

Chemistry, energy flow, and community structure in some Venezuelan fresh waters

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With 17 figures and 17 tables in the text

Abstract

Physical, chemical, and selected biological features of 9 freshwater habitats in Venezuela are discussed and compared. Included are one Andean lake (Mucubají), two Andean rivers (Rio Sto. Domingo, Rio Aracay), and one stream at low elevation (Rio Limon), a large, desiccating lake at low altitude (Lake Valencia), two lowland reservoirs (Lagartijo and Guanapito), and a darkwater reservoir (Guri). The potential bases for ecological comparison of the biota are discussed and those considered to be most effective are used in the subsequent comparisons.

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Introduction

Venezuela includes a sufficient diversity of fresh waters to support a broadly-based comparative tropical limnology. Altitudinal gradients are well represented due to the intrusion of the Andes on the west, hence lakes and flowing waters ranging from more than 3000 m to sealevel can be sampled and compared within a relatively brief period. Similarly, the rain shadows of the coastal mountains, where hard and even saline waters can be found, grade into the wet forests to the south, where the surface water is characteristically soft. Wet lowland areas are in turn divided according to the content of dissolved organic matter, which varies from moderate to extreme. In addition, there are some notable unique limnological features, including the desiccating Lake Valencia and the large blackwater Guri Reservoir.

Except for a few scattered works of limited scope, Venezuelan limnology is currently founded on publications of GESSNER growing out of the German Limnological Venezuela Expedition in 1952 (GESSNER 1955, GESSNER & HAMMER 1967), and the more recent and comprehensive works originating from the Limnological Laboratory of the Universidad Central (WEIDEMANN et al. 1970, MARTINEZ 1970, CRESSA 1971, DE REYES 1972). There remains an elementary need for broad survey and comparative study, which the present work is intended to satisfy partially.

Representatives of most of the major freshwater habitat types are discussed here. The physical and chemical properties of the habitats are stressed, as are primary production and respiration rates and probable identity of limiting factors. The discussion includes some of the detail of community composition and structure, but this is mainly limited to the autotrophic components.

Simultaneous studies of a large number of habitats are ordinarily deficient in the temporal dimension. We wish to stress this shortcoming in the observations and analysis of this work. Seasonality is of unquestionable importance in the tropics, however different its physical manifestations may be from temperate experience, hence biological processes are to some extent under seasonal control. The redeeming virtues of the following work, which does not span an entire year, are that a standard set of methods was used on a wide range of habitats, and that the observations were all made during the same season. We therefore hope that the data provide a sound if somewhat incomplete basis for comparison of the freshwater systems.

Methods

Analyses of water and biological samples were conducted in the field, or after 1—3 days upon return to Caracas, or after several weeks, according to the lability of the variable in question. All labile chemical properties (e. g. pH, O_2 , alkalinity) were

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determined in the field, as were primary production and respiration. Conservative chemical properties (e. g., conductance, total N and P) were determined in Caracas. Community composition and structure were determined from preserved samples after termination of the field work.

Physical and chemical data

Temperatures were taken with a laboratory thermometer or with a thermometer calibrated against a thermometer. Thermal profiles in lakes were always obtained by incremental lowering of the thermometer. Flow rates in running water were ordinarily computed from a velocity cross-section obtained with a current meter. Light penetration was determined by means of a submersible photometer with a selenium photocell.

The pH data were taken in the field with a battery-operated meter. Alkalinity was determined by titration with sulfuric acid to a pH of 4.4, and is expressed as ppm $CaCO_3$. Calcium was determined by titration and sulfate by the barium sulfate precipitation method (GORTERMAN 1969). Conductance was measured with a dipcell instrument and is reported as specific conductance @ 25 °C. Total N and P were determined by digestion methods similar to those described by GORTERMAN (1969). The various fractions of total N and total P were not separated because the samples had to be stored a few days before they could be analyzed. Oxygen concentrations were determined by the Winkler method with azide modification.

Biological data

Unconcentrated samples of phytoplankton were taken at a series of depths in each of the lakes included in the study. These samples were preserved with Lugol's solution. At a later date, the samples representing the euphotic zone of a given lake were combined in equal proportions to constitute an integrated sample. The integrated sample was then examined to determine species composition of all autotrophs and heterotrophs ranging between 0.5 and 200 μ . All phytoplankton and planktonic protozoa were thus included in the tabulations, provided that the species were sufficiently abundant to show up during census.

The abundance of each species was determined by UTERMÖHLL'S method. Census was halted when 100 counting units (cells, colonies, or filaments) of the most abundant species had been counted. All species which had appeared at least once by the end of the census were included in the species lists, and all other species were omitted. The species lists are thus more ecological than taxonomic in orientation, as rare species that might have been located by concentrating the plankton were not tabulated. Considerable care was taken, however, to separate all valid species. Species designations are given in the tables wherever possible. When the description of a species from references did not quite match the specimens from a lake, the species name is given in parentheses. Where no species could be named, a number is assigned with the genus name.

The product of the census is a list of abundances for each of 20—50 species of plankton. These abundances, which were originally recorded in terms of counting units, were supplemented by two additional bits of information for each species. 1. The cell volume, and thus the volume of each census unit, was computed from cell dimensions for each species in each lake. 2. The average size of independently-moving units was determined for each species. Independently-moving units are defined and referred to here as plankton units. These range in complexity between a single cell for such species as *Rhodomonas* to several hundred cells comprising an independent aggregate of some *Myxophyceae*. The average volume of a plankton unit for a given species (exclusive

of structural material and sheaths) thus indicates the average particle size into which the standing crop of that species is divided. The number of plankton units per unit volume of lake water specifies the number of biomass packages of a species present in the lake at the time of census. The standing crop was also computed in terms of net weight for each species on the basis of cell volume with the assumption that the density of plankton protoplasm is near 1.0 gm/ml.

The census excludes the crustacean plankton, rotifers, and *Chaoborus*, as these organisms are generally larger than 200 μ or too sparse to be counted along with the phytoplankton and smaller heterotrophs. All of the autotrophs were enumerated, even though some were sufficiently small to require phase contrast.

Primary production was measured by the C-14 method according to the plan detailed by LEWIS (1974). Ordinarily, short in-situ incubations of inoculated light and dark bottles were followed by filtration of an aliquot onto Millipore HA paper. The filter was subsequently dissolved in a scintillation cocktail and counted on a scintillation counter. Specific incubation methods varied somewhat between habitats. These variations are described below in connection with specific habitats. The amount of sunlight reaching the waterbody during the incubation period was measured with a calibrated recording pyrheliometer of the differential thermal expansion design.

Respiration was measured by the oxygen-difference method. In some cases, the oxygen-difference method was also used to measure primary production.

Two major assumptions are made in the interpretation of the C-14 data. (1) The C-14 measure of production as obtained by the specific methods of this study is considered to be a very close approximation of true net production. (2) Net production per unit area of aquatic habitat is assumed to be directly proportional to total sunlight per unit area within any 1-day period. The general accuracy in considerable detail is still a matter of controversy, but they have been examined in considerable detail in connection with a tropical lacustrine study using the same method and proved to be quite sound (LEWIS 1974).

Net production per unit area for a specific incubation period or for a specific day is not an ideal statistic for comparative purposes. The ideal statistic, of course, is total annual net production estimated from continuous sunlight records and frequent production measurements spanning more than one year. For practical reasons, this is scarcely possible in comparative studies of numerous habitats. It is not difficult, however, to make a rather simple compromise between the most obvious and the most difficult measures of production.

The amount of sunlight reaching the earth's surface at a given location is highly predictable and is under non-biological control, hence it is unnecessarily imprecise to characterize the productivity of an environment without removing from consideration the random variation in irradiance over short incubation periods. A step in this direction is the computation of daily production from production over a short period and the proportion of the day's light delivered during that period. That is,

$$\int_{sr}^{ss} p_n dt \sim \int_{t_1}^{t_2} p_n dt \cdot \int_{sr}^{ss} i_{ndt} : \int_{t_1}^{t_2} i_{ndt} \quad (1)$$

Where p_n is rate of net primary production per unit surface, t is time, sr and ss are sunrise and sunset, t_1 and t_2 are the onset and termination of a period during which production is measured, and i_n is rate of surface irradiance. This is standard practice when irradiance is known (although it frequently is not). The most frequent criticism of this

estimate is that a diurnal photosynthetic rhythm may invalidate the proportion. Current evidence for lakes argues to the contrary, provided that the integral rates rather than the rates of production at specific depths are of primary concern (LEWIS 1974). Computation involving equation (1) is much more satisfactory than a direct use of production per incubation period, as it removes the effect of transient light conditions that might render an incubation period non-representative of the day on which it is scheduled. It is nevertheless quite possible for a single day's irradiance to depart significantly from the seasonal or annual mean. The comparative value of one or a few measures of primary production on a given habitat is thus of greater analytical significance if more of the nonbiological variation from production data for analytical purposes is removed.

Further removal of nonbiological variation from production data for analytical purposes is simple if irradiance data are available, but it is not commonly done (however, see RUDNE 1958, GOLDMAN 1970, WEITZEL 1973, THURER 1973, LEWIS 1974, THURER et al. 1974). The net production can be expressed as an ecological efficiency:

$$Eff = \frac{\int_{t_1}^{t_2} p_n dt}{\int_{t_1}^{t_2} i_{ndt}} = PN_p : I_n \quad (2)$$

Ordinarily, PN_p is given as $mg/C/m^2$ over a specified time interval ($t_2 - t_1$), and I_n is given as cal/cm^2 (= Langley, ly) over the same interval. The units of the efficiency measure will thus be $mg/C/m^2/ly$. Efficiency will be reported in this form through most of the following work. If a dimensionless efficiency measure is preferred, conversion of mgC to calories can easily be made (ca. 10 cal/mgC). Measurements expressed as $mgC/m^2/ly$ can simply be multiplied by 0.1 to give the dimensionless % efficiency. Alternatively, the efficiency as a proportion of photosynthetically available radiation (400—700 nm) may be desired, in which case the efficiency derived from total radiation should be multiplied by 2.

Ecological efficiency of net production (eq. 2) is the best statistic for analytical purposes, as it reflects the condition of the phytoplankton rather than the sunlight conditions for the day on which a measurement is made. The relative variance of production per day as calculated from equation (1) and efficiency as calculated from equation (2), however, proved to be very much the same for Lake Lanau, for which extensive data are available (Tab. 1). The variation of efficiency is in fact slightly higher owing to a few outlying observations on the high end of the scale that are not

Tab. 1. Relative variability of various production statistics for Lake Lanau. Incubation periods were 3—3.5 hr in length and were initiated during the early second quarter of the day (ca. 0900). $N = 62$ for all statistics in the table. Areal production was computed from equation (1) in the text, efficiency from equation (2). Raw data from LEWIS (1974).

Statistic		Coefficient of Variation
Incident sunlight during incubations	($cal/cm^2/3$ hr)	41 %
Incident sunlight, whole day	($cal/cm^2/day$)	30 %
Maximum production per volume	(P_{max} , $mgC/m^3/3$ hr)	76 %
Areal production per incubation	($mgC/m^2/3$ hr)	65 %
Areal production per day	($mgC/m^2/day$)	51 %
Efficiency of production	($mgC/m^2/ly$)	57 %

found on the frequency distribution of daily production values (Fig. 1). The high efficiency values are masked in the daily production curves because they invariably occur during stormy weather when nutrients are brought to the surface (Lewis 1974). The predictive power of a given number of measurements is in fact about the same for either production efficiency (eq. 2) or daily production (eq. 1) if the only goal is to estimate annual production. The analytical power of the efficiency statistic is much greater, however, in that it more faithfully reflects the condition of the phytoplankton. Sunlight and primary production are weakly coupled wherever nutrient limitation is common (in Lanao, $r = 0.54$, $p < 0.01$ for sunlight and net production), hence the daily production statistic is certain to be less sensitive to changes in the productive capacity of the plankton than is the efficiency statistic. The efficiency is for this reason a more valuable diagnostic tool than daily production, and it is apparently not substantially weaker in predictive power for total annual production, so efficiency will be extensively used below.

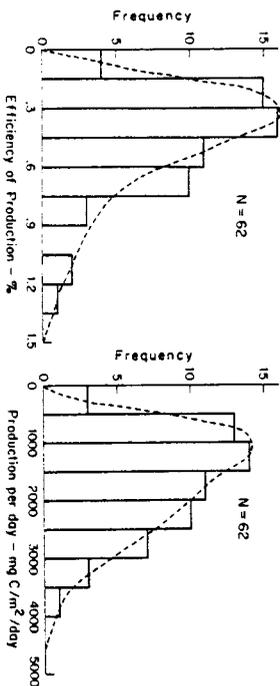


Fig. 1. Frequency distributions of daily net production (Eq. 1) and efficiency of net production (Eq. 2) over the annual cycle in Lake Lanao, Philippines. Raw data from LEWIS (1974).

Ecological efficiencies of net production for freshwaters of moderate to high productivity will generally be between 1—15 mgC/m²/ly (= 1—1.5%). We suggest the further conversion of efficiency to a measure of daily production for an average or standard solar day. This step serves 2 purposes. (1) The daily production is intuitively more meaningful than the efficiency. (2) Habitats that differ in latitude or altitude differ in the total annual insolation, and this should be recognized in the course of comparisons. The efficiency has a unique analytical use in that it is an index of the response of the autotrophic component to a unit of energy supply, and does not require the analyst to confound the response per unit of supply with the total supply. The computation of net production per standard day reintroduces the consideration of total energy supply, but on the basis of an average supply figure rather than a single measurement or small set of measurements. Production per standard day has all of the merits of the efficiency statistic, plus the additional advantage of improved predictive power for cases in which habitats are known to receive substantially different solar input.

At least 4 limnological studies within the lowland tropics have included long-term radiation records. TAILING (1965) reports an annual total of 1.50 kcal/m²/yr on Lake Victoria (0° latitude). GANN (1969) and VINEK & SMITH (1973) report 1.68 kcal/m²/yr for Lake George (0° latitude). BISHOP (1973) gives 1.53 kcal/m²/yr in his Malaysian stream study, and LEWIS (1974) reports 1.49 kcal/m²/yr for Lake Lanao (8° lati-

tude). These are all just over 400 cal/cm²/day. For present purposes, 400 cal/cm² will be accepted as the insolation per standard day at 0—1000 m altitude and 0—15° latitude. The production per standard day for aquatic habitats in this region is thus equal to the ecological efficiency (mgC/m²/ly) times the insolation per standard day (400 ly/day).

Lake Mucubajii

Lake Mucubajii is a small cirque lake located at 3550 m in the Venezuelan Andes (Fig. 2). Morphometric data from WEINZANN et al. (1970) include area (0.26 km²), maximum depth (15.5 m), mean depth (5.63 m) and other physical details. The small watershed is dominated by plants typical of the Venezuelan paramos, including *Espeletia* and *Hypericum*. The west side of the lake is surrounded by the typical cirque amphitheater, and the northeast side is open to the winds. The discharge from the lake on 19—6—74, at the end of the dry season, was 215 l/sec. (18,600 m³/day), which is negligible in relation to the lake volume.

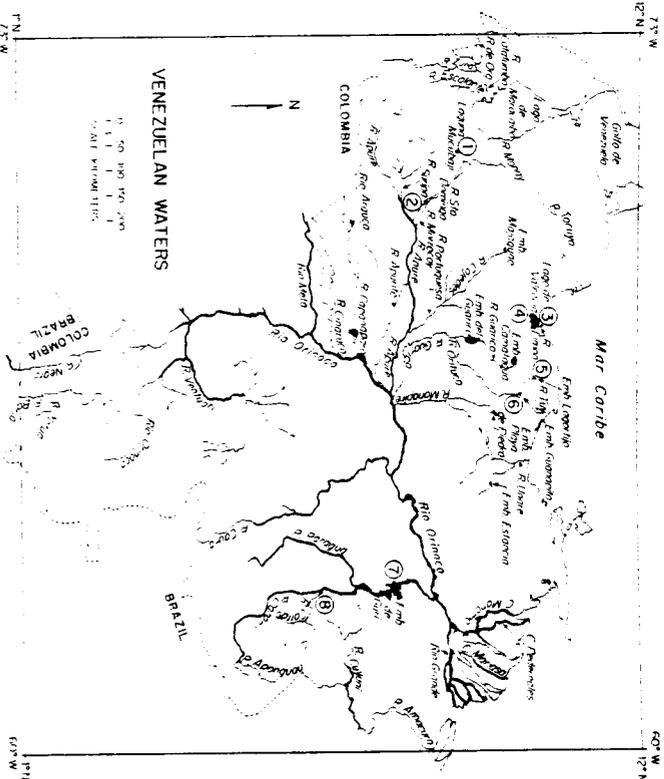


Fig. 2. Map of Venezuela showing major river courses, lakes and study areas.

The chemical data of Tab. 2 indicate the low concentration of dissolved solids, which is explained by the low solubility of parent material in the watershed and minimal contact of runoff with soil and rock before it reaches the lake. The alkalinity and conductance are nearly the same as reported by

Tab. 2. Descriptive physico-chemical data for some freshwater habitats in Venezuela.

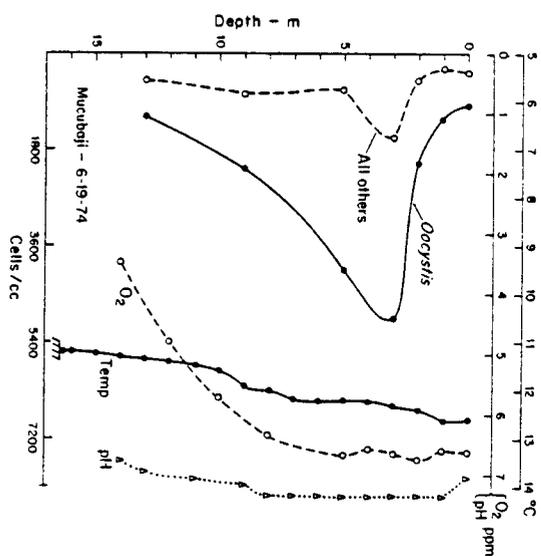
Location	Date	Conductance 25 °C ($\mu\text{mho/cm}$)	Alkalinity mg/l	pH	Temperature °C	Calcium mg/l	Sulfate mg/l	Total N mg/l	Total P mg/l
Lake Mucubaji ¹	6-19-74	12.6	5.2	7.40	12.4	1.2	0.2	0.112	0.006
Rio Sto. Domingo									
Station 1 (2540 m)	6-20-74	24.3	8.4	7.40	10.5	1.4	0.2	—	—
2 (1670 m)	6-20-74	40.1	14.5	7.70	14.8	3.2	1.0	0.112	0.016
3 (660 m)	6-21-74	45.2	16.3	7.65	18.7	3.9	1.7	—	—
4 (200 m)	6-21-74	70.1	28.5	7.70	22.2	7.2	4.6	0.056	0.038
Rio Aracay (1780 m)	6-21-74	48.6	17.4	7.85	19.6	3.9	1.5	—	—
Rio Limón									
Station 1 (1180 m)	6-28-74	—	10.1	7.15	17.9	—	—	—	—
2 (900 m)	6-28-74	—	18.4	7.34	—	—	—	—	—
3 (560 m)	6-28-74	71.0	29.6	7.80	23.0	8.2	0.0	—	0.045
Canal El Roble	7-1-74	805	240	7.15	—	15.4	48.0	—	4.480
Caño Charal	7-1-74	505	164	7.25	—	12.0	18.0	—	2.220
Caño Central	7-1-74	525	174	7.35	—	13.4	43.0	—	1.320
Rio Güey	7-1-74	775	247	9.30	—	9.2	—	—	7.060
Lake Valencia	7-2-74	1830	340	9.10	27.60	9.0	505.0	—	0.038
Lagartijo Reservoir ²	7-9-74	185	95	8.45	29.80	18.0	—	0.250	0.010
Guanapito Reservoir	7-10-74	240	115	8.30	26.50	24.5	12.0	—	0.020
Guri Reservoir	7-17-74	9.0	3.2	6.40	28.40	∨ 1.0	—	—	0.006
Rio Carrao	7-15-74	10.5	0.0	4.60	—	∨ 1.0	—	—	—

¹ Values for lakes are in all cases for 2 m depth.

² Alkalinity, calcium, and nitrogen data are annual averages as determined by WEIBZAHN et al. (unpubl.).

The respiratory oxygen demand of the plankton from 6 depths in Mucubaji was measured by incubation of replicate samples from each depth in the dark for 5 hr. The samples were treated with WINKLER chemicals at the end of the incubation and the oxygen content was determined by titration and compared with the initial oxygen. There was no detectable decline in oxygen over the 5-hr period. In view of the sensitivity of WINKLER titrations and the large number of samples incubated, it seems safe to conclude that the respira-

Fig. 3. Chemical conditions and cell counts for Lake Mucubaji on 19 June 1974.



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GESSNER & HAMMER (1967), although the pH is somewhat higher. The temperature profile in Fig. 3 shows a weak stratification. This is evidently more than a diurnal trend, since the weak thermocline at 8—9 m is a clear boundary for oxygen saturation. There is considerable depletion of oxygen in the deep water, especially considering the oligotrophic nature of the lake. It thus appears that stratification is relatively stable in this lake despite its great altitude. Although irregularities in the weather of the warm season could easily mix the lake completely, nocturnal mixing evidently does not affect the entire water column during the warm season, hence the lake does not meet the criteria of the polymictic type identified by HUTCHINSON & LÖFFLER (1956). The water temperatures recorded by GESSNER (1955, GESSNER & HAMMER 1967) for February also show a weak but definite stratification. GESSNER's suggestion that the lake circulates completely a night does not seem justified in view of deepwater oxygen depletion shown by both his data and ours.

tory oxygen demand of the plankton is well below $10 \text{ mgO}_2/\text{m}^2/\text{hr}$. This is consistent with the other data, which together are indicative of the low overall metabolic rate of the lake. Even if the oxygen depletion rate were as high as $10 \text{ mgO}_2/\text{m}^2/\text{hr}$ ($3 \text{ mgC}/\text{m}^2/\text{hr}$), the oxygen deficit at 14 m could have been produced in no less than 20 days even if no oxygen whatever had been transferred from above by eddy diffusion or density flow.

The data at hand suggest two possible seasonal sequences for Lake Mucubajji. The lake may behave similarly to lakes at lower altitude, and one might thus expect the lake to be essentially warm monomictic with strong non-seasonal fluctuations in stability of the upper water column. Alternatively, Mucubajji may be more similar to the epilimnion of a tropical warm monomictic lake such as Lake Lanao (Lewis 1973a) in that a temporary warm stratification might develop and persist for rather long periods but would be subject to disruption by nonseasonal events prior to the end of the sunny season. It is impossible to say without seasonal data which of these explanations is more accurate.

The productivity of Lake Mucubajji was measured by C-14 uptake on 19 June at the time the chemical samples were taken (Fig. 4). During the 3-hr incubation period, total fixation corrected for dark fixation was $82 \text{ mgC}/\text{m}^2$. The depth of maximum fixation was 2 m. Surface inhibition of photosynthesis is expected due to the moderately high transparency of the lake. The amount of sunlight delivered to the lake during incubation was $291 \text{ cal}/\text{cm}^2$. The ecological efficiency was thus $0.28 \text{ mgC}/\text{m}^2/\text{langley}$.

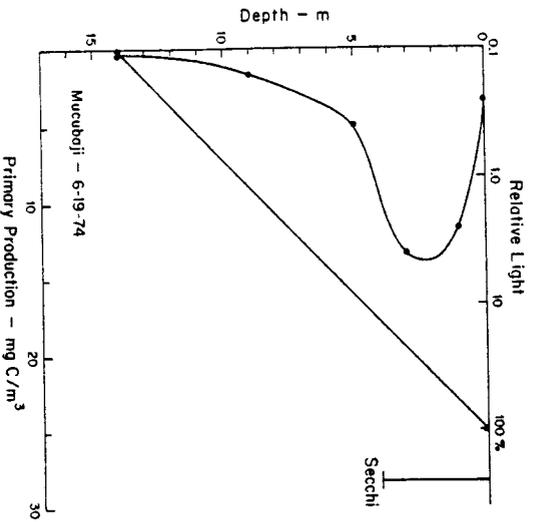


Fig. 4. Primary production and light penetration in Lake Mucubajji on 19 June 1974. Duration of the incubation was 3.0 hr (see text).

Since only 65% of the earth's atmosphere is distributed above 3500 m a.s.l., the lake receives more light than it would at a lower altitude. The difference due to altitude can be considerable, as shown by the European data of STEJNMAJER (1939) cited by HUTCHINSON (1957). The radiation input can be tentatively estimated as 50% greater than at sea level, or about $600 \text{ cal}/\text{cm}^2/\text{day}$ on the average. Production on a standard day would thus be $600 \text{ langleys}/\text{day} \times 0.28 \text{ mgC}/\text{m}^2/\text{langley}$, or $168 \text{ mgC}/\text{m}^2/\text{day}$. GESSNER & HAMMER (1967) measured the productivity of nearby Laguna Negra, a smaller lake with similar water quality. They obtained by the oxygen-difference method a net production of $186 \text{ mgC}/\text{m}^2/\text{day}$ for a 24-hr incubation. This value may not be fully comparable with the present value for Mucubajji, as it is not clear whether GESSNER calculated gross or net production. The values are nevertheless quite similar.

The productivity measurement and other data indicate that Mucubajji is unproductive, as expected, but not remarkably so. LÖNNER (1968) gives some even lower values for mountain lakes of Asia and Africa. The extreme lower ranges of productivities for lowland tropical lakes that have been studied over a yearly cycle are all above the value obtained for Mucubajji. It is not clear at present whether the lower temperature or poverty of nutrients is more important in explaining the low productivity of this and perhaps of other Andean lakes. The littoral vegetation of Mucubajji is so poorly developed that production by rooted aquatics probably does not figure prominently in the energy budget, even though the lake is small.

The plankton census is summarized in Tab. 3. Species having an abundance less than about 5 census units/cc will not be found on the list. The list is remarkably short, as it includes just 10 autotrophic species plus the two mixotrophic *Peridinium* species and only one species of heterotrophic flagellate. A number of investigators have noted the poverty of plankton species, particularly phytoplankton, in high-mountain lakes of the tropics. First GESSNER (1955), then KRUEGER & BOURELILY (1956) and FITZMANN-KUSEL (1968), working mainly with desmids, have commented on the gradual disappearance of species with increasing altitude until only a few species remain in the highest lakes. The remaining species, according to these authors, tend to be the cosmopolitan ones also present at lower altitudes. There is little tendency for development of a special flora by any means other than simplification of the flora from lower altitudes. For example, FITZMANN-KUSEL (1970) examined the desmids from a series of lakes in Central America and the northern Andes and among 116 species found only 1 new species. The GESSNER hypothesis seems further supported by the whole phytoplankton assemblage of Mucubajji during summer 1974. The species of Tab. 3 include a number of cosmopolitan species and no really special component that would be absent in lowland lakes.

Tab. 3. Phytoplankton and small planktonic heterotrophs of Lake Mucubajii.

	Volume per plank. unit μ^3	Plank. unit per ml	Biomass $\mu\text{g/ml}$
Autotrophs			
Cyanophyta			
<i>Aphanobce</i> sp. 1	20	9	180
<i>Lynghya limnetica</i>	100	2	200
Sub total		11	380
%		1	<< 1
Chlorophyta			
<i>Glacocystis planctonica</i>	120	154	18,480
<i>Chlorocella</i> sp. 1	30	70	2,100
<i>Oocystis</i> sp. 1	1,100	267	293,700
<i>Oocystis</i> sp. 2	250	438	109,500
<i>Oocystis</i> sp. 3	30	232	6,960
<i>Ankistrodesmus falcatus</i>	30	132	3,960
<i>Scenedesmus dentalatus</i>	320	17	5,280
<i>Closterium</i> sp. 1	200	22	4,400
Sub total		1,332	444,380
%		87	24
Pyrrrophyta			
<i>Peridinium</i> sp. 1	4,000	149	596,000
<i>Peridinium</i> sp. 2	60,000	13	780,000
Sub total		162	1,376,000
%		11	75
Total Autotrophs		1,505	1,820,760
%		99	99
Heterotrophs			
Flagellate sp. 1	500	31	15,500
%		1	< 1

The phytoplankton standing crop of Mucubajii expressed as plankton units is quite low, but the standing crop biomass is relatively high due to the large cell volumes of the *Peridinium* species. LÖFFLER (1972) has noted on the basis of extensive sampling in high-mountain lakes of the tropical Americas that *Peridinium* is commonly an important element of the plankton in such biotopes. GESSNER & HAMMER (1967) found that *Peridinium* was abundant in Mucubajii in September, but their samples were taken with a net and thus do not properly represent the abundance of smaller phytoplankton.

If *Peridinium* can be considered to have special trophic status, then the remaining autotrophs are dominated by *Oocystis*, both in terms of biomass and plankton units. Studies of whole plankton in the lowland tropics have thus far shown that the Chlorophyta, while present in considerable diversity, almost never dominate the standing crop (e.g. TALLING 1966, LEWIS 1973b), but montane lakes may differ categorically. The Chlorophyta and Pyrrrophyta may in fact replace the diatoms and possibly Myxophyceae as dominants in the high-mountain lakes of the tropics, but this is presently uncertain. The

recent work of WINDMER et al. (1974) on Tinticaca shows that *Oocystis* and other greens are major elements of the crop, although both diatoms and bluegreens are better represented than in Mucubajii. Tinticaca is unusual, however, owing to its great size. Myxophyceae, particularly *Lynghya*, are frequently reported in collections from high-mountain lakes in the tropics. LÖFFLER (1968) found *Lynghya* in two high East African lakes, and THOMASSON (1956) found planktonic *Lynghya* and *Anabaena* in the Peruvian Andes. THOMASSON in fact notes that the Chlorophyta and Cyanophyta tend to be much more important in both arctic and alpine lakes than in other regions. Whether the Cyanophyta are as important as the Chlorophyta and Pyrrrophyta in terms of energy flow and standing crop remains to be seen.

Rio Santo Domingo and Rio Aracay

The Rio Santo Domingo flows from the region of Lake Mucubajii in the Andes to the Rio Apure at about 200 m a.s.l. (Fig. 2). The river was sampled at 4 locations along its length. Locations of the stations are given by altitude in Tab. 2.

The stations along the Rio Sto. Domingo form an altitudinal series between paramos and lowland. The Rio Aracay was sampled between stations 2 and 3 at its junction with the Sto. Domingo. Throughout its course along this series, the Rio Sto. Domingo is virtually unshaded. The first two stations on the Sto. Domingo and the single Rio Aracay station receive water which drains from a very sparsely-populated area that is essentially unfarmed. Station 3 on the Sto. Domingo is located in an area of moderately intensive agriculture and grazing, and Station 4 is undoubtedly influenced by agricultural practices, especially erosion.

Tab. 2 shows that water at the first station already contains about twice as much dissolved solids as Lake Mucubajii, which approaches the solids content of rainwater. The electrolyte content of the river water, as judged from the conductance, increases steadily between 2500 m and 200 m by a factor of about 3, but the rate of increase as the river descends is not entirely regular. Station 3, for example, receives water which contains little more than Station 2, although the river descends 1000 m between these two stations. The alkalinity, calcium content, and sulfate content of the water show the same trend. The composition of the feeder streams must vary somewhat, and this would account for irregularity in rate of electrolyte buildup with decreasing altitude. The increase in electrolyte content as the river descends is presumably due partly to evaporation and partly to decrease in grade of the watershed, which implies slower percolation and runoff and a greater abundance of weathered minerals and soils exposed to rainwater. The Rio Aracay is slightly higher

in electrolytes than the Rio Sto. Domingo at the same altitude, but is chemically very similar.

The Sto. Domingo warms rapidly despite its rapid descent because it is unshaded. Warming between 2500 m and 600 m is almost uniform at 0.04 °C per 100 m loss of elevation. Loss of grade below 600 m causes more rapid warming at the lower elevations. It should be noted that this and other gradient features are subject to seasonal change.

The water of the Rio Sto. Domingo is very clear except at Station 4, where it is somewhat silty. Between 2500 and 600 m, however, the water has a definite green cast, as does the water of the Rio Aracay. Although this might be only an apparent color, it was decided that the river might support significant photosynthesis in the flowing water. The rate of net primary production of the flowing water was therefore estimated by the C-14 technique.

The standard C-14 technique was applied to the water at Stations 1—3 on the Sto. Domingo and at the Rio Aracay, except that a few minor modifications of the incubations were included due to the special circumstances in the river. Two replicate light bottles and a single dark bottle were filled at each station and allowed to incubate either in the river or in a water bath of about the same temperature under full sunlight for 3 to 4 hr. The amount of water over the samples was not considered to be important, as the Sto. Domingo is largely shallow white water between Stations 1 and 3, as is the Rio Aracay. No incubation was done at Station 4 on the Sto. Domingo.

The results of the incubations are shown in Tab. 4. The fixation is given in terms of the amount per day as computed from the amount of uptake, the duration of the incubation, and the amount of sunlight. Results are expressed in terms of fixation per standard day (400 ly, sealevel). Correction has been made for greater amounts of sunlight at higher stations.

Tab. 4 shows a definite photosynthetic uptake at all stations as indicated by the considerable difference between light and dark bottles in all instances. The total amount of production is near 0.5 mgC/m²/day at all stations, which

Tab. 4. Net production in the free water of the Rio Sto. Domingo and Rio Aracay, June 20—21 1974.

Location	mgC/m ² /day Light	Dark	Net	mgC/m ² /day Net ^a	Ecol. Efficiency ^{b,c,d} mgC/m ² /ly
Sto. Domingo					
Station 1	0.812	0.108	0.704	0.352	0.0009
2	0.585	0.036	0.549	0.275	0.0007
2 ^{***}	1.209	0.036	1.173	0.586	0.0015
3	0.645	0.184	0.461	0.230	0.0006
Aracay	0.623	0.114	0.509	0.254	0.0006

^a Based on an approximated mean depth of 0.5 m at all stations.

^b Production when half the incident light is blocked.

^{c,d} Incident light was in this case only estimated from previous measurements.

is of course extremely low. There is no evidence of increasing productivity between the upper and lower stations, but a more extensive study might show some difference. Examination of water samples under the inverted microscope showed that the photosynthetic components of the flowing water are extremely sparse and much less numerous than particles of microdebris. The organisms that are present are either detached benthic forms, principally diatoms, or bacteria-size cells of unknown trophic status. Presumably these two components explain the C-14 uptake that was observed.

On the whole we must conclude that photosynthesis in the flowing water of Rio St. Domingo is easily measurable but quantitatively insignificant. It would, however, be interesting to continue the study at lower altitude, which was not possible in this case. Presumably the two explanations of the unattached autotrophs to build up standing crop with sufficient speed to match the flow of the river, and (2) the physical unsuitability of extreme water turbulence for algal cells and colonies. Both of these inhibitors of photosynthesis operate less effectively at low grade, hence the present results should be considered representative only of the high-energy reaches of the Sto. Domingo.

At Station 2 on the Sto. Domingo, one light bottle was shaded with translucent polyethylene to demonstrate possible photoinhibition of primary production in the Sto. Domingo. The thickness of the polyethylene was adjusted by reference to a light meter until exactly 1/2 of the incident sunlight was blocked. Thus the shaded bottle received only half the irradiance of the other bottles. The fixation in the shaded bottles is given in Tab. 4 along with the data for unshaded bottles. Although replication was insufficient to support firm conclusions, it appears that photoinhibition at midday is substantial.

Photosynthesis by periphyton was not measured here but it is likely to exceed the amount of photosynthesis in the free water. There were no visible algal mats at Stations 1—3 on the Sto. Domingo or on the Rio Aracay, however. This is presumably due to the high energy of the river and perhaps in part to its direct exposure to the sun as well. Further investigation may therefore show that the attached algae are also quite unproductive.

Rio Limon

The Rio Limon is a stream that empties into Lake Valencia (Fig. 2). The Limon flows throughout the year, although its volume is small during the dry season. The river was sampled at 3 stations whose locations are given by altitude in Tab. 2. Station 3, which was the main study site, is situated just 160 m above the surface of Lake Valencia. The rate of flow at the main study site was 0.56 m²/sec during the study period (26—28 June 1974), which

can be considered representative of the dry season. The watershed above Station 3 is partly forested and does not receive significant industrial or domestic waste. The stream is thus in a nearly natural condition above Station 3. The riverbed is almost entirely shaded by trees and the grade of the river in the main study areas is not so steep as that of the Sto. Domingo.

Tab. 2 summarizes the water quality data from Rio Limon. The water is relatively soft and low in nutrients. The water was clear and not noticeably colored by humic substances at the time of study. The central portion of the river and the riffles were relatively free of attached algae, but toward the sides of the stream an algal mat was well developed, as it was in the pools. The genus *Hildenbrandia* (identified by H. B. N. HYNES) was distributed on large rocks even in the faster moving portions of the stream in a manner similar to that observed by HYNES (1971) in Trinidad.

The percentage of light reaching the stream varies according to the percentage of diffuse and direct light. By comparing a series of measurements beneath the canopy over the stream and in an unshaded area outside the streambed, some average penetration percentages were derived. The sky at any instant was considered to be either "cloudy" if a cloud occluded part or all of the sun's face, or "sunny" if this was not the case. A more exact classification would be desirable but is not possible here. Pyrheliometer readings indicate that during sunny periods the amount of light reaching the stream surface at Station 3 is on the average 6.2% of the light in an unshaded area. In his study of a Malayan stream similar to Rio Limon, BISHOP (1973) observed that 4.5—7.4% of light reached the surface in areas that were canopied. During cloudy periods about 25% of the light falling on an unshaded spot reaches the surface of the Rio Limon. This difference is presumably due to the greater proportion of diffuse light during cloudy periods. The percentages are of interest in connection with productivity studies, as they provide a measure of the effectiveness of the tree canopy in intercepting the light before it reaches the stream autotrophs. The absorption of light by the water itself is not significant during the dry season because the water depth is not great (ca. 25 cm average), hence all light incident on the stream surface is considered to be available for stream autotrophs attached to the substrate.

Investigations at Station 3 on the Rio Limon were of 3 types: (1) production and respiration in the free water, (2) production and respiration of the algal mat community, (3) production of *Hildenbrandia*.

Production and respiration in the free water

Primary production and respiration in the free water were measured by means of the oxygen-difference method on 26 June 1974. Water samples were

taken from the stream, mixed, and put into light and dark BOD bottles. At the same time a third (initial) bottle was fixed for Winkler titration. The light and dark bottles were then placed in the stream, where they remained for 6.0 hr (0900—1400). The bottles were then fixed and titrated to determine oxygen content. The results are given in Tab. 5.

Tab. 5. Amounts of oxygen in light bottles and dark bottles and initial oxygen content of water used in the determination of respiration and photosynthesis of the free water on the Rio Limon 26 June 1974. Incubation time was 6 hr.

Replicate	mg/l O ₂		
	Light Bottle	Dark Bottle	Initial
1	7.92	7.89	7.94
2	7.96	7.96	8.02
3	8.00	8.00	7.98
mean	7.96	7.95	

Tab. 5 shows that the rate of both respiration and photosynthesis in the free water is so low as to be undetectable by the oxygen difference method. Considering the length of incubation and number of replicates, we conclude that both respiration and net photosynthesis in the free water are < 10 mgO₂/m³/hr (3 mgC/m³/hr).

A more precise determination of net production in the free water was achieved by use of the C-14 method, which produced results conforming with the oxygen difference determination. The C-14 bottles were incubated in the stream between 1035 and 1335 on 26 June. The amount of carbon fixed in the light and dark bottles is given in Tab. 6.

Tab. 6. Amount of carbon fixed in the free water of the Rio Limon on 26 June 1974 (1035—1335).

Replicate	mgC/m ³ /incubation period	
	Light Bottles	Dark Bottles
1	5.76	0.14
2	5.11	0.29
3	5.33	0.29
4	7.42	0.00
mean	5.90	0.17

The mean photosynthetic fixation (light minus dark) is 5.7 mgC/m³ for the incubation period, or 12.3 mgC/m³/day for the standard day. This is approximately 20 times the amount of photosynthetic fixation in the free water of the Sto. Domingo, which is only slightly lower in dissolved solids at Station 3 than the Rio Limon (Tab. 2). The explanation for this great difference in biological activity within the free water is not obvious, but it may be related to rate of flow, amount of allochthonous organic input, or

degree of exposure to sunlight. Although the rate of photosynthetic carbon fixation in the water of the Rio Limon is much greater than that of the Sto Domingo, it is still very low.

The rate of net primary production in the free water can be expressed in terms of area if the average depth of the stream is known. Averages from several cross-sections in the study area give a mean depth of 0.20 m. The net production for a standard day on an areal basis is thus 2.46 mgC/m²/day over the water surface. An ecological efficiency can also be calculated, but special difficulties are involved because the stream surface is shaded. The amount of light delivered to the tree canopy over the stream during the incubation period was 187 cal/cm² according to the pyrheliometer. Of this amount, 25% could be expected to reach the stream surface if the sky were cloudy and 6.2% if the sky were clear. The duration of cloudy weather during the incubation period can be approximated from the pyrheliometer chart as 50% of the entire period. On this basis the percent of light reaching the streambed is approximated as 15% of the light reaching the tree canopy, or 28 cal/cm². The ecological efficiency is thus 0.041 mgC/m²/ly.

Production and respiration of the algal mat

All except the most turbulent portions of the stream were covered by a mat of attached algae. Examination of the mat showed that its composition was variable. In some locations the mat was almost entirely composed of bluegreen algae, mainly of the genera *Oscillatoria* and *Lynghya*. In other places the mat was predominately diatomaceous. The diatomaceous mat was most widespread and was extremely diverse in species composition. The predominant genera included *Surirella*, *Melosira*, *Synedra*, *Amphipleura*, and *Navicula*. The mats also contained bacteria, protozoa, sessile rotifers, and small insect larvae. In the production and respiration studies, mat samples were taken without regard to composition.

Production and respiration of the mat were measured by the oxygen-difference method, but some special modifications were introduced due to the difficulties caused by the mat. It was observed that the mats must remain attached to substrate during incubation or, if they are detached, great care must be taken to assure that bubbles attached to the underside of the mat are not transferred into the incubation vessel. The incubations discussed below were done both with intact mats on the surfaces of small rocks and with mats that had been carefully detached from sand or rocks. No difference could be detected between these techniques after the method of detachment had been perfected. It is understood that incubation inside a vessel may lead to underestimates of productivity in the current.

Samples of mat were selected at random along the stream and removed intact or detached in units of approximately 1 cm². These were gently transferred underwater into a light or dark BOD bottle or widemouth jar containing water of known oxygen content from the stream. The incubation was then performed in the closed bottles on

the stream bottom. At the end of the incubation, it was necessary to separate the mat from the water prior to doing the WINKLER test, hence the water was carefully siphoned into a smaller bottle prior to addition of the WINKLER chemicals. The titrations and computations were then done in the standard manner except that the total oxygen change (mgO₂) was computed instead of the oxygen change per unit volume (mgO₂/l). The total oxygen change was then divided by the area of mat inside the bottle to yield an estimate of oxygen change per unit mat surface during the incubation period. To improve replication, gross photosynthesis was measured on separate days (26–27 June) from respiration (28 June).

On 26 June gross production measured over 4.5 hr with detached mats in BOD bottles was 750 mgO₂/m²/hr (n = 3, range 740–760). Gross production measured in widemouth jars was 720 mgO₂/m²/hr (n = 1). The weighted average on this data is thus 740 mgO₂/m²/hr. Total sunlight for the period was 252 langleys.

On 27 June, gross production over 3.0 hr on intact mats incubated in BOD bottles was 580 mgO₂/m²/hr (n = 5, range 440–760). The amount for detached mats incubated in BOD bottles was 510 mgO₂/m²/hr (n = 5, range 280–680). The composite estimate is thus 545 mgO₂/m²/hr. The amount of sunlight during the period was 155 langleys.

On 28 June, respiration measured on intact mats incubated 5 hr in BOD bottles proved to be 130 mgO₂/m²/hr (n = 3, range 40–230). Respiration on detached mats averaged 140 mgO₂/m²/hr (n = 3, range 80–250). The mean respiration rate for the algal mat is thus estimated at 135 mgO₂/m²/hr.

Net primary production for an entire day cannot be computed until respiration is separated from gross photosynthesis. Respiration of the mat on 26 June can be estimated from the respiration data as 135 mgO₂/m²/hr, hence net photosynthesis for 26 June was 740–135 or 605 mgO₂/m²/hr. The total net photosynthesis for the 4.5-hr incubation period was thus 2720 mgO₂/m². From the amount of sunlight which fell during the period we can compute the total net production for a standard day, 4320 mgO₂/m²/day. The final estimate of net photosynthesis on the algal mat is the average of this figure for 26 June and the estimate obtained on the following day, 27 June. The final estimate of net production is 3740 mgO₂/m²/day (1189 mgC/m²/day).

Energy balance can be computed for the algal mat from the mean amounts of respiration and photosynthesis given above. Respiration averages 135 mgO₂/m²/hr. Although mat communities presumably vary diurnally in respiratory rate (e.g. BEYERS 1963), an average taken from a 5-hr trial in the afternoon-evening hours (1730–2230) is probably sufficiently representative for present purpose. The total daily respiration would thus be 24 × 135 or 3240 mgO₂/m²/day. This is compared with the net production per standard day of 3740 mgO₂/m²/day. The mat community thus evolves about 500 mgO₂/m²/day, i. e., it is autotrophic on the whole despite its contingent of

attached heterotrophs and the respiratory demands of the algal cells themselves, which probably accounts for the bulk of mat respiration.

An ecological efficiency can be computed for the autotrophic component of the algal mat provided that adjustment is made for the interception of light by the tree canopy. On 26 June, the incubation period is classified as 17% sunny on the basis of the pyreheliometer trace. The average irradiance during the sunny periods was 1.4 ly/min and the total duration was $270 \times 17\%$, or 41 min. Thus 1.4×41 or 57 cal/cm² were delivered to the canopy over the stream during sunny periods and the balance, 211 cal/cm², during cloudy periods. The proportion of light reaching the stream bed under sunny conditions is only 6.2%, hence the amount of light delivered during sunny periods was 3.4 cal/cm². The proportion for cloudy periods is 25%, hence the total amount delivered during cloudy periods was 53 cal/cm². The total estimated sunlight striking the water surface during the 26 June incubation is therefore 56 cal/cm². The ecological efficiency is 2720/56 or 49 mgO₂/m²/ly (15.6 mgC/m²/ly). A similar calculation for the data taken on 27 June gives 22% for the proportion of sunny weather, 3.4 cal/cm² for the light delivered during sunny periods, 24.9 cal/cm² during cloudy periods, and an ecological efficiency of 43 mgO₂/m²/ly (13.7 mgC/m²/ly). The final estimate of ecological efficiency is thus 46 mgO₂/m²/ly (14.6 mgC/m²/ly, 1.46%). This is much higher than the highest efficiencies obtained by Bisnor (1973) for the forested zone of the Sungai Gombak. Bisnor's highest efficiencies were about 0.025% (reported as 0.05% due to subtraction of photosynthetically unavailable radiation). The efficiencies for the mat in Rio Limon are more similar to the values obtained by Orum (1957 a, b) for Florida springs (ca. 2.5%). The critical factor may be shading, which is probably greater at Bisnor's forest stations than on the Rio Limon.

Primary production by *Hildenbrandia*

The red alga *Hildenbrandia* grows over fixed stones in the Rio Limon as a tightly-attached layer 1—3 cells thick. The productive capacity of this alga has apparently never been measured and little is known of its general ecology (Hyvies 1970). The growth habit and distribution of the species in the Rio Limon suggest that it persists by virtue of features other than rapid growth rate, such as general unpalatability. The alga is common in the upper reaches of the Rio Limon as well as at Station 3 where the production was measured.

The production rate of *Hildenbrandia* was measured by the C-14 method. A rock bearing the alga was broken with a hammer and small pieces of rock with an undamaged *Hildenbrandia*-coated surface were selected for the experiment. Each piece was measured so that the area of the mat could be calcu-

lated. The rock fragments having 1—3 cm² of mat were then placed inside light and dark widemouth bottles and inoculated with C-14. Replicate control bottles containing water but no *Hildenbrandia* were also inoculated and incubated. After the incubation the mat was entirely scraped from the rock surface, filtered onto millipore HA paper, and put into the scintillation cocktail for counting.

The results of the *Hildenbrandia* incubations, corrected for uptake in the control bottles, are given in Tab. 7. The mean fixation for the incubation period, 7.6 mgC/m², can be used to compute the production for a standard day, 13.5 mgC/m²/day. This is 1% of the net production of the net diatomaceous and bluegreen algal mats on the stream bottom. *Hildenbrandia* is thus not an important autotrophic component of the streams in terms of energy flow and probably possesses a number of special strategies, including the ability to withstand strong current, which allow it to coexist with the more rapidly-growing diatomaceous and bluegreen mats.

Tab. 7. Amount of carbon fixation by *Hildenbrandia* mats from the Rio Limon in a 4-hr incubation period (1125—1535) 27 June 1974 in 125-ml bottles.

Replicate	mat area-cm ²	Fixation per unit area mgC/m ² /incubation period
Dark Bottles	1	1.5
	2	9.0
	mean	5.2
Light Bottles	1	2.9
	2	5.0
	3	5.0
	4	4.0
	mean	4.2
		7.6

Energy balance for the Rio Limon

Sufficient information is available for the Rio Limon at Station 3 that an overall energy balance can be computed for the study period. Net production figures are given above for autotrophs in the free water, for the diatomaceous and bluegreen mats growing in water of slow to moderate flow, and for the *Hildenbrandia* mats growing on stones in water of moderate to fast flow. No estimate is available for the contribution by the sparse population of diatoms attached to stones in swift water, but this source will be considered minor. Of the three autotrophic components that were studied, the diatomaceous and bluegreen mats are by far most important, as their daily net production is approximately 500 times greater per unit area than that in the free water and 100 times greater than for *Hildenbrandia* mats.

The total contribution of all components is of course determined not only by their relative rates of production but also by the percentage of the

stream which is occupied by each. All of the values given above are expressed in terms of a pure stand of the component in question. The composition of the stream bottom is mixed, hence the computations for the entire stream must account for percent coverage by different components. *Hildenbrandia*, which grows very slowly, occupies no more than 1% of the stream bottom, hence its overall contribution to the system is quantitatively trivial ($< .13$ mgC/day for the average m^2 of stream bottom). Production in the free water is considerably more important on a system basis because this component is distributed over the entire stream (2.5 mgC/day for the average m^2 of the stream bottom).

The total system contribution of the diatom-bluegreen mats is the most difficult to calculate because the mats are irregularly distributed over the streambed. Estimate of mat coverage was made by measuring the width of the stream at 15-m intervals in the study area. At each point where such a measurement was made, the distance covered by mat was also noted. The average stream width was 3.1 m ($n = 15$, range 1.0–6.5 m) and the average distance covered by mat was 1.9 m ($n = 15$, range 0.0–6.0 m). On an areal basis we thus estimate that 1.9/3.1 or 61% of the stream in the study area is mat-covered. The net production for a pure stand of mat as given above is 1189 mgC/ m^2 /day, hence the average square meter of streambed has a mat production equal to 0.61×1189 or 725 mgC/day. The mat production thus dominates the system. The relation of components is shown in Fig. 5.

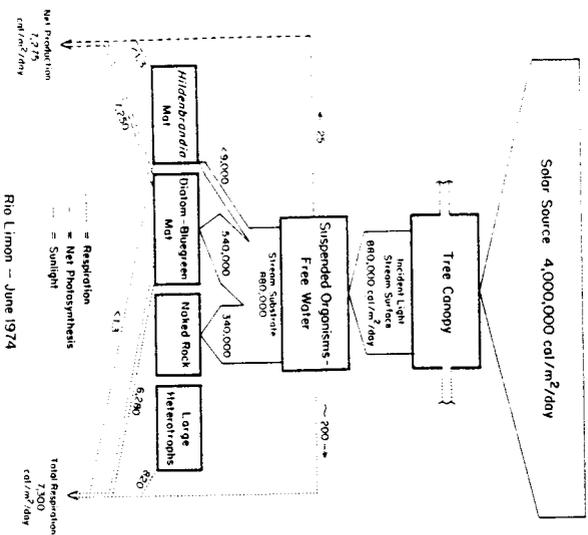


Fig. 5. Energy flow diagram for the Rio Limon at Station 3.

By means analogous to those used for net production, we can compute the respiration of components per average m^2 of stream bottom. Respiration of the free water is known to be < 72 mgC/day, and is probably nearer to 10 than 72 mgC/day. *Hildenbrandia* respiration is conservatively approximated without a direct estimate as less than its own net photosynthesis (< 0.13 mgC/day). The diatom-bluegreen mats are again the big components (628 mgC/day). The total of the three components could then be estimated at about 650 mgC/day total respiration per average m^2 of stream bottom. To this figure must be added the respiration of large heterotrophs (fishes, macroinvertebrates) whose respiration was not measured. The relative importance of this component is not likely to be great due to the low standing crop and metabolic rate of the larger organisms. For the sake of completeness, it seems worthwhile to make an approximation from the literature without benefit of measurement. Macroinvertebrates were not more than moderately abundant in the stream. It appears from the review by Hynes (1970) that a conservatively high estimate of the standing crop of macroinvertebrates under such conditions would be near 5 g wet wt/ m^2 , although the general fund of such information is inadequate. Bisson (1973) found about 7 g wet wt/ m^2 in the upper reaches of the Sungai Gombak. One of the most careful estimates on a small temperate stream is that of Cummins et al. (1966), which yielded an estimate several times greater than 5 g wet wt/ m^2 , but the stream was apparently richer than the Rio Limon, hence the lower figure is probably satisfactory. We could add to this another 5 g/ m^2 of small fishes, principally *Poecilia* and small characins in the pools and sidewaters. Bisson collected about 4 g/ m^2 from the Sungai Gombak, so 5 g/ m^2 seems to be a reasonable estimate.

The median respiratory rate for small aquatic invertebrates according to a literature compilation (Nat. Acad. Sci. 1958) is approximately 0.4 mg O_2 /gm wet wt/hr. Vrardun (1956) gives the respiration rate of aquatic benthic invertebrates in Lake Erie as 0.77 mg O_2 /gm wet wt/hr. It is pointed out in the review by Prosser & Brown (1961) that organisms inhabiting high-oxygen environments typically have higher than average oxygen demand, and they cite values as high as 4 mg O_2 /gm wet wt/hr for aquatic insects. If we specify a demand of 2 mg O_2 /gm wet wt/hr, then we obtain 10 mg O_2 /m 2 /hr or 240 mg O_2 /m 2 /day for the stream, which is probably conservatively high. From the same sources we approximate the demand of the fishes as .15 mg O_2 /g wet wt/hr, or 18 mg O_2 /m 2 /day. The total demand of the larger heterotrophs in terms of carbon is thus approximated as 82 mgC/m 2 /day. This brings the total respiratory demand of the stream to 732 mgC/m 2 /day.

The flow of sunlight, net production and respiration is summarized in Fig. 5 in terms of calories (1 mgC \sim 10 cal). Allochthonous energy sources

are of course not detailed here, but their contribution is incorporated indirectly in the form of respiratory contributions by heterotrophs. It should be noted with reference to the distinctions recently drawn by FISNER & LIKENS (1973) and earlier by ODUM (1956), that the emphasis of this analysis on energy flow is separate from any considerations of total input and output of organic matter at the study site. The relations and proportions indicated in Fig. 5 are also deficient in the temporal dimension, as the highly productive mats must be washed away during the spates of the rainy season.

From the estimates of net production and respiration, the P/R ratio (gross production over respiration) can be computed for the community according to the rationale of ODUM (1956) and RYTHIER (1956). Gross production for the system is taken as the sum of net production and mat respiration, or 1353 mgC/m²/day. The P/R ratio is thus 1353/732, or 1.8. The stream can therefore be considered autotrophic at the time of measurement. Even if the assumption that mat respiration is mainly autotrophic were invalid, the P/R ratio could not be below 1.0. This implies that the output of organic matter from the stream exceeds the input to it, although the size of the net export in relation to total export cannot be judged from the data at hand.

ODUM (1956) noted the high productive potential and generally autotrophic character of flowing-water communities, although he lists a number of heterotrophic communities as well. FISNER & LIKENS (1973), however, have speculated that most small woodlands streams are strongly heterotrophic. These views are not truly divergent provided that we recognize the importance of shading and the magnitude of allochthonous organic input in regulating the P/R ratio.

The amount of sunlight reaching the Rio Limon is actually quite low, as indicated previously (the percentage of total light reaching the stream would average between 10—20%, depending on daily cloud cover), hence the system would be logically classified as a shaded stream. The shading is in this case offset in part by high efficiency of net production (14.6 mgC/m²/ly), which presumably reflects the development of a shade-adapted autotrophic component. The importance of this compensation is evident from a comparison with ecological efficiencies for net production measured on a highly-productive tropical lake, which averaged only 4.4 mgC/m²/ly ($n = 61$, range 1—13 mgC/m²/ly, LEWIS 1974). It is possible that the net production efficiencies of tropical streams are in fact generally higher than those of temperate streams owing to greater stability of some physical conditions. If this proves to be true, tropical streams will have greater tendencies to autotrophy, although this remains to be proved.

The degree of allochthonous subsidy to respiration is also a critical determinant of the P/R ratio, as indicated by ODUM (1956). Since the heterotrophic component contributes substantially to R and is partly or largely

nourished by allochthonous material, the value of P can be greatly altered by changes in allochthonous input without any change in the autotrophic component of the community. Here also possibilities exist for basic differences between temperate and tropical woodland streams, as the timing and extent of allochthonous input may in fact differ between the tropics and the temperate zone.

Lake Valencia

Lake Valencia is of exceptional interest among Venezuelan lakes because it has been steadily desiccating over at least the last two centuries. The lake occupies a graben in the Valley of Aragua between coastal and interior mountains running East-West (Fig. 6). The amount of rain in the valley



Fig. 6. ERTS photo of Lake Valencia and insert showing the Rio Limon and other features.

averages 1.07 m/year according to the 46 years of data (1901—1946) tabulated by Бюскн (1956). Potential evaporation of 1.97 m per year is quoted by ТАМЕРS & ТИНЕЛЕН (1966) from government studies. The total watershed of the lake, excluding the lake surface, is given by Бюскн as 2646 km², or between 5 and 10 times the lake surface area over the last decade. АРМАНЫ (1973), working from government documents, cites a population density of 350 persons/km² in 1970. The watershed is divided into numerous (ca. 11) small watersheds, each of which is, or was, drained by a small river. All of these watersheds except the upper portion of the Rio Limon (near the lake called Tapatapa) are completely deforested, and much of the land has been frequently burned for many years. Бюскн (1956, 1968) speculates, as did АЛЕХАНДЕР VON ХУМВОЛДТ a century and a half earlier, that deforestation and burning have contributed substantially to desiccation.

The hypothesis that desiccation of the lake has its origin in settlement and development of the watershed has been disputed by СРУХЕНТ & РОУСЕ (1961) on archeological grounds and by ТАМЕРS & ТИНЕЛЕН (1966) who provide an alternate explanation based on natural changes in groundwater flow. This controversy has not yet been satisfactorily resolved, although it seems certain that the demands of civilization upon the water supply of the lake have at least aggravated desiccation. In his comprehensive geological work, РЕЙТЕРS (1968, 1971) gives evidence that the lake has experienced at least one previous episode of desiccation, hence the present trend, like the prehistoric ones, may well have begun under the impetus of climatic factors not linked with human activity, as suggested by ТАМЕРS & ТИНЕЛЕН.

The basin has been endorheic for at least 245 years, possibly longer. During this period the lake has declined from its discharge level of about 427 m to a present level of about 404 m. If the decline in lake level had been evenly spread over the period since 1727, the year which Бюскн sets as the final year of discharge, the change in level would thus amount to about 10 cm per year (see GISSNER 1955, Tab. 2). The decline in lake level has in fact probably been much more rapid in recent years, as indicated by a number of unpublished studies (АРМАНЫ 1973) as well as casual observation.

In 1965, the mean depth of Lake Valencia was 19.8 m, maximum depth was 40.8 m, and surface area was 363 km² (ВЕЙНЗАХН 1971). Since the lake level has declined substantially since 1965, we will for present purposes estimate the current mean depth as 18.0 m, maximum depth as 39.0 m, and area as 350 km². The current volume of the lake is thus near 6.3 km³.

Nutrient sources

The streams and canals flowing into Lake Valencia are extensively polluted by industrial and domestic wastes. The effluents with the exception

of Rio Limon and Rio Maricao in fact carry almost no natural drainage during the dry season, but considerable flow is sustained by wastewater, which originates principally from wells. In addition, the city of Valencia now pumps 6 m³/sec over the mountains from an adjoining watershed.

Tab. 2 gives basic chemical data for the 5 main dry season affluents to Lake Valencia. The Rio Limon, which has already been discussed, was sampled in a protected area and consequently typifies the expected water quality of the affluents without human intervention. The Canal El Roble, Caño Charal, Caño Central and Rio Güey all carry substantial amounts of pollutants into Lake Valencia, as indicated by the chemical data. Canal El Roble and Rio Güey are grey in appearance, as they bear higher concentrations of organic matter than Caño Charal and Caño Central. This is also evident from the chemical data, which show that Canal El Roble and Rio Güey are considerably higher in conductance and total P than the other two sources.

The respiratory oxygen demands of the four major sources of organic matter were approximated by a modified BOD procedure. A large bottle of water was taken from the Rio Limon, mixed thoroughly, and used to fill 18 BOD bottles. Two of the bottles were fixed immediately with Winkler reagents, and the remaining 16 were divided into 4 groups of 4 bottles each. The 4 bottles of one group were inoculated with 1.0 cc of water from Canal El Roble. The 4 bottles in each of the remaining 3 groups were inoculated in the same manner with 1.0 cc of water from Caño Charal, Caño Central, and Rio Güey. All of the bottles were incubated at ambient temperature (25—27°C) in the dark. One bottle from each group was removed and treated with WINKLER reagents after 3 hr, one after 6 hr, one after 12.5 hr and the last after 26 hr.

The water of the Rio Limon at Station 3 is known to have an oxygen demand of <0.01 mg/l/hr, hence the entire oxygen consumption within the bottles was assumed to originate from the organic matter and bacteria present in the inoculum from the contaminated water sources.

As expected, the rate of oxygen consumptions was at first rapid and in all cases declined greatly toward the end of the 26-hr period (Fig. 7). The oxygen concentrations after 3 hr had elapsed were uniformly anomalous, which was considered to be due to an error in determination of initial oxygen. For this reason the curves shown in Fig. 7 are extrapolated between 0 and 3 hr on the basis of oxygen consumption between 3 and 6 hr. The data otherwise displayed a great degree of internal consistency.

The oxygen change curves in Fig. 7 are considered to be progressing toward asymptotes. The asymptotes, which presumably correspond to the respiratory consumption of all labile organic matter in the bottles, are estimated from the curves in Fig. 7 as shown. One cc of each of the 4 inocula is thus considered to have an oxygen depletion potential equal to the asymptote con-

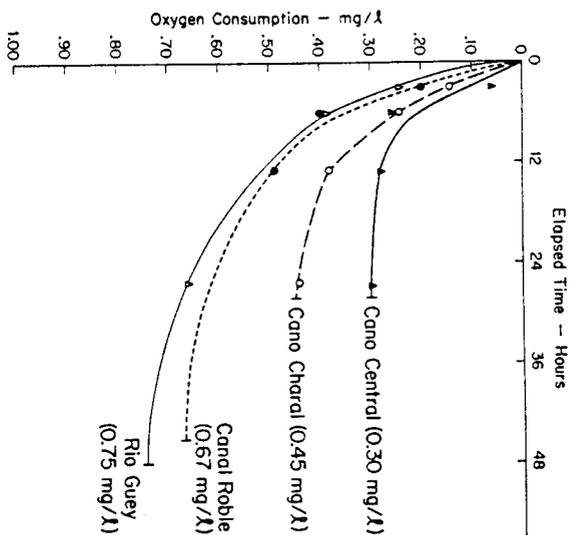


Fig. 7. Oxygen consumption caused by the addition of 1.0 cc of water from each of the 4 polluted water sources to 300 cc of unpolluted water from the Rio Limon. Approximate asymptotes for oxygen consumption are indicated in parentheses.

centration (mg/l) times the bottle volume (0.33 l). The Canal El Roble, for example, has an oxygen demand of 0.22 mgO₂/ml. The discharge rate of the rivers can be multiplied by the oxygen demand per unit volume to obtain a total oxygen demand (Tab. 8). The total demand from the four polluted sources is 72.8 × 10⁶mgO₂/day. On an areal basis over the lake surface this is 210 mgO₂/m²/day, which is attributable to the 4 sources is shown in Tab. 8. On a volume basis for the entire lake, the oxygen demand due to these 4 sources is .012 mg/l/day. This is considerably below the respiration rate

Tab. 8. Rate of flow, suspended solids (dry weight), total oxygen demand, and total phosphorous loading due to the 4 principal nutrient sources for Lake Valencia. Data are for 2 July 1974.

	Discharge m ³ /day	Suspended Solids-mg/l	Oxygen Demand mgO ₂ /m ³ lake/day	P loading mgP/m ² lake/day
Canal El Roble	67,400	—	42	0.87
Caño Charal	119,500	238	51	0.76
Caño Central	262,600	448	75	0.97
Rio Güey	55,600	1290	40	1.12
Rio Limon*	48,400	< 10	2**	0.006
Total	553,500	—	210	3.73

* Within the protected watershed at station 3.

** Estimated, too low to measure.

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measured in the water column (1.3 mgO₂/l/day, see below). The organic material is probably distributed efficiently over the lake due to the low shoreline development of the basin.

The P loading rate due to the affluents is considerable, as shown in Tab. 8, and probably matches in its ultimate effect the oxygen consumption directly attributable to the affluents. The total P input from the 4 major sources as an annual rate per unit lake surface amounts to about 1.4 gm/m²/yr. Assuming that the majority of this P is from domestic sources, this is equivalent to about 0.5 kgP/capita/yr, which is only slightly below the typical input listed by WOLLENWENDER (1968) for north temperate areas (0.8 kgP/capita/yr). On areal basis, Lake Valencia is evidently one of the most heavily-loaded large lakes in the world. The loading rate for P estimated here is comparable to that of Lake Erie and is somewhat worse than Lake Washington (prior to treatment) according to WOLLENWENDER's graphical treatment of surface loading and mean depth. It is not known, of course, whether perennially warm lakes of the lowland tropics are significantly different in sensitivity of metabolic response to P loading than temperate lakes. WOLLENWENDER's relation may well have to be redrawn for such lakes.

The loading rate of Valencia per unit volume (0.08 gP/m³/yr) is not so extreme as the areal rate due to the relatively great mean depth of the lake. The volume loading rate is thus comparable to that of lakes having only mesotrophic status in Florida (SHANNON & BREZONIK 1972). The Florida lakes are shallow, however, and do not contain heterotrophic water layers comparable in size to that of Valencia, hence a comparison of volume loading rates does not seem appropriate.

The data on hand permit only a first approximation of the P loading rate, although the values reported here are entirely reasonable in view of the land use patterns in the watershed. The present estimate is almost certainly conservatively low, as small affluents and direct input of nutrients along the shore are not included. Seasonal variation in input is not considered either, but the P loading rate, which is essentially all attributable to human activity, is presumably much more stable temporally than the water input to the lake.

A final aspect of the water flowing into Valencia is its total salt content. With the exception of Rio Limon, all of the affluent streams are rather high in dissolved solids (Tab. 2). All are nevertheless considerably more dilute than the lake. Thus despite their high organic content these affluents retard salination.

Vertical profiles an lake chemistry

Only fragmentary chemical data on the lake were available until a rigorous chemical breakdown of the water was conducted by I. N. O. S. (Instituto Nacional de Obras Sanitarias, 1971). The data are summarized in

Table 9. The slightly higher values for total electrolytes (specific conductance), sulfate, and pH in the 1974 data of the present work (Tab. 2) are probably due to continued salination in the 3-year interval between studies. The two sets of measurements are quite consistent wherever they overlap.

Tab. 9. Water chemistry data for Lake Valencia, upper water column, July 1971 as reported by I. N. O. S. (1971). Most values are averages from 19 stations scattered over the lake.

Conductance	pH	Dissolved solids mg/l	Color pt units	Alkalinity mg/l	mg/l					
					Mg	Ca	Na	K	Fe	
1747	9.0	1309	5	363	84	83	196	27	0.05	
					mg/l					
SO ₄	Cl	F	SiO ₂	Tot-N	NH ₄ -N	NO ₃ -N	PO ₄ -P			
486	2.0	2.0	17	1.7	0.05	0.06	0.06			

The total electrolyte content of Lake Valencia is presently quite unusual for freshwaters insofar as the salt concentration is much higher than the vast majority of fresh waters in humid regions but not yet high enough to fall within the range of common salinities for fresh water of arid regions. This of course reflects the transitional status of the lake, and will be of considerable biological interest in relation to the composition and relative abundance of species in the lake.

Measurements of total dissolved solids by a number of investigators extending back to 1830 have been compiled by BONAZZI (1950). The increase in total solids since 1830, when the concentration was 500 mg/l, has been approximately exponential. The concentration of dissolved solids passed 1300 mg/l at the time of the I. N. O. S. study in 1971, and must presently be very near 1400 mg/l. The concentration of alkalis has increased the pH to a level that must approach the physiological tolerance of some taxa. Presumably carbonates are now beginning to precipitate, although the effects are not yet visible in the superficial sediments.

The thermal profile shown in Fig. 8 was taken on a relatively calm day, hence the increase of temperature toward the surface can be interpreted as diurnal heat accumulation. The amount of heat in excess of 27.0° C, the water temperature in the straight portion of the profile, is nearly 500 cal/cm². This is somewhat more heat than could have accumulated during the day on which the profile was made, hence part of this heat is either advected or residual from the previous day. The latter is most likely on a lake the size of Valencia. The lake may therefore not have mixed to the thermal discontinuity during the previous night, although recent mixing to the discontinuity is virtually certain due to the presence of oxygen just above thermocline. It is probable that the lake mixes to about 15 m on days with moderate winds and to 5—

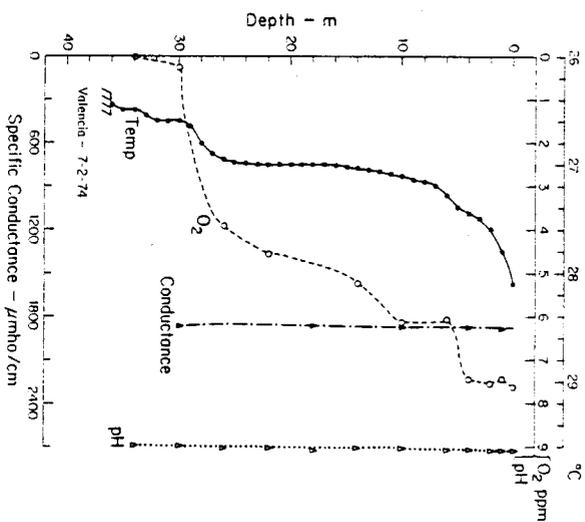


Fig. 8. Temperature and chemical profiles in Lake Valencia.

10 m on calm nights due to convection. Considerable wind or wind with cooling is probably needed to mix the entire epilimnion to a depth of 28 m, but this is probably not an infrequent occurrence. The mixing of the entire water column is unlikely except during severe storms or the seasonal cooling period. This hypothetical mixing scheme is consistent with the distribution of oxygen and dissolved solids in the water column at the time of sampling and with more detailed observations on Lake Lanao in the Philippines, which is nearly identical in size, latitude, and exposure (Lewis 1973a).

Lake Valencia is almost entirely epilimnetic, as a stable thermocline is located just over the bottom in the deepest water. There are undoubtedly many days or even weeks during which the epilimnion does not mix completely, however, and in these instances there will be a chemical divergence between upper and lower portions of the epilimnion. A mild divergence of this type is evident in the oxygen profile of Fig. 8. Such unstable chemical divergences within the epilimnion are important in the regulation of nutrient cycling in Lake Lanao (Lewis 1974), and therefore probably in Lake Valencia as well.

Production and respiration

Planktonic autotrophs are of much greater importance in Lake Valencia than macrophytes. Macrophyte stands are poorly developed, probably due to a combination of high turbidity and changing water level.

The amounts of primary production and respiration in the upper water column were determined by a 3-hr in situ oxygen incubation on 4 July. The profiles are shown in Fig. 9 along with transparency data for the same date. The integral net production for the period (11:45—14:45) was 254 cal/cm², delivered during the cloudless 3-hr period (11:45—14:45) was 254 cal/cm², hence the ecological efficiency was 16.9 mgO₂/m²/ly, or 5.37 mgC/m²/ly. A standard day would thus give 6760 mgO₂/m²/day, or 2148 mgC/m²/day.

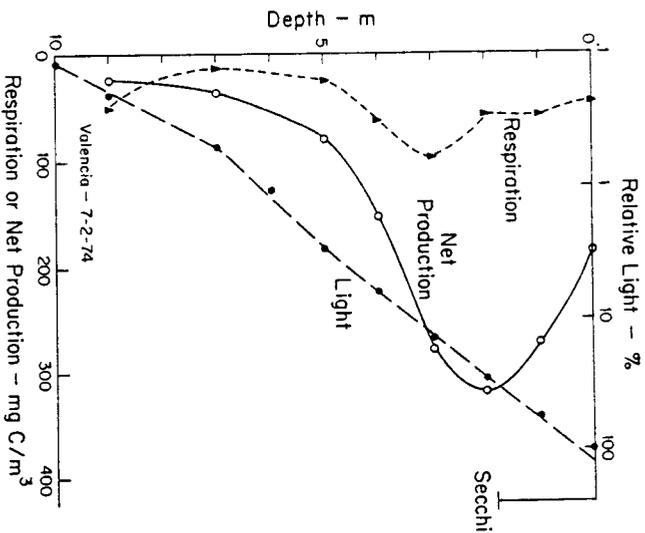


Fig. 9. Primary production, respiration, and light penetration in Lake Valencia.

The expected inhibition of photosynthesis near the surface is visible in Fig. 9. The lake is not transparent due to the high algal standing crop, hence significant photosynthesis occurs only in the upper 6—8 m of the water column. Primary production at the time of incubation was probably nutrient-limited, as the epilimnion was not mixing substantially below the zone of production, and full sunlight was reaching the lake surface. Under these conditions, tropical plankton communities in moderately deep lakes are capable of showing a net production 2—3 times greater than that observed in Valencia (TALLING 1965, 1966; LEWIS 1974). The inference to be drawn from this and the low levels of P in the upper water column (Tab. 2) is that photosynthesis was nutrient-limited at the study site.

The large nutrient loads added to the lake via the affluent canals, which were distant from the sampling station, may remain at or near the surface upon entering the lake, as the water from these sources is almost as warm as the surface water and considerably less saline. This nutrient-rich water is thus likely to be mixed into the euphotic zone, where the nutrients are scrubbed out by the plankton. It is also possible that the affluents form profile-bound density currents near the bottom, but the chemical profiles do not support this possibility. Nutrients reaching the euphotic zone from the shore are evidently still insufficient to saturate the nutrient requirements of autotrophs, at least in midlake during calm sunny weather. The annual net productivity and standing crop of autotrophs are nevertheless likely to be much greater presently than without continuous artificial nutrient input, and gross productivity is almost certain to be greatly enhanced by nutrient loading.

The respiration data are perhaps more revealing of the trophic status of the lake than are the measurements of net primary production. The respiration profile shown in Fig. 9 averages 56 mgO₂/m²/hr between 0 and 10 m, or about 1344 mgO₂/m²/day (432 mgC/m²/day). Respiratory oxygen consumption within the top 3 m would thus equal the entire net photosynthetic oxygen output for water column on 2 July. The respiratory rate of Lake Lanao, which has dimensions similar to those of Valencia but receives no sewage input, averages 82 mgC/m²/day (95% limits, 62—103 mgC/m²/day) despite a very high net productivity (mean, 1700 mgC/m²/day). Respiration rate in Lake Valencia was thus some 5 times higher than the average for Lanao, and is outside the highest of values ever observed in Lanao. It appears that the lake has moved considerably toward heterotrophy.

The phytoplankton collected in July, from the euphotic zone are itemized in Tab. 10. The assemblage is in all senses dominated by bluegreens, which are both abundant and diverse in the plankton. Mere presence of bluegreens is of course not extraordinary for lakes of the lowland tropics, but bluegreens are usually exceeded in variety by the Chlorophyta. The great variety of bluegreens in Valencia is probably attributable to the enrichment of the lake with nutrients and salts. Although the balance of the community is unusual due to the large variety of bluegreens, the species composition itself is not remarkable among tropical plankton communities. It therefore appears that enrichment of the lake may have exaggerated the variety and standing crop of bluegreens without grossly changing the species composition. Salination may ultimately progress to still another stage in which species composition also changes.

It is noteworthy that neither the mixotrophic nor heterotrophic flagellates were present in significant numbers despite the heterotrophic tendencies of the lake. Evidently the enrichment of the lake is a stimulus to the bacterial populations but not to other small heterotrophs.

Tab. 10. Census of phytoplankton and small heterotrophs in Lake Valencia.

	Volume per plank. unit μ^3	Plank. units per ml	Biomass μ^3/ml
Autotrophs			
Cyanophyta			
<i>Aphanocapsa delicatissima</i>	25	71	1,775
<i>Aphanobacter</i> sp. 1	5	572	2,860
<i>Chroococcus</i> sp. 1	30	3,300	99,000
<i>Chroococcus</i> sp. 2	120	71	8,520
<i>Merismopedtia glauca</i>	344	86	29,584
<i>Synchroococcus</i> sp. 1	1	620	620
<i>Rhabdoderma</i> sp. 1	2	858	1,716
<i>Dactylococcopsis facicularis</i> f. <i>solitans</i> (straight)	15	1,073	16,000
<i>Dactylococcopsis facicularis</i> f. <i>solitans</i> (coiled)	15	191	2,865
<i>Anabaenopsis raciborskii</i>	600	36	21,600
<i>Anabaena tolstii</i>	150	60	9,000
<i>Anabaena</i> (aphanizomonoides)	400	44	17,600
<i>Spirulina</i> (<i>laxissima</i>)	20	95	1,900
<i>Oscillatoria</i> (<i>limnetica</i>)	225	371	80,000
<i>Oscillatoria</i> sp. 1	150	95	15,000
<i>Lynxeya limnetica</i>	100	925	92,500
<i>Lynxeya limnetica</i> f. <i>minor</i>	5	766	3,800
subtotal		9,174	404,340
%		64	55
Chlorophyta			
<i>Coccomyxa</i> sp. 1	4	1,526	6,124
<i>Chlorella</i> sp. 1	30	238	7,140
<i>Oocystis</i> sp. 1	300	155	40,500
<i>Ankistrodesmus setigerus</i>	50	24	1,200
<i>Closteridium</i> sp. 1	80	24	1,920
<i>Selenastrum gracilis</i>	5	667	3,335
<i>Selenastrum</i> sp. 1	5	238	1,190
<i>Tetraedron</i> sp. 1	100	24	2,400
<i>Trebularia</i> sp. 1	15	24	360
<i>Scenedesmus</i> (<i>ecornis</i>)	200	48	9,550
Unknown green #1	800	48	38,400
Unknown green #2	60	240	14,400
subtotal		3,256	132,499
%		23	18
Cryptophyta			
Cryptophyceae			
<i>Rhodomonas minuta</i>	180	95	17,100
subtotal		95	17,100
%		1	2
Bacillariophyceae			
<i>Melosira granulata</i>	800	84	67,200
var. <i>angustissima</i>	50	48	2,400
<i>Nitzschia amphibia</i>	30	476	14,280
<i>Nitzschia kurzlingiana</i>	100	1,073	107,300
<i>Nitzschia palea</i>		1,681	191,180
subtotal		12	26
%		100	100
Total Autotrophs		13,446	741,319
		100	100

Conclusions

Lake Valencia is quite obviously experiencing a precipitous physical, chemical and biological evolution. The volume of the hypolimnion, as defined by the seasonal thermocline in deep water, has undoubtedly declined steadily to its present negligible level as the mean depth of the lake has decreased. Such a change is likely to speed the recycling of limiting nutrients and thus increase gross productivity. Simultaneously, nutrient input has increased absolutely and will continue to increase on an areal or volume basis due to the desiccation of the lake even if no further absolute increase occurs. An increase of total respiration is likely as well. This will very likely be accompanied by major shifts in phytoplankton composition. As respiratory oxygen demand increases, the probability of anoxia becomes greater and will increasingly affect shallow water areas. Changes in distribution of the mayfly *Campurms* already provide evidence of this trend (WEINEZAHN, unpublished). As desiccation proceeds, community metabolism will very likely become increasingly like that of such shallow tropical lakes as Lake George, Uganda, which have high respiration, high volume-specific standing crop dominated by bluegreens, and extreme diurnal chemical rhythms (GANF 1972, 1974; GANF & VINEK 1973). Even now, the energy flow through the decomposer chains has evidently increased greatly. Biotic changes due to oxygen depletion seem inevitable if the present trend is not arrested.

Lagartijo Reservoir

There is more comprehensive limnological information on Lagartijo Reservoir than any other Venezuelan waterbody. Seasonal studies by WEINEZAHN et al. have been in progress since 1967, and have thus far culminated in detailed accounts of primary production (MARTINEZ 1970), *Chaoborus* (CRUSSA 1971), and the phytoplankton (DE REYES 1972). The survey data taken on Lagartijo during July 1974 in connection with the present work are therefore discussed against the background of the much more detailed information available from earlier studies.

Lagartijo Reservoir was formed by construction of a dam on the Rio Lagartijo just above its confluence with the Rio Tuy (fig. 2). The reservoir is of economic importance as a water source for Caracas, hence the watershed is partly protected and there are no large sources of artificial nutrients near the lake.

The physical features of Lagartijo Reservoir are summarized in Tab. 11. The morphometry of the lake is rather unusual among reservoirs, as mean depth is great despite the dendritic shape and small size. Much of the flooded river valley that now forms the lakebed is abruptly sloped. The littoral zone is therefore insignificant, especially toward the dam, and the lake is highly

Tab. 11. Physical data on Lagartijo Reservoir as determined by WEINZAHN et al. (unpubl.) and reported in MARTINEZ (1970).

Altitude m	Area km ²	Volume km ³	Mean Depth m	Max Depth m	Shoreline km	Watershed km ²
190	4.55	.080	17.5	54.8	75.3	298

sheltered by the steep hills rising along the shoreline. The reservoir is thus reminiscent of a ford.

Although seasonal changes in rainfall are unquestionably significant to the nutrition of the plankton in Lagartijo, the flushing rate of the reservoir is not so high as in many reservoirs. Ratio of watershed size to lake area is 65, and rainfall in this part of Venezuela is relatively low, ordinarily much below 2 m/yr (Fig. 10). Twenty-six cm of runoff from the watershed is sufficient to equal

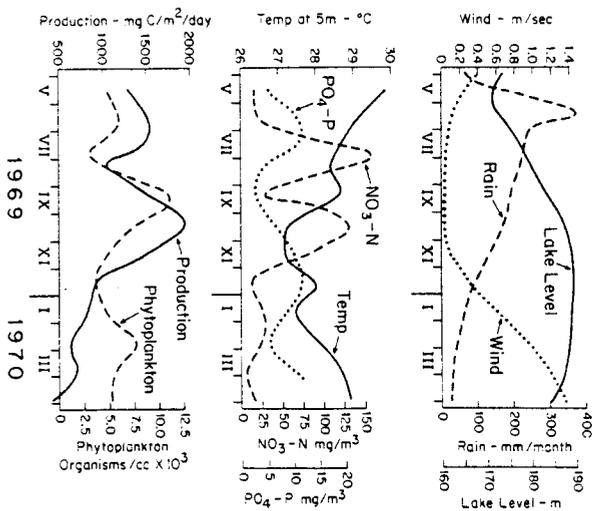


Fig. 10. Physical, chemical, and biological variation in Lagartijo Reservoir as determined by WEINZAHN et al. and reported in MARTINEZ (1970) & CRESSA (1971). Chemical and biological measurements were monthly, others more frequent. Temperature is for 5 m depth in the water column, nitrate, phosphate, and phytoplankton are averages for the upper 12 m of the water column.

the volume of the lake, but this amount of runoff is unlikely to accumulate over a short interval except during the wettest month of the rainy season. Fig. 10 shows that the rainy season of 1969 spanned June—November and that the remaining 6 months were quite dry. This is a true seasonal pattern, although the onset of the seasonal rains is somewhat irregular. In 1974, for ex-

ample, heavy rains were delayed past June. Fig. 10 also shows the buffering effect of the watershed on lake level. Lake level is greatest at the end of the wet season and beginning of the dry season. The seasonal trend in wind strength is inversely related to the seasonal trend in rainfall.

Thermal cycle and chemistry

The water near the lake surface shows a seasonal trend that is marked by generally declining temperatures during the rainy season, a minimum at the end of the rainy season, and a general warming throughout the dry season. Fig. 10 shows this trend clearly and in addition illustrates temporary departures from the seasonal trend during 1969—1970. MARTINEZ (1970) remarks that the lake does not become isothermal during the cool season, although the deep water cools considerably. During the cool season, the water of the Lagartijo River is cooler than the hypolimnetic water, hence the river water flows along the lake bottom as a density current (MARTINEZ 1970). Although the hypolimnion is recharged with oxygen during the cool season, oxygen is apparently transferred mainly by density currents and not by wind-generated mixing from the surface.

Lagartijo can be considered anomalous in the sense that a natural lake with a smaller watershed and similar dimensions would almost certainly be monomictic under the same climatic regime (LEWIS 1973a). Failure of complete seasonal destratification in Lagartijo is readily understandable considering the large flow of cold water into the hypolimnion during the cooling season. Cooling of the hypolimnion by river water occurs as rapidly as cooling of the surface layer by radiative and evaporative heat loss, hence a density difference is preserved between the water layers despite seasonal change in mean temperature of both layers. The invulnerability of the layering to wind stress is also effectively increased by the topography, which shelters the lake, and by the shape of the lake, which provides for little fetch. Similar perennial stratification will undoubtedly be observed in other tropical lakes that experience marked hypolimnetic cooling by rivers. Such lakes are likely to have high ratios of watershed to lake surface area so that runoff can supply the large volume of water needed to cool the hypolimnion.

The thermal profile for July 1974 (Fig. 11) is somewhat remarkable in that the hypolimnetic temperature (23.60 °C) is considerably lower than the minimum temperature reported by MARTINEZ (1970) for 1969—70 (25.0 °C). The epilimnetic temperatures are essentially identical, however. Obviously the events during the cooling period differed for the two years, possibly by a simple variation in the magnitude of the hypolimnetic influx of cool water from the Rio Lagartijo.

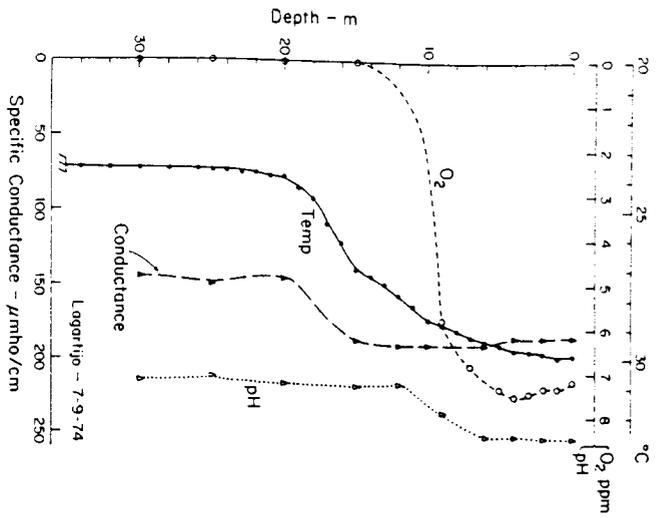


Fig. 11. Profiles of specific conductance, temperature, pH, and oxygen 2 km from the dam on Lagartijo Reservoir.

The water of Lagartijo is a well-buffered bicarbonate type (Tab. 2). In addition to the substances tabulated in Tab. 2, the lake contains the following average concentrations of other substances in the euphotic zone: nitrate-nitrogen, 60 mg/m³; phosphate-phosphorous, 10 mg/m³; iron, 0.25 mg/l; chloride, 8 mg/l; silicate, 22 mgSiO₂/l; and magnesium, 10 mg/l (WEINZAHN et al., unpublished). Fig. 10 shows a clear relationship between temperature of the upper water column and nitrate and phosphate concentrations in the euphotic zone. Dissolved nutrients are present in the upper water column only when temperature is declining. This is almost certainly explained by the greater likelihood of partial vertical mixing during the cooling season (i. e., atelomixis, LEWIS 1973a). It is interesting to note in Fig. 10 that the non-seasonal interruption of cooling in August and September is accompanied by decline of soluble nutrients near the surface, presumably due to the decrease in vertical exchange between layers during this period.

The chemical profiles for early July 1974 indicate the marked divergence in chemical properties of the two main water layers just at the end of a dry season. Complete anoxia below 15 m is evidence of a quite rigid dry-season separation between epilimnion and hypolimnion. The hypolimnion contains considerably smaller amounts of ions, as this water flowed into the hypo-

limnion during the rainy season. The water in the epilimnion has a higher conductance due to evaporative concentration of dry season runoff flowing into the epilimnion and considerable evaporation at the lake surface itself.

Production and respiration

MARTINEZ data show a quite clear relationship between primary production and nutrient supply (Fig. 10). Primary production is evidently suppressed by deficiency of N and P when there is little exchange between epilimnion and hypolimnion. Vertical movement of nutrients in response to turbulence in the water column is thus probably the critical factor controlling primary production most of the year. The regulatory mechanism of primary production is in this respect apparently similar to that of Lake Lanao, Philippines (LEWIS 1974).

The profile of net production and respiration in Lagartijo was measured by the oxygen-difference method during July 1974 (Fig. 12). The production profile shows no evidence of light inhibition, as the sky was overcast during the incubation. The net production for the period was 1300 mgO₂/m², or 413 mgC/m². The amount of sunlight was only 132 cal/cm², hence the ecological efficiency was 3.12 mgC/m²/ly. For a standard day the production would thus amount to 1252 mgC/m²/day. The annual average reported by

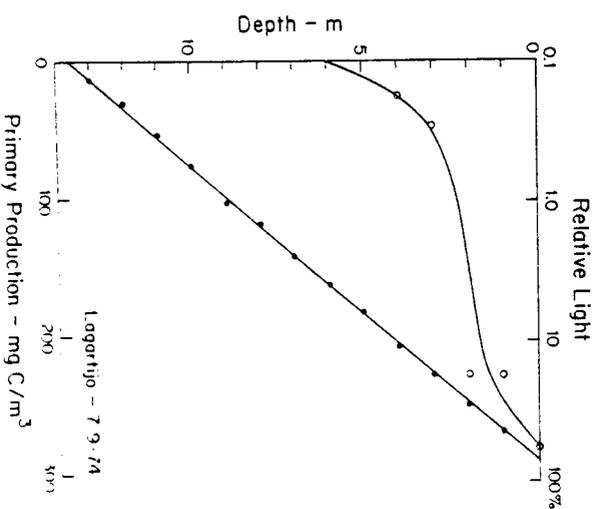


Fig. 12. Net primary production and light penetration in Lagartijo Reservoir for an incubation period lasting 3.75 hr on an overcast day.

MARTINEZ is 1126 mgC/m²/day (n = 14), or only about 10% less than the estimate obtained during the survey.

Mean respiration for the upper 4 m of the water column was 30 mgO₂/m²/hr, or 229 mgC/m²/day. Respiration per unit area for the upper 5 m of the water column was thus nearly equal to the net production for a standard day. If respiration on July 4 was not atypical, the P/R ratio for the upper 5 m of the lake is near 2.0, hence for the entire lake P/R is likely to lie between 1.0 and 1.5 even if respiration below 5 m is considerably lower than in the top 5 m.

The phytoplankton of Lagartijo Reservoir have been rigorously studied by DE REYES (1972). Tab. 12 lists the species that were identified by DE REYES

Tab. 12. Phytoplankton species occurring in Lagartijo Reservoir, according to DE REYES (1972).

Cyanophyta	Chlorophyta (continued)
<i>Anacystis montana</i>	<i>S. cuspidatum</i>
<i>Chroococcus turpidus</i>	<i>S. aradum</i>
<i>Agmenellum quadrifidum</i>	<i>S. sp.</i>
<i>Oscillatoria subbrevis</i>	<i>Sphaerosoma excavatum</i>
<i>Spirulina</i> sp.	<i>Coscinium choresiacum</i>
<i>Anabaena arphazizomenoides</i>	<i>Spirotenia</i> sp.
<i>A. volzii</i>	Euglenophyta
<i>Cylindrocapsa stagnale</i>	<i>Phacus triquetrus</i>
(= <i>Anabaenopsis raciborskii</i>)	<i>Leptocleisis ovum</i>
Chlorophyta	<i>Trachelomonas bacillifera</i>
<i>Elakatorhix gelatinosa</i>	<i>T. volvoecia</i>
<i>Golenkonia radiata</i>	<i>T. sp.</i>
<i>Dicystosphaerum pulchellum</i>	Chrysoophyta
<i>Schroederia setigera</i>	<i>Melosira granulata</i>
<i>Coelastrum microporum</i>	<i>Cyclotella meneghiniana</i>
<i>Oocystis lacustris</i>	<i>Synedra acus</i>
<i>O. marsonii</i>	<i>Nitzschia gracilis</i>
<i>Chlorella</i> sp.	Pyrrrophyta
<i>Ankistrodesmus falcatus</i>	<i>Sphaerodinium cinctum</i>
<i>Chodatella subbasila</i>	<i>Peridinium inconspicuum</i>
<i>Tetradion muticum</i>	<i>P. pyrmatium</i>
<i>T. caudatum</i>	<i>Cryptomonas erosa</i>
<i>T. trigonum</i>	
<i>Trebularia triarppendiclaria</i>	
<i>Scenedesmus ecomis</i>	
<i>S. acuminatus</i>	
<i>Crucigenia rectangularis</i>	
<i>C. tetrapedia</i>	
<i>Closterium acutum</i>	
<i>Saurastrium detexum</i>	

in the plankton during 1966—68. DE REYES lists 58 species, but a number of heavy diatoms and other species that are considered to be only incidental elements of the plankton are omitted from Tab. 12.

Tab. 13 gives the results of the census conducted on samples taken during July 1974 in connection with our survey. Comparison of the species compo-

tion with that indicated in Tab. 12 is informative in several respects. Tab. 12 contains a number of species that do not appear in Tab. 13. This is expected, as Tab. 13 includes only those species satisfying a predetermined criterion of abundance. In addition, Tab. 13 contains a few species that are not listed in Tab. 12. This is partly explained by the taxonomic confusions that cannot be entirely eliminated, but there must also have been some change in species composition in the years between 1968 and 1974. For example, we find *Lyngbya* in abundance during July 1974, but DE REYES did not find this genus during 1966—68 despite intensive study. The obvious diagnostic features

Tab. 13. Census of phytoplankton and small heterotrophs in Lagartijo Reservoir.

Autotrophs	Volume per plank. unit μ ³	Plank. units per ml	Biomass μg/ml
Cyanophyta			
<i>Aphanocapsa delicatissima</i>	250	72	17,908
<i>Chroococcus</i> sp.	30	2,149	64,470
<i>Rhabdodetma sigmoides</i>	10	5,301	53,010
<i>Dactylooscopus acicularis</i>	10	143	1,430
<i>Anabaenopsis raciborskii</i>	240	7,700	1,848,000
<i>Anabaena volzii</i>	300	72	21,600
<i>Lyngbya limnetica</i>	70	5,530	386,800
subtotal		20,967	2,393,218
		93	89
Chlorophyta			
<i>Cocconeuxa</i> sp. 1	10	215	2,150
<i>Oocystis</i> sp. 1	60	179	10,745
<i>Selenastrium</i> sp. 1	15	72	1,080
<i>Selenastrium</i> sp. 2	3	143	429
<i>Scenedesmus ecomis</i>	120	143	17,192
<i>Crucigenia tetrapedia</i>	100	18	1,800
Unknown sp. 1	30	215	6,450
subtotal		985	39,846
		4	2
Euglenophyta			
<i>Trachelomonas</i> sp. 1	1,500	72	108,000
subtotal		72	108,000
		< 1	4
Chrysoophyta			
Cryptophyceae			
<i>Rhodomonas minuta</i>	30	72	2,160
<i>Cryptomonas erosa</i>	500	287	143,500
subtotal		359	145,660
		2	5
Bacillariophyceae			
<i>Nitzschia amphibia</i>	50	217	10,750
subtotal		217	10,750
		1	1
Total Autotrophs		22,598	2,697,474

of the genus make errors of identification unlikely in this case, hence we must conclude that *Lynghya* was either not present during 1966-68, or was sufficiently rare to go undetected in all samples. A similar situation has been documented for Lake Lanao (Lewis 1973b), in which *Botryococcus* was observed to be a major species in an early study, but did not appear at all in the plankton years later. There is no reason to suspect marked directional changes in lake chemistry in either of these cases, hence major changes in the importance of various species may prove to be even more dramatic in tropical than in temperate lakes.

Bluegreens dominated the July sample from Lagartijo. *Anabaenopsis ractoriskii* accounted for more than half the standing crop, and *Lynghya limnetica* for much of the rest. Bluegreen blooms are common under natural conditions in the lowland tropics, and these two species are common components of such blooms. The species composition is not remarkable.

Guanapito Reservoir

Guanapito Reservoir, like Lagartijo, was formed by blockage of drainage from the protected Guatopo National Park near Caracas (Fig. 2). Guanapito is slightly larger (ca. 10 km²) and less dendritic than Lagartijo, but the topography of the watershed is similar. The dam spans the Rio Orituco, which is a small river with a highly seasonal flow. At the end of the dry season the lake may lie as much as 10 m below the spillway, as it did during July 1974 at the time of the survey sampling. Maximum depth is near 40 m at the spillway level. Guanapito lies on the interior side of the Guatopo high country, which receives considerably less rainfall than the coast side, where Lagartijo is situated. Approximate annual rainfall at Guanapito is near 100 cm, and at Lagartijo it is about 200 cm/yr (Ministerio de Agricultura 1960).

Temperature and chemical profiles

At the time of the survey, Guanapito was actively mixing only to 6-7 m, at which depth there was a slight but significant thermal gradient that should be considered a thermocline, as it was obviously not a diurnal boundary (Fig. 13). Above this, the zone of diurnal heating occupied the uppermost 2 m, but the chemical characteristics of the top 6 m were highly uniform, which would suggest daily mixing to a depth of 6 m. Below 7 m was a zone of uniform temperature approximately 6 m thick with an intermediate oxygen and pH, and below this was a second slight but significant thermal transition containing a marked oxygen gradient. The bottom 8 m was more uniform in temperature and was anoxic.

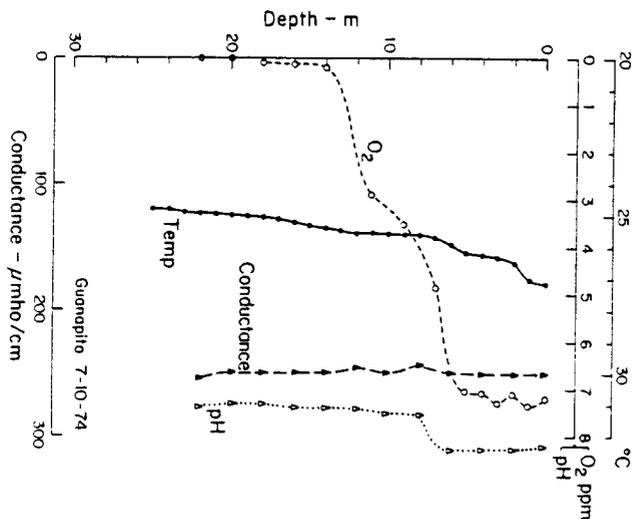


Fig. 13. Temperature and chemical profiles in Guanapito Reservoir.

The vertical profiles are reminiscent of Lake Lanao (Lewis 1973a) and are amenable to a similar explanation.

There are two thermoclines, one centered at 6 m and the other at 15 m. The first thermocline is in equilibrium with gentle winds and sunny weather, which prevailed at the time the data were taken. From the considerable oxygen depletion just below this upper thermocline it appears that no mixing had occurred below 6 m for at least several days and probably a week or more, but it is also evident from the presence of some oxygen below 6 m that mixing cannot have been restricted to the top 6 m for the entire season. The second thermocline is in equilibrium with heavy winds, and even so lies relatively close to the surface due to the limited fetch and protected shoreline. Wind-generated mixing to about 14 m must have occurred in the recent past during an episode of stormy weather, and since that time the epilimnion had been split into an upper circulating layer and a deeper stagnant layer due to heat accumulation near the surface in calm sunny weather. The chemical divergence of the epilimnetic layers is expected due to their separation. Another episode of windy weather would mix the lake once again to 14 m, perhaps even deeper, and thereby bring about atelomixis.

The vertical profiles do not show any evidence of residual cool underflows as in Lagartijo Reservoir, and the deep water is considerably warmer than

that of Lagartijo. This is explained either by complete absence of an underflow, or by complete mixing subsequent to a seasonal underflow.

The water is harder than that of Lagartijo, presumably due to the lower rainfall near Guanapito.

Primary production

Primary production and light penetration are given in Fig. 14. Primary production was measured by oxygen difference. The bottles that would have been used to compute initial oxygen concentration were lost, hence the net production has been estimated by subtracting an estimated respiration from the measured gross photosynthesis. Respiration was estimated as the same proportion of gross production as in Lagartijo. Since respiration is small relative to gross photosynthesis at midday, this approximation should not cause great error.

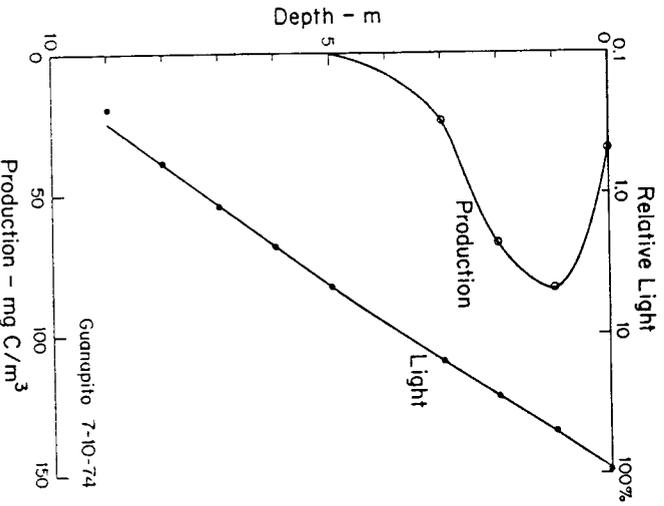


Fig. 14. Primary production and light penetration in Guanapito Reservoir.

Net primary production totalled 600 mgC/m² for the incubation period.

The sunlight for the period was 176 cal/cm², hence the ecological efficiency was 3.9 mgO₂/m²/ly, or 1.24 mgC/m²/ly, yielding a total net production of 496 mgC/m²/day for a standard day. This is quite low considering the high

Tab. 14. Census of phytoplankton and small heterotrophs in Guanapito Reservoir.

	Volume per plank. unit μm^3	Plank. units per ml	Biomass $\mu\text{g/ml}$
Autotrophs			
Cyanophyta			
<i>Chroococcus (minutus)</i>	30	2,428	72,857
<i>Rhabdoderma sigmoides</i>	10	1,000	10,000
<i>Dactylococcus fascicularis</i>			
<i>fa. solitarius</i>	30	190	5,714
<i>Anabaenopsis raciborskii</i>	240	482	115,714
<i>Oscillatoria limnetica</i>	75	94	7,071
<i>Oscillatoria planctonica</i>	150	152	22,857
<i>Lynxbya limnetica</i>	50	5,046	252,300
<i>Lynxbya limnetica</i> var. <i>minor</i>	6	1,220	7,320
subtotal		10,612	493,533
%		51	27
Chlorophyta			
<i>Glaucozystis planctonica</i>	120	190	22,857
<i>Chlorella</i> sp. 1	25	333	8,333
<i>Oocystis</i> sp. 1	125	761	95,238
<i>Tetradion minimum</i>	100	809	80,900
<i>Trebharia</i> sp. 1	30	47	1,414
<i>Crucigenia rectangularis</i>	80	12	957
Unknown # 1	50	714	35,714
subtotal		2,866	245,413
%		14	14
Chrysophyta			
<i>Cryptophyceae</i>			
<i>Cryptomonas</i> sp. 1	1,500	47	70,500
subtotal		< 1	70,500
%			4
Bacillariophyceae			
<i>Cyclotella stelligera</i>	300	1,857	557,143
<i>Synedra acus</i>	300	667	200,000
<i>Synedra acus</i> var. <i>radians</i>	125	380	47,619
<i>Adnantes microcephala</i>	25	96	2,393
<i>Nitzschia acicularis</i>	50	667	33,333
subtotal		3,657	840,488
%		18	46
Total Autotrophs			
%		17,192	1,649,914
%		83	91
Heterotrophs			
Protozoa			
Flagellate 1	20	3,095	61,901
Flagellate 2	40	95	3,828
Flagellate 3	30	47	1,418
Flagellate 4	500	47	23,500
Ciliate 1	500	143	71,633
subtotal		3,427	162,283
%		17	9

dissolved solids and high temperature of Guanapito. Standing crop of phytoplankton, which accounts for the greatest amount of light extinction, is nevertheless quite high. These factors implicate nutrient depletion as the cause of low production.

Low primary production in a tropical lake with a temporary, high-lying thermocline is once again reminiscent of Lake Lanoo (Lewis 1974). Division of the epilimnion limits the nutrient pool so severely that nutrient depletion shortly becomes marked and limits photosynthesis. Depletion is probably relieved by atelomixis under the control of nonseasonal weather changes.

The plankton census is summarized in Tab. 14. The standing crop is dominated by diatoms, which is a contrast with all of the other lakes. The importance of *Cyclotella* is noteworthy, as the diatoms in lakes of this kind are ordinarily dominated by *Melosira*, *Nitzschia*, and *Synedra*, although other genera may be present in small numbers. Small flagellates are also more important here than in the other lakes.

Guri Reservoir

The Guri Reservoir, which was created in 1968, is the largest freshwater body in Venezuela. The reservoir is currently about 2.5 times the size of Lake Valencia, and when the dam is extended from its present height of 110 m to its stage II height of 160 m, the water surface will be about 10 times that of Valencia (Tab. 15).

Tab. 15. Statistics for Guri Reservoir taken or computed from various government sources.

Watershed Area	Discharge		Volume ¹		Area		Mean Depth		Flush Rate		
	Mean	Max	Min	I	II	I	II	I	II	I	
km ²		m ³ /sec		km ³		km ²		m		%/yr	
95000	5000	17000	200	17.7	103.0	800	3280	22	31	900	150

¹ I signifies stage I of dam construction, presently complete. II signifies stage 2 of construction, not yet initiated.

The Guri Reservoir is part of a hydroelectric development plan on the Caroni River in the undeveloped region of east Venezuela (fig. 2). A dam was first constructed on the Caroni just above its confluence with the Orinoco (Macagua Dam), but the impoundment created by the dam, Lago Gil, is not large. Guri dam was subsequently constructed some 30 km to the south along the Caroni.

The reservoir receives water from two major rivers, The Caroni and the Paragua, plus a number of minor rivers. The ratio of watershed to lake area

is currently 119 and will decline to 29 when the dam height is increased. The immediate area of the reservoir is moderately dry (80—160 cm/yr rain), but the annual rainfall increases markedly toward the southern part of the watershed, which includes some area receiving as much as 300 cm/yr. May through August are generally wet months. Mean annual temperature is between 20 and 24°C in the southern half of the watershed and 24—28°C in the northern half. A large portion of the land immediately surrounding the reservoir supports a "chaparral" vegetation consisting of savannahs bearing short trees such as *Curratella americana*. There is to the south and east of this dry area a belt of deciduous forest. The flooded portion of the watershed, whose trees extend from the water surface, was largely of this classification. The bulk of the watershed to the south, which is generally higher (500—2000 m), consists of wet forests. The human population density of the watershed is negligible.

Despite the great size of the watershed, the water volume of the reservoir is sufficiently great to prevent rapid flushing. Mean annual replacement time is currently 41 days and will increase to 240 days when the lake volume is increased. The seasonal flow is well-buffered due to the unaltered nature of the watershed. Although the Guri is not a markedly dendritic reservoir, it contains a large number of islands that greatly increase the shoreline area and retard mixing. A significant portion of the lakebed is covered with trees, none of which were felled prior to construction.

Temperature and chemical profiles

Interpretation of vertical profiles from Guri is more difficult than for Lagartijo or Guanapito, since there was a significant discharge at the Guri Dam at the time of sampling. Vertical profiles thus reflect flowthrough as well as wind mixing in Guri.

The thermal profile is clearly divided into zones (fig. 15). The upper 5 m is a zone of diurnal heating. The total heat stored within the top 5 m in excess of the isothermal zone below was about 375 cal/cm², or only slightly more than would have accumulated by midday on a sunny day. Either some of the heat was advective gain from the shore, or there was some heat storage in the upper 5 m overnight, so that the upper 5 m was the limit of wind mixing over the previous 24 hr. The latter possibility is likely in view of the calm weather. Between 5 and 20 m is a zone of nearly isothermal water which may owe its homogeneity either to flowthrough or wind mixing to 20 m during windy weather, probably both. Mixing below 20 m is not likely during the warm season due to the inhibition of circulation and wind stress by emergent trees and islands. There is a clear thermal discontinuity at 20 m, and between 21 and 28 m lies a second zone of very uniform temperatures, which is probably a remnant of seasonal mixing.

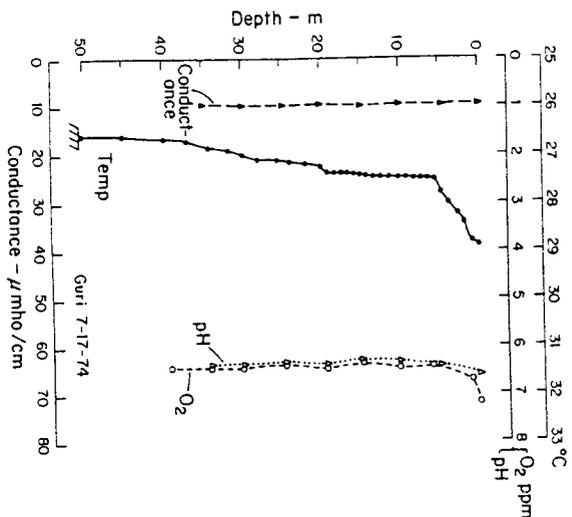


Fig. 15. Temperature and chemical profiles in the Guri Reservoir.

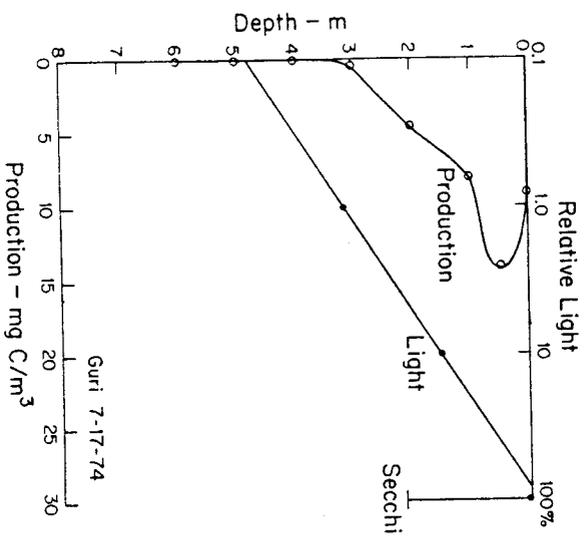


Fig. 16. Primary production and light penetration in the Guri Reservoir.

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The chemical profiles are homogeneous to 50 m. This is not necessarily indicative of recent mixing to this depth, however, as the water is so sterile that biologically-induced changes in dissolved components must occur very slowly except in the uppermost 2 m. As chemical profiles did not extend to 50 m, it is not possible to say whether some chemical changes would occur in the lowermost 10 m.

The low pH of the water (Fig. 15) and extremely low electrolyte content are characteristic of darkwater rivers such as those entering the Guri Reservoir. The lake is in fact a dark-water reservoir, as the chemistry of the dark river waters is not substantially changed as a result of impoundment. The water is teal-colored due to the presence of limno-humic substances derived from the humid forests to the south. Light penetration is consequently inhibited (Fig. 16) even though turbidity is negligible and plankton standing crop is lower than in any of the lakes included in the survey.

Primary production and respiration

Primary production in Guri was so low that it could not have been detected by oxygen difference. The net production profile as determined by C-14 for a 3.5-hr incubation in almost full sunlight is shown in Fig. 16. Extremely low maximum rate is explained by nutrient limitation, and the vertical compression of the profile is explained by poor light penetration.

The total net production for the period was 31.9 mgC/m^2 . The lake received 196 cal/cm^2 of sunlight during the incubation period, hence the ecological efficiency was $0.16 \text{ mgC/m}^2/\text{ly}$. Production for a standard day would thus be $65 \text{ mgC/m}^2/\text{day}$.

Respiration was measured at 1 m and 5 m by incubation of 4 replicate dark bottles for 5.5 hr and subsequent comparison of their oxygen content with 4 initial oxygen determinations at each depth. No statistical difference was detected at either depth. Respiration was thus below $0.010 \text{ mgO}_2/\text{m}^2/\text{hr}$, as might be expected.

Tab. 16 summarizes the plankton census. These data are of particular interest, as little is known of the plankton composition in such dark waters, especially under reservoir conditions. Desmids are reputed to be important in such soft waters. A great variety of desmids can in fact be found in Guri (R. HOSFORD, pers. communication), but Tab. 16 suggests that other forms may be more important to the energetics of the plankton.

The phytoplankton are remarkably varied in Guri, as is evident in Tab. 16. Despite the extreme nutrient poverty of the water, a considerable number of bluegreens were present. These were for the most part very small non-filamentous forms, and can in this respect be considered different from the typical bluegreen component of uncolored lowland tropical lakes. The eco-

Tab. 16. Census of phytoplankton and small heterotrophs in Guri Reservoir.

	Volume per plank. unit μ^3	Plank. units per ml	Biomass $\mu\text{g/ml}$
Autotrophs			
Cyanophyta			
<i>Aphanocapsa delicatissima</i>	4	9	36
<i>Aphanobcece</i> sp. 1	8	9	72
<i>Chroococcus minutus</i>	30	9	270
<i>Merismopedta tenuissima</i>	20	10	200
<i>Rhabdoderma sigmoides</i> fa. <i>minor</i>	5	1,343	6,715
<i>Dactylococopsis fascicularis</i>			
fa. <i>solitaria</i>	20	67	1,331
<i>Dactylococopsis (rabdihroides)</i>	10	76	760
<i>Cyanarctus</i> sp. 1	3	57	171
<i>Lyngeya himetica</i>	50	20	1,000
subtotal		1,600	10,555
		66	2
Chlorophyta			
<i>Gloerocystis planctonica</i>	140	19	2,660
<i>Pediastrum tetras</i>	120	9	1,080
<i>Coelastrum</i> sp. 1	360	16	5,760
<i>Chlorella</i> (<i>ellipsoides</i>)	10	371	3,710
<i>Chlorella</i> sp. 1	15	9	135
<i>Ankistrodesmus falcatus</i>	40	9	360
<i>Ankistrodesmus</i> sp. 1	70	9	630
<i>Tetraedron asymmetricum</i>	300	9	2,700
<i>Scenedesmus quadricauda</i>	300	23	6,900
<i>Scenedesmus (arcuatus)</i>	150	19	2,850
<i>Crucigenia tetrapedia</i>	40	9	360
<i>Cosmarium</i> sp. 1	10	19	190
subtotal		540	27,525
		22	6
Chrysophyta			
Cryptophyceae			
<i>Rhodomonas minuta</i>	250	48	11,929
<i>Rhodomonas minuta</i>			
var. <i>nanoplanktonica</i>	25	29	714
<i>Cryptomonas</i> sp. 1	300	67	19,971
subtotal		144	32,634
		6	7
Bacillariophyceae			
<i>Rhizosolenia eriensis</i>	35	9	315
subtotal		9	315
		<1	<1
Pyrrophyta			
<i>Gymnodinium</i> sp. 1	125	19	2,375
<i>Gymnodinium</i> sp. 2	125	9	1,125
<i>Peridinium</i> sp. 1	13,000	29	377,000
subtotal		57	380,500
		2	84
Total Autotrophs		2,350	451,509
		96	99
Heterotrophs			
Flagellate 1	30	9	270
Flagellate 2	50	9	450
Flagellate 3	10	67	670
subtotal		85	1,390
		4	<1

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logical role of these very small bluegreens, which are routinely overlooked whenever nets are used, may prove to be rather different from that of the largest filamentous and coccoid forms that are so frequently prominent in nutrient-rich lakes.

Important species at the time of sampling included a number of green algae, as might be expected, but only one very small desmid. Cryptomonads and Pyrrophyta were much more important than in other lakes except Mucubají. The selective advantage of flagellates in nutrient-poor mountain lakes of the temperate zone is becoming increasingly evident (TRIZER & SCHWARZ 1976). The dark waters of the tropics may confer similar advantages on flagellates, particularly since the lighted zone is very limited.

Heterotrophic flagellates were also rather numerous in Guri, which contrasts in this respect with all of the other lakes except Guanapito.

Rhizosolenia is a noteworthy element of the flora, as it is not found in the other lakes.

Carrao river

The Rio Carrao, which empties into the Caroni, was sampled at Canaima. Some chemical properties of the water are indicated in Tab. 2. The water contains larger amounts of organic acids than the water of Guri, which is a mixture of waters. The high organic content and low electrolyte content of the water are characteristic of drainages from humid forests contributing to the composition of Guri Reservoir.

Comparison of habitats

Energy and biomass

Tab. 17 compares energy flow in the 8 principal habitats of study. For lakes it was also possible to compute biomass and biomass turnover from the census data. There is a clear division between the flowing systems, in which the production and respiration by suspended organisms is extremely low, and the lakes, in which suspended organisms govern the energy flow of the entire system. The Rio Limon study shows, however, that the energy flow in flowing systems may be comparable to that of the most productive lentic systems, provided that circumstances are right for the development of an illuminated algal mat. Tendency toward heterotrophy, as measured by the absolute amount of respiration and by the P/R ratio, was at least as pronounced in the lakes, especially Valencia and Lagartijo, as in the Rio Limon.

The success of autotrophs in Rio Limon must be attributed to a favorable nutrient supply and light climate, which are jointly responsible for a high

Tab. 17. Summary of energy flow, biomass, and turnover in the waterbodies of the study.

Location	Primary Production mgC/m ² /std. day	Efficiency %	Community Respiration ^{2,3} mgC/m ² /day	Biomass Autotrophs ⁴ μ ³ /cc	mgC/m ²	P/B Autotrophs ⁵	Biomass Turnover Autotrophs (days)
Lake Mucubaji	168.	0.028	< 720.	1,820,000	18,200	0.0092	108.
Rio Sto. Domingo (free water)	0.29	0.00007	> 36.	—	—	—	—
Rio Aracay (free water)	0.25	0.00006	> 36.	—	—	—	—
Rio Limon ¹ (free water)	2.46	0.0041	> 4.	—	—	—	—
mats	1189.	1.46	1030.	—	—	—	—
entire stream	728.	0.89	730.	—	—	—	—
Lake Valencia	2148.	0.54	3816.	741,000	4,816	0.44	2.27
Lagartijo Res.	1252.	0.31	1832.	2,697,000	24,273	0.051	19.4
Guanapito Res.	496.	0.12	—	1,643,000	11,986	0.041	24.1
Guri Res.	65.	0.016	< 720.	451,509	1,398	0.047	21.5

1. Efficiency computed from sunlight reaching stream surface, not tree canopy.
2. Integrated between water surface and top of hypolimnion in lakes.
3. Rates specified as less than a certain figure were below detection limits.
4. Carbon per unit area is carbon per unit volume integrated over the euphotic zone.
5. P/B applies to euphotic zone as defined by 1% light level.

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efficiency of light utilization (Tab. 17). Although several of the lakes have large nutrient inputs, nutrients within the system are not confined to the zone of production, as in the stream, but tend to accumulate below the lighted zone where photosynthesis is impossible due to light limitation. Only the shallowest lakes (e. g. Lake George, GANF & VIMER 1973; Lake Nakuru, METACK & KURIAM 1974) escape the frequent nutrient depletion that is expected when the nutrient inventory of a lake becomes unequally partitioned between euphotic zone and the deeper water. It is therefore not surprising that the Rio Limon was using light more efficiently than any of the lakes of the study. Physical stress (spates) could of course remove the autotrophs in the Rio Limon, which would reduce its efficiency. Alternatively, seasonal or non-seasonal mixing could relieve nutrient shortages in the lakes and raise the efficiencies of light utilization.

Among the lakes, the biomass figures are in some respects surprising. Biomass of autotrophs (phytoplankton) in Lagartijo and Guanapito is very close to biomass of autotrophs found in Lakes Lanao and Manait in the Philippines (LEWIS 1973c, 1974). Lake Valencia, which might be expected to have the highest standing crop owing to its rich supply of allochthonous nutrients, had a lower standing crop than either Lagartijo or Guanapito. Mucubaji, which might have been expected to have a low standing crop, was comparable to Lagartijo and Guanapito. Guri also had a higher standing crop than expected. This, as in Mucubaji, was due to the presence of some large phytoflagellates.

An explanation for the unexpected crops of Valencia, Mucubaji, and Guri emerges from the calculated biomass turnover (Tab. 17) and from the census data. Valencia has a very high turnover, which is only possible if the mean cell size is relatively small. Mucubaji has such a long turnover time that very large biomass units are implicated. The census data in fact show that Valencia contains an unusually large proportion of very small biomass units, while Mucubaji and Guri contain substantial numbers of large motile cells. Turnover is thus consistent with community composition in these lakes. Evidently the highly enriched environment of Lake Valencia favors autotrophic species with very quick metabolic response, perhaps as a result of competition for nutrients that are erratically plentiful according to the mixing conditions in the lake. Mucubaji and Guri, which must experience chronic nutrient poverty, favor organisms with sufficient motile power to carry them to an ideal depth. The other lakes lie between these extremes, both in their nutrient budgets and in the composition of their communities.

Community structure

Some aspects of community structure are evident in the raw census data. For example, large numbers of species were encountered in Valencia and Guri,

they may be present. Unlimited deviation from average water quality would of course tax the physiological capabilities of most species and thus lead to domination by organisms with special tolerances, as demonstrated by the classical studies of THIEBEMANN (1939) and many subsequent studies. Evidently neither Guri nor Valencia is so extreme, although Valencia may well become so in the future.

The low diversity of the Mucubaji community is perhaps explained by the harsh physical conditions in the high-mountain environment, which might greatly restrict the field of potential competitors in the community. This view is supported by the importance in Mucubaji of certain taxa that seldom dominate the plankton of lowland lakes (*Peridinium*, *Oocystis*).

If the foregoing hypotheses are sound, Lagartijo and Guanapito can be regarded as modal plankton habitats, hence their communities are moderately diverse and are dominated by species that have a wide distribution and are generally abundant in many other lakes. Valencia and Guri are sufficiently deviant from the modal habitat that the common dominants are not so important, even though they are present. These lakes consequently have diverse plankton assemblages. Mucubaji is still more divergent from the modal habitat, and the number of competitors is consequently so restricted that the diversity is low.

Conclusions

The communities of this study can be ranked or clustered according to their physico-chemical characteristics, rates of energy flow, biomass and biomass turnover, community composition, and community structure. The apparent affinity of any two communities will vary greatly according to the criteria by which affinity is determined. For example, the communities of Mucubaji and Guri are quite similar in composition, but grossly different in structure. Similarly, energy flow in Rio Limon is comparable to that in Lake Valencia, but the physico-chemical environments are markedly different.

Our data strongly suggest that a meaningful comparative ecology, at least for aquatic habitats such as these, cannot be based on any single community trait. Ecologists perhaps know this intuitively, but too frequently allow their interests to be channeled toward one community property. It is a worthwhile observation that Lake Valencia and Guri Reservoir have similar community structure, but the value of this observation is immeasurably greater if we also know that the two communities differ by more than an order of magnitude in energy flow and are dominated by markedly different taxa. The evaluation of more than one community property vastly narrows the number of tenable hypotheses that might be adopted to explain major differences between communities, and this is the first major step toward a comparative community ecology.

Summary

Physical, chemical, and selected biological features of 9 freshwater habitats in Venezuela are discussed and compared. Included are one Andean lake (Mucubaji), two Andean rivers (Rio Sto. Domingo, Rio Aracay), and one stream at low elevation (Rio Limon), a large, desiccating lake at low altitude (Lake Valencia), two lowland reservoirs (Lagartijo and Guanapito), and a darkwater reservoir (Guri). The potential bases for ecological comparison of the biota are discussed and those considered to be most effective are used in the subsequent discussion.

Lake Mucubaji, a small cirque lake at 3550 m, contains very soft water (12 $\mu\text{mho/cm}$) and was quite unproductive (168 $\text{mgC/m}^2/\text{day}$, net). The phytoplankton standing crop was nevertheless quite high due to the presence of large diatoms. Chemical and thermal profiles strongly suggest that, contrary to some previous predictions for this lake type, complete nocturnal mixing does not ordinarily occur. The Andean rivers, Sto. Domingo and Aracay, were sampled at several elevations. Chemical data show a 3-fold increase in electrolyte content between 2500 and 200 m. Photosynthesis in the free water was detectable but very low (efficiency of solar conversion, 0.00007%). Bacteria-size cells of unproven trophic status may partly account for carbon fixation. Photoinhibition was demonstrated by experimental shading of water. The Rio Limon, a low-altitude stream flowing under a tree canopy, has about the same electrolyte content as the lower-most reaches of the Andean rivers. Photosynthesis in the free water was considerably higher than in the Andean rivers (conversion, 0.0041%) but still very low. Photosynthesis rates of algal mats in the stream were very high (1189 $\text{mgC/m}^2/\text{day}$) despite considerable shading. The photosynthetic rate of *Hildenbrandia*, which coats fixed stones, was very low, hence the success of the species is attributed to factors other than rapid growth. An energy balance was constructed for Rio Limon, including all major photosynthetic and respiratory components, and the stream proved to be autotrophic at the time of study (P. R. = 1.8). Lake Valencia, a large endohetic waterbody, is very high in electrolytes (1830 $\mu\text{mho/cm}$) and receives large amounts of domestic and industrial effluents. Sampling of canals and rivers yielded estimates of 3.73 $\text{mgP}/\mu\text{m}^2$ lake/day for phosphorous loading and 210 $\text{mg O}_2/\mu\text{m}^2$ lake/day for labile organic matter oxygen equivalent. Net production was high (2148 $\text{mgC/m}^2/\text{day}$), which is not unusual for lowland lakes of this latitude, but respiration was also high (3816 $\text{mgC/m}^2/\text{day}$, 0—10 m). Autotrophs include a greater variety of bluegreens than is usual, but species composition itself is not remarkable. Future trends are discussed. The reservoir Lagartijo, which contains moderately hard water (185 $\mu\text{mho/cm}$), was not so productive as expected (1252 $\text{mgC/m}^2/\text{day}$), presumably owing to nutrient depletion. An unusual year-round stabilization of the water column is adhered in this lake by inflowing cool water, and this probably limits annual production. Guanapito, which is somewhat more saline (240 $\mu\text{mho/cm}$), was even less productive (500 $\text{mgC/m}^2/\text{day}$) due to extreme drawdown and consequent stagnation leading to nutrient depletion. Guri is a large blackwater reservoir with very low electrolyte content (9 $\mu\text{mho/cm}$) and high organic acid concentration. Net production was very low (65 $\text{mgC/m}^2/\text{day}$) due to nutrient poverty and poor light penetration, and respiration was below detection limits. Guri contains considerable populations of bluegreens but the species composition is considerably different from other lakes. Phytoflagellates were also abundant.

Among the lotic communities, development of significant autotrophy seems to occur when conditions are suitable for development of mats. Mats are vulnerable to spates, and are thus more likely to develop under some conditions than others. Net

production of streams may on an areal basis be as high as that of lakes. Lake productivity is limited not only by nutrient loading, but also by stability of the water column, which governs recycling rates. Of the lakes in this study, only Lagartijo and Guanapito had average phytoplankton standing crops. Guri and Mucubají had higher crops than expected owing to the presence of large phytoflagellates with a low biomass turnover. Lake Valencia had a lower crop than expected due to predominance of species with very small cells. Guri and Valencia had similar community structures with high richness and equitability among phytoplankton species despite their differences in energy flow and biomass. Mucubají was poorest in species and had low equitability. Differences in community structure are explained by a hypothesis based on a modal physico-chemical condition.

The conclusion is that energy flow, biomass, and community structure vary between tropical freshwater systems in an essentially independent manner, hence each of these major variables must be measured if ecosystem comparisons are to have maximum analytical value.

Zusammenfassung

Physikalische, chemische und weitere Eigenschaften von neun Süßwasserbiotopen Venezuelas werden beschrieben und miteinander verglichen. Untersucht wurden der Anden-See Mucubají, die beiden Anden-Flüsse Rio Sto. Domingo und Rio Aracay, der in geringerer Berghöhe fließende Rio Limón, der große, der Austrocknung ausgesetzte Valencia-See, die beiden Flachland-Stauseen Lagartijo und Guanapito sowie der Schwarzwasser führende Stausee Guri. Es werden die möglichen Grundlagen für einen ökologischen Vergleich dieser Biotope dargestellt und die am besten geeigneten erscheinenden Methoden in dieser Arbeit zur Anwendung gebracht.

Der Mucubají, ein kleiner, kreisrunder See in 3550 m Höhe, führt sehr weiches Wasser ($12 \mu\text{S} \cdot \text{cm}^{-1}$) und erwies sich als sehr schwach produktiv ($168 \text{ mg C/m}^2/\text{d}$, netto). Infolge Anwesenheit großer Dimoflagellaten war die Biomasse des Phytoplanktons sehr groß. Die aufgenommenen chemischen und thermischen Profile deuten überzeugend daraufhin, daß eine vollständige Durchmischung in der Nacht normalerweise nicht stattfindet, womit sich ein Widerspruch zu früheren Annahmen für eine solche Seeart ergibt. In den andinen Flüssen Sto. Domingo und Aracay wurde zwischen 2500 und 200 m Höhe eine dreifache Zunahme des Elektrolytgehaltes festgestellt. Zwar war die Photosynthese im freien Wasser meßbar, aber sehr gering. Die Ausnutzungsquote der einfallenden Lichtstrahlung betrug nur 0,00007%. Es wird angenommen, daß kleinste Zellen von Bakteriengröße und nicht nachgewiesenen trophischen Rang wenigstens zum Teil für die Photosynthesaktivität verantwortlich waren. Eine lichtbedingte Hemmung dieser Aktivität wurde durch Besatzungsexperimente nachgewiesen. Der Rio Limón, der von einer Baumdecke beschattet wird, weist etwa den gleichen Elektrolytgehalt wie die Unterläufe der andinen Flüsse auf. Die Photosynthese jedoch verlief hier im freien Wasser beträchtlich stärker als in den Bergflüssen, war aber immerhin noch sehr gering. Die Strahlungsausnutzung erreichte den Wert 0,004%. Die Photosyntheserate der Algenmatten im Strom war trotz der beträchtlichen Beschattung unvergleichlich hoch, nämlich bis zu $1189 \text{ mg C/m}^2/\text{d}$. Demgegenüber war die Photosyntheserate von *Hildenbrandia*, die auf den Steinen wuchs, sehr schwach. Eine Energiebilanz, die alle wichtigen Photosynthese- und Atmungs-Komponenten berücksichtigte, wurde für den Rio Limón aufgestellt. Der Strom erwies sich zur Zeit der Untersuchung als autotroph (P.R. = 1,8). Der Valencia-See, ein großer endorheischer Wasserkörper, ist sehr reich an Elektrolyten ($1830 \mu\text{S} \cdot \text{cm}^{-1}$) und empfängt große Mengen an häuslichen und industriellen Abwäs-

sern. Probenentnahmen aus den Kanälen und Flüssen brachten für die Phosphatzufahren Schätzwerte von $3,73 \text{ mg P/m}^2$ Secareal/d als Phosphonfracht und $210 \text{ mg O}_2/\text{m}^2$ Secareal/d in Sauerstoffäquivalenten für die zugeführte organische, abbaufähige Substanz. Die Nettoproduktion des Sees war hoch ($2148 \text{ mg C/m}^2/\text{d}$), aber für Flachlandseen dieses Breitengrades nicht ungewöhnlich. Die Ammoniumkonzentration war auch hoch ($3816 \text{ mg C/m}^2/\text{d}$, $0-10 \text{ m}$). Das autotrophe Phytoplankton umfaßte eine außerordentlich große Mannigfaltigkeit von Cyanophyten; jedoch ist ihre Zusammensetzung nicht so bemerkenswert. Kleinfrühe Entwicklungstendenz dieses Gewässers werden besprochen. Der Stausee Lagartijo, der mäßige kalkhaltiges Wasser führt ($185 \mu\text{S} \cdot \text{cm}^{-1}$), war weniger produktiv als erwartet ($1252 \text{ mg C/m}^2/\text{d}$), vermutlich infolge einer Nährstofferschöpfung. In diesem See bildet sich infolge ständig zufließenden kühlen Wassers eine ungewöhnlich stabile Lagerung der Wassermassen aus. Dieser Umstand führt wahrscheinlich zur Begrenzung der jährlichen Primärproduktion. Der Stausee Guanapito mit etwas höherem Elektrolytgehalt ($240 \mu\text{S} \cdot \text{cm}^{-1}$) war noch unproduktiver, nämlich wegen extremen Niedrigwassers und darauffolgender Stagnation, die eine Nährstofferschöpfung bedingte. Der Schwarzwasser-Stausee Guri mit sehr geringem Elektrolytgehalt ($9 \mu\text{S} \cdot \text{cm}^{-1}$) und hohem Gehalt an aldehydionem organischen Stoffen zeichnete sich durch große Säurekonzentrationen aus. Infolge geringen Nährstoffgehaltes und schwacher Lichtdurchlässigkeit des Wassers erreichte die Nettoproduktion nur Werte um $65 \text{ mg C/m}^2/\text{d}$. Die Sauerstoffzehrung (Respiration) lag innerhalb der methodischen Fehlergrenzen. Der Guri-Stausee enthält beträchtliche Biomassen von Cyanophyten. Die Artenzusammensetzung ist auffällig anders als in den übrigen untersuchten Seen. Phytoflagellaten waren ebenfalls reichlich vorhanden.

In den lotischen Gemeinschaften bildet sich anscheinend eine starke Autotrophie aus, wenn die Voraussetzungen für die Entwicklung von Algenmatten gegeben sind. Allerdings sind solche Matten bei Hochwasser verwundbar. Bezogen auf das Oberflächenareal kann die Nettoproduktion von Fließgewässern wohl so groß wie in Seen sein. Die Produktivität der stehenden Gewässer wird nicht nur durch die zugeführten Nährstoffmengen beschränkt, sondern auch durch die Stabilität der Wasserstille und damit die Umschichtungsverhältnisse. Unter den untersuchten Seen wiesen nur der Lagartijo und der Guanapito mittlere Biomassen von Phytoplankton auf. Aufgrund des Reichtums an Phytoplankton-Peridinen mit geringen Biomassen Umsatz wiesen der Guri und der Mucubají kleinere Biomassen als erwartet auf. Der Valencia-See andererseits zeichnete sich durch eine unerwartet geringe Biomasse aus; hier herrschen kleinzellige Phytoplankter vor. Zwar wiesen der Guri-Stausee und der Valencia-See einander ähnliche Populationsstrukturen auf, der Energiefluß und die Biomassen aber unterschieden sich sehr stark voneinander. Der Mucubají-See wies die wenigsten Phytoplanktonarten auf mit ungleichmäßiger Verteilung. Es wird angenommen, da die beobachteten starken Unterschiede der Populationsstrukturen auf physico-chemischen Voraussetzungen der Biotope beruhen.

Es wird der Schluß gezogen, daß Energiefluß, Biomasse und Populationsstruktur in voneinander auffällig unabhängiger Weise von einem tropischen Süßwassersystem zum anderen wechseln. Deshalb muß jede dieser Hauptvariablen gemessen werden, wenn Vergleiche von Ökosystemen optimalen analytischen Wert aufweisen sollen.

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