)_3$ precipitates. During the rainy season this material will be swept into the lake and contribute to the high concentration of iron.

Eventually most of this particulate ferric hydroxide will precipitate from the epi- into the hypolimnion, where it will be reduced to the ferrous state. Consistently we found high concentrations of Fe in the deep water layers, where they reached up to 6.35 mg l^{-1} = 114 µmol l^{-1}. In the presence of H_2S iron forms the quite insoluble FeS, thus the concentrations of both Fe and H_2S are limited by the solubility of FeS. A calculation revealed that in Laguna Hule the solubility product of FeS at the prevailing pH of 6.5 is already reached (Davison & Heaney 1978), thus any further increase of H_2S due to bacterial activity or increase of Fe due to for example allochthonous input should lower the concentration of Fe or H_2S. It should be mentioned that this calculation is based on some uncertainties, the most important is the problem what part of the iron detected in the hypolimnion was really present in true ionic form. However, the calculation shows, that the H_2S concentration cannot increase substantially above the 4.1 µmol l^{-1} observed. Anyhow, this increase is not to be expected since its upper concentration is limited by the reduced availability of sulfate (8.6 µmol l^{-1}). During the partial circulation of the lake the amount of iron present in the upper part of the hypolimnion will be mixed into the epilimnion, where it represents the second and probably most important source of the observed high epilimnetic iron concentration.

Manganese behaves in many aspects quite similar to iron. Its concentration in the hypolimnion of Laguna Hule, however, is not likely to be controlled by the presence of H_2S due to the relatively good solubility of MnS. The concentration peak of 1.18 mg l^{-1} = 21.5 µmol l^{-1} at 12 m is probably the result of a dynamic interaction between oxidation,

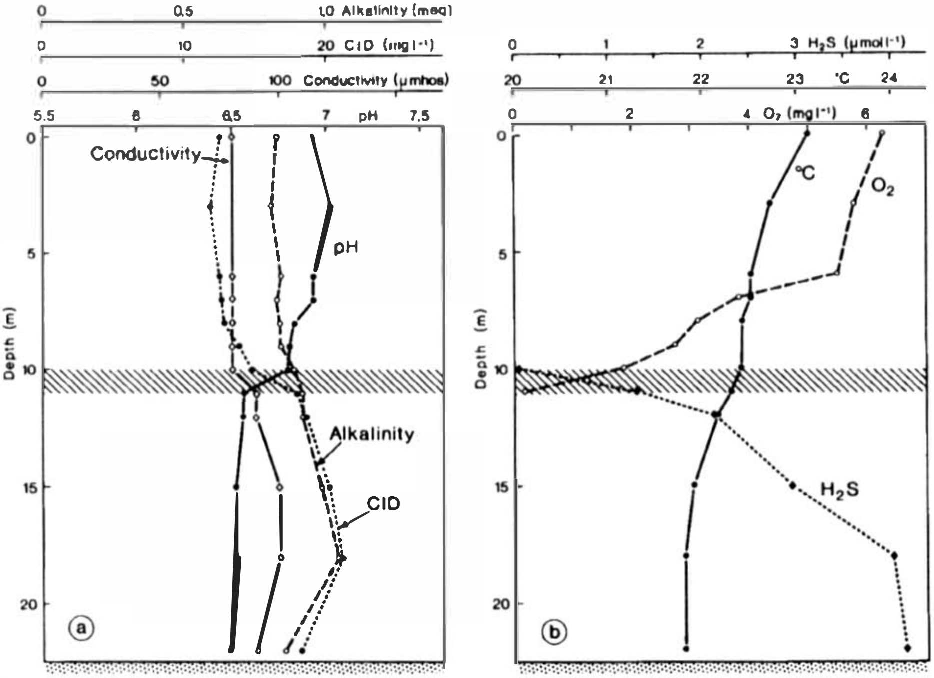

Fig. 5 a. Vertical distribution of iron and manganese, b. Vertical distribution of ammonia and nitrite. Shaded area indicates depth of chemocline.

formation of particulate Mn compounds of higher oxidation value, and reduction processes at the oxic/anoxic interphase. Apparently this peak is confined to a thin layer, since we missed it when we sampled one week before.

Fig. 5 shows the vertical distribution of ammonium and nitrite in Laguna Hule. NH_4^+ amounted to 5 µmol in the epilimnion, which is comparable to the concentration observed in Laguna de Río Cuarto (Gocke *et al.* 1987). It increased to more than

70 µmol l^{-1} in the anoxic deep layer (at 22 m, near the sediment) compared to about 300 µmol l^{-1} in the hypolimnion of the much deeper LRC. NO_2- increased from <0.1 µmol in the epilimnion to about 0.9 µmol l^{-1} in the hypolimnion. At 22 m (0.5 m above the sediment) a decrease to about 0.3 µmol l^{-1} was observed (Fig. 5). Both NH_4^+ and NO_2^- started to increase exactly at the depth of the chemocline.

The relative proportion between the inorganic N-compounds NO_3^-, NO_2^- and NH_4^+ is related to lake stratification and presence or absence of oxygen. It is controlled mainly (at least in the aphotic layers) by bacterial activity. Ammonium is released from organic substances and, if the absence of oxygen prevents its bacterially mediated oxidation to nitrate, it increases since uptake due to phytoplankton does not occur. Sometimes huge amounts of NH_4^+ are observed, especially in the deep layers of oligomictic lakes (Wetzel 1983). Nitrite concentrations usually are very low. Sometimes higher concentrations are found at the oxic/anoxic interphase, since NO_2^- is an intermediate of the oxidation of NH_4^+ to NO_3^- Nitrite may also occur for a short time after the depletion of oxygen, when NO_3^- is used by denitrifying bacteria as an electron acceptor (Rheinheimer 1991).

Under the prevailing conditions the occurrence of nitrite in the hypolimnion of Laguna Hule seems to be somewhat mysterious. As discussed above, the water layers below 10-11 m most probably did not participate in the partial circulation of the water column. Instead, it must be assumed that they had been excluded from mixing at least for several months. If this is true, then NO_2^- should have been completely used up due to denitrification. Experimental errors can be ruled out since the determination of NO_2^- is both very sensitive and very specific. Some compounds, for example, Fe^{3+} (Merck, 1987), may interfere in the dye forming reaction, but only at concentrations significantly above those found in the lake. Hence, there must be a physical or biological reason concerning the occurrence of NO_2^-

The most simple explanation would be that a total or at least quite deep-reaching circulation had occurred shortly before our sampling and that since then the lake had stratified again. This, however, is unlikely as shown by the high concentration of reduced chemical compounds in the hypolimnion (Fig. 5). But, despite the stratification it seems probable that the separation of the epi- and hypolimnion of Laguna Hule is not sufficiently stable to completely prevent the intrusion of oxygen into the deeper layer. This intrusion could be facilitated by turbulent mixing at the thermocline, a process favoured by shear stress between the upper and lower water layers caused by strong winds (Hutchinson 1957, Wetzel 1983). Strong winds at first glance seem to be improbable due to the protected location of Laguna Hule. During our sampling period (January, February), however, winds were so strong that we had difficulties to keep our anchored boat at a fixed position. Apparently the caldera with its secondary cone favours a jet effect of the wind. A hint to the incomplete separation of epi- and hypolimnion of the lake is given by the fact that the thermocline is very weakly developed (Fig. 4). The steady or intermittent intrusion of traces of oxygen, which may lie below the detection limit of the Winkler technique or which may be used up immediately, probably allows the formation of nitrite by nitrifying bacteria. At the same time the oxygen is used for the oxidation of H_2S by purely chemical reactions and/or by sulfur-oxidizing bacteria, which may explain the shape of the H_2S-curve between the chemocline and 18 m (Fig. 5).

Biological Properties Fig. 6 shows the vertical distribution of Chl *a*. From 14 µg l^{-1} at the surface the concentration increased steadily to 40.6 µg l^{-1} at 6 m. Below this depth Chl *a*-concentrations decreased but even in the anoxic hypolimnion substantial amounts were still found. The values were corrected for phaeophytin concentrations, which, however, were quite small throughout the water column. The latter finding, together with the

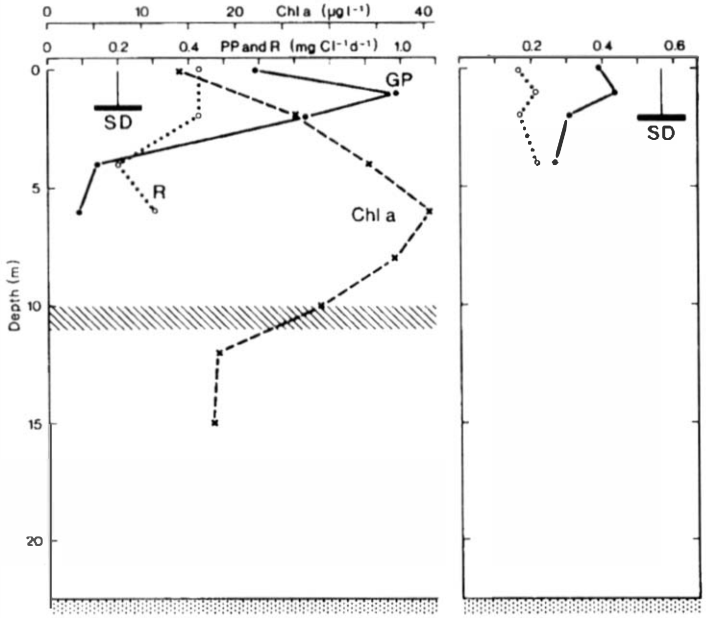

Fig. 6. Vertical distribution of chlorophyll *a*, gross primary productivity and community respiration on February 7, 1989 (left side) and on May 20, 1979 (right side). Secchi depth = SD.

high hypolimnetical amounts of chlorophyll *a* indicate a rapid sedimentation of algae, which must have occurred quite recently before our sampling. Otherwise the deterioration of the Chl *a* should have been much more pronounced. At the same time of year, but two years later, Umaña (1993) found much smaller chlorophyll *a* concentrations and, consequently, a considerably larger Secchi depth (nearly 3 m compared to our 1.5 m).

The gross primary productivity is also given in Fig. 6. It showed an inhibition at the surface and peaked at 1 m depth, where almost 1.0 mg C per liter per day was produced. The compensation depth during the daylight hours was found at 5 m, calculated on a 24 h basis it occurred at roughly 3.5 m. The gross primary productivity per day was 2.74 g C m^{-2}, the community respiration per day down to 6 m was 1.98 g C m^{-2} and the daily net primary productivity amounted to 0.76 g C m^{-2}. The Secchi depth was only 1.5 m. In May 1979 (Fig. 6) the productive layer was thinner and the integrated productivity per square meter was smaller than in February 1989, values were 1.35 g C $m^{-2}d^{-1}$ (gross primary productivity), 0.78 g C $m^{-2}d^{-1}$ (community respiration down to 4 m) and 0.57 g C $m^{-2}d^{-1}$ (net primary productivity). The Secchi depth was 2.0 m.

The pronounced difference between the gross primary productivity values of both studies is interesting to discuss. In February 1989 the day was much sunnier than in May 1979, which may explain in part the difference. It is believed, however, that the entrainment of the upper part of the hypolimnion into the epilimnion in January/February, which causes an increase in epilimnetic nutrient concentration, is the main reason for the high gross productivity in February. It is obvious that the circulation and its spatial and temporal variability in tropical lakes is as important for magnitude and seasonal distribution of productivity as in temperate lakes (Melack 1978). Apparently the entrainment process was still going on or must have stopped just before our productivity measurements. Otherwise the O_2 saturation of the upper layers should have been much higher than the observed 81 % (see above) due to oxygen production by the algae. The peak in primary productivity in Laguna de Río Cuarto, which occurred in March/April, was explained by the same phenomenon (Gocke *et al.* 1990).

The fact, that in LRC the primary productivity was still quite small in February is not explainable by our limited set of data. It may merely reflect year to year differences. Additionally the different altitudes of 360 m (LRC) compared to 740 m (LH) may play an important role. With much caution it may be concluded that the primary productivity of both lakes is roughly comparable.

The present study is only a small step towards a better understanding of Laguna Hule. The whole Caldera Bosque Alegre, in which the lake is situated, is of outstanding scenic beauty and offers excellent opportunities both for limnological or terrestrial research and for studies on limnetic and terrestrial ecosystem interrelationships. It is therefore very much to be welcomed, that the suggestions made by Bergoeing & Brenes (1978) and later by scientists of the Escuela de Ciencias Biológicas of the Universidad Nacional de Costa Rica to incorporate the system into the area of the Parque Nacional Poás was followed in part by the Costa Rican government. The recent declaration concerning the Bosque Alegre to become a Refugio Nacional de Vida Silvestre will hopefully help prevent the whole system being altered or damaged. Thus, a wonderful environment for studies is left for later generations.

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RESUMEN

La Laguna Hule está situada en la vertiente atlántica de la Cordillera Volcánica Central de Costa Rica. Se encuentra en una caldera a una altitud de 740 m sobre el nivel del mar. Tiene un área de 56.9 hectáreas, un volumen de 7.8 x 10^6 m^3 y una profundidad máxima de 22.5 m. Durante el tiempo de estudio (enero y febrero de 1989) el limite entre la capa óxica y anóxica se situó a 10 m, significando que el 33 % del volumen de la laguna estuvo anóxico. Se encontraron concentraciones relativamente bajas de H_2S (hasta 4.1 μmol l^{-1}) simultáneamente con altas cantidades de Fe y Mn (114 respectivamente 21.5 μmol l^{-1}) en el hipolimnion. La termoclina estuvo apenas desarrollada (la diferencia total de la temperatura entre la superficie y el fondo del lago alcanzó solo 1.3°C). Tanto esta reducida diferencia como las concentraciones relativamente altas de amonio y hierro en el epilimnion y la baja saturación de la capa superficial del agua con oxígeno (81 %) indican que, durante o poco antes del tiempo de estudio, había ocurrido una circulación parcial del lago causando una incorporación (entrainment) de aguas del hipolimnion en el epilimnion. Este proceso de mezcla no produjo una circulación total, pero llevó probablemente a una intrusión de pequeñas cantidades de O_2 a las capas debajo de la quimioclina lo que hizo posible la formación de nitritos por bacterias nitrificadoras en el hipolimnion. El día 7 de febrero la productividad primaria bruta alcanzó 2.74 g C $m^{-2}d^{-1}$ y la respiración de la comunidad planctónica entre la superficie y 6 m de profundidad llegó a 1.98 g C $m^{-2}d^{-1}$. Tomando en cuenta tanto los resultados del estudio presente como los del mayo 1979 y comparando la Laguna Hule con la Laguna de Río Cuarto que se encuentra a una distancia de pocos kilómetros, se concluye que la magnitud y la distribución temporal de la circulación controlan la productividad primaria anual en la Laguna Hule.

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