THE ORGANIC MATTER BUDGET AND ENERGY FLOW OF A TROPICAL LOWLAND AQUATIC ECOSYSTEM

By

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TO MY PARENTS

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Abstract of Dissertation Presented to the Graduate Council of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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This study examines the influence of regional coupling mechanisms on the organic matter budget of a lowland tropical lake and documents the principal energy flows that contribute toward making the watershed a cohesive ecological unit. The downhill flow of organic matter (OM) and water from the terrestrial (6,860 km^2) to the aquatic (717 km^2) ecosystem was quantified and evaluated as to its effect on physical conditions and metabolic activity of Lake Izabal, Guatemala. The lake type is warm polymictic due to its shallow mean depth (11.6 m). Its water mass has a short residence time (6.6 months), and the annual gross productivity is high (1,592 g OM/m^2).

The hydrologic regime exerted control on OM flow into the lake. Mean runoff for the watershed was calculated as 65 percent of mean annual rainfall (2,992 mm), most of which occurred during the 9-month wet season (greater than 100-mm monthly rainfall). Organic matter runoff was characterized by an initial "flushing" of the watershed at the beginning of the wet season, when the particulate fraction (greater than 0.80 microns

diameter) constituted a large portion of the total organic flow. During the remainder of the year, OM runoff was nearly all contained in the dissolved fraction (less than 0.80 microns diameter). Approximately 50 percent of the total OM runoff occurred during the 3 wettest months of the year.

During the dry season when OM inputs from the watershed were low, the lake experienced a net gain in OM when gross primary productivity exceeded community respiration. During the wet season, there was a net loss of OM in spite of increased inputs of allochthonous organic detritus. This loss increased as the wet season progressed, due to a combination of decreased rates of gross primary productivity and increased rates of community respiration. The periodicity of OM accrual and loss provides a mechanism, apparently controlled by hydrologic patterns, by which steady-state conditions can be achieved on an annual basis.

Daily rates of gross primary productivity ranged from 1.15-7.31 g O_2/m^2 day and planktonic respiration rates from 0.50-8.38 g O_2/m^2 day. The average daily values for the organic matter budget were calculated for the 8-month sampling period and were represented by five principal flows. The two OM sources were gross primary productivity (3.730 g/m^2 day) and OM imports (0.632 g/m^2 day). The three OM losses were by OM exports (0.452 g/m^2 day), planktonic respiration (3.875 g/m^2 day), and respiration of the bottom muds (0.36 g/m^2 day). The mean residence time for the average OM content of the lake (71.08 g/m^2) was 16.3 days.

Seasonal periodicity was expressed in the net plankton by a bimodal pulse of abundance. Peaks in plankton density occurred at the end of the dry season (April-May) and followed the initial period of heavy rainfall (August-September). Causal factors for this response remain undetermined.

The connection of the lake to the marine environment, via a 42-km long waterway, allows additional mechanisms for ecosystem coupling. Evidence was collected to demonstrate the control of the Na:Cl ratio of lake water by dry-season penetration of brackish water into the lake. The waterway also provides marine vertebrates and invertebrates access to a fresh-water environment. Periodicity of OM metabolism in the lake, high productivity of surrounding lagoons and coves, and brackish water penetration from the coastal marine ecosystem are discussed as factors influencing consumer activity and seasonal migration. The lake's fisheries, dependent on the marine contingent of fishes, may best be managed by utilizing the understanding of regional coupling mechanisms to prevent fisheries deterioration and to ensure continued yields.

INTRODUCTION

Many years ago Forbes (1887) discussed lakes as microcosms, and in so doing emphasized their isolation from the terrestrial ecosystem. Much of the limnological work since that time has taken this myopic view of lakes with little regard to the activities beyond their boundaries. It is these extra-lacustrine activities that give lakes their characteristics, and they can be dealt with effectively only by expanding the ecosystem boundaries to include the whole of the watershed. The cohesive nature of the watershed, and its well-defined boundaries, are characteristics that make it a conceptually attractive unit for ecological study.

Powered by the proper energy sources, water is the common denominator that couples this ecological unit by virtue of its geological constraints (downhill flow) and its biological indispensibility. The characteristics of this water, its flux from the terrestrial to the aquatic subsystem, and the effect of this flux on the lacustrine ecosystem are all important components of the present study.

The study was conducted in the Izabal Watershed on the Caribbean slope of Guatemala. Because of the high rainfall and seasonal climate of the region and the suspected short residence time of the lake's waters, I hypothesized that upstream activities in the terrestrial subsystem would be reflected by short-term (<1 year) responses in the downstream subsystem of the lake. The main focus of the study was to examine the metabolic activity of the lake in response to organic matter inflow from the watershed.

Talling (1969), in reference to the poorly understood seasonality of shallow tropical lakes with no long-term thermal stratification, pointed out that "any periodicity [discovered] acquires a new interest." In the Izabal Watershed, this interest may necessarily extend beyond the boundaries of the lake to determine the extent of ecosystem coupling and matter exchange between subsystems. The connection of the lake to a marine environment adds to the difficulty of evaluating the watershed as an isolated unit or closed system. This adds new dimensions for possible mechanisms for ecosystem coupling.

Depending on the degree to which these coupling mechanisms create interdependency on a regional scale, schemes for ecosystem management and land use planning should demonstrate awareness of both the potential benefits and inherent dangers of manipulation of isolated subsystems. Therefore, as Odum (1971) emphasized, "it is the whole drainage basin, not just the body of water, that must be considered as the minimum ecosystem unit when it comes to man's interests." Thus, there is an urgent need for understanding these interactions on a regional level.

Terrestrial Ecosystem Exports

Naturally forested areas are extremely effective in recycling materials, thereby preventing losses to downhill processes (Bormann et al. 1969). However, organic matter fixed by terrestrial photosynthesis undergoes some leakage that eventually appears downstream. The degree to which this leakage occurs depends on factors which characterize the ecosystem. Some of the factors that significantly affect organic matter runoff are: (1) seasonal phenomena, (2) runoff intensity, (3) ecosystem perturbation, and (4) topography and other geological characteristics of the watershed.

In temperate regions, the organic matter inputs to streams located in forested areas are seasonal, being highest in the autumn during the seasonal leaf drop (Kaushik and Hynes 1968). In tropical latitudes where rainfall is the seasonal control, a deciduous forest presumably could experience a similar pulse during the dry season. However, since water is the medium that transfers organic matter downhill, one might expect the downhill transfer of organic matter to be seasonally coincident with high rates of runoff.

Although there are no data from tropical regions to support the assumption that water runoff and organic matter runoff are positively correlated, there is some evidence for this in the temperate zone. In a Piedmont stream in the southeastern USA, Nelson and Scott (1962) found that, although the dissolved and colloidal organic matter fraction of river water increased with discharge rate, the particulate fraction increased at a much more rapid rate. At low to moderate flows the dissolved and colloidal organic matter concentrations were two to ten times higher than the particulate, while, during high flow rates, the particulate organic fraction increased to double the concentration of the dissolved. Causal factors which increased the particulate portion so dramatically during high discharge were: (1) greater surface runoff associated with heavy rainfalls, and (2) the flushing effect of high water. Therefore, with increased rates of river discharge, organic matter flows increase at a proportionately greater rate than water flows. There is no reason to expect that these factors would operate differently in tropical latitudes. Therefore, measurements of the organic matter runoff from the Izabal Watershed to Lake Izabal would necessarily include a range of runoff intensities in order to characterize size fractions of organic runoff and to achieve a good estimate of absolute quantities.

Perturbation of terrestrial ecosystems by deforestation decreases the ability of watersheds to prevent downstream losses by destroying the mechanisms and adaptations for the recycling of matter. Regions of the Izabal Watershed have received some alteration from deforestation and agriculture. Again, specific data for estimating the magnitude of organic runoff change by deforestation must be drawn from temperate-zone ecosystems.

The northern hardwoods of the Hubbard Brook Experimental Forest, New Hampshire, provide the model on which to judge effects of perturbation. There, drainage streams exported 5.3 grams of organic matter per m^2 of watershed area annually (Bormann et al. 1969). After clear-cutting of the forest, organic matter losses doubled during the first two years. These ecosystem exports represent inputs for downstream ecosystems (Likens et al. 1970). If the downstream ecosystem were a lake, then depending on its size, these can represent a significant source of organic matter and illustrate the importance of one-way coupling between a terrestrial and aquatic ecosystem. The absolute values for tropical regions may be different, but nevertheless deforestation could be expected to result in increases in organic matter runoff. The only assumption necessary for arriving at this conclusion is that the mechanisms for recycling matter possessed by ecosystems of both latitudes would be lost or severely damaged upon destruction of the forests.

Finally, the topography and other geological characteristics of watersheds are factors that should be considered in the regulation of organic matter runoff. Runoff waters from the steep mountain environment in the Amazon Basin have higher concentrations of dissolved and suspended organic matter than those of the lower Amazon (Gibbs 1967). However, in large watersheds there may be a great deal of spatial variation in topography and geology as well as the previously discussed variables of runoff intensity and ecosystem perturbation. The larger the watershed, the more these spatial variations tend to become integrated by the confluence and mixing of tributaries by the time downstream measurements are taken. Also the metabolic activities of riverine ecosystems could be expected to modify both the quantity and quality of organic matter after it is received upstream. In the Izabal Watershed, the majority of the drainage areas become confined to one major river before the waters discharge into the lake. Thus, any peculiarities in organic matter sources will tend to cancel one another by the time the water discharges into the lake.

Inflows to Aquatic Ecosystems

Now that the characteristics of organic matter runoff have been discussed and loosely established, it is essential to determine the qualitative and/or quantitative influence that this organic source may have on downstream aquatic ecosystems. Showing that the energy fixed in the form of organic matter in the terrestrial ecosystem can be utilized in the aquatic ecosystem would establish that an energetic coupling or flow occurs on a regional level.

There is good evidence that aquatic ecosystems adapt to organic detritus inputs by utilizing them as a source of energy. This has been demonstrated for estuaries (Teal 1962; Darnell 1967; Heald 1971; Cooper and Copeland 1973) and in flowing waters (Odum 1956; Nelson and Scott 1962). That the Lake Izabal ecosystem should be an exception to this concept would seem anomalous. Some workers have had the insight to compare the relative contribution of organic matter import to the total metabolism of coastal embayments. Of the total organic increment, allochthonous inputs accounted for about one-half the total for the Strait of Georgia (Seki et al. 1968), 7-21% in Moriches Bay on Long Island (Barlow et al. 1963), and about 97% in the turbid and polluted Chao Phya River estuary in Thailand (Pescod 1969). In addition to its importance to the total metabolism of some areas, organic detritus has been shown specifically to be a principal food item for many estuarine vertebrates and invertebrates (Darnell 1961, 1967; Odum and de la Cruz 1967; W. Odum 1971). The basis for the nutritive and presumably the energetic value of particulate detritus is the high quality of organic matter (e.g. proteins) associated with the micro-organisms that colonize the particles. Wherever ecosystems exist that have organic detritus inputs, there is good evidence that the organisms are adapted to utilizing the organic component as a source of energy.

Lakes, however, have apparently received the least attention of all aquatic ecosystems that may derive some of their energy from organic matter transported from outside their boundaries.

Again, specific examples that demonstrate this are drawn from studies in temperate latitudes. Two independent approaches have been used to measure allochthonous organic matter sources for lakes. One is to directly monitor the organic matter runoff from a watershed--the approach used in the present study. This was done by McConnell (1963) in small impoundments of the semi-arid southwestern USA. There, relatively unleached oak litter entered a lake by surface runoff at an annual rate of about 750 g dry weight per m^2 of lake surface. This allochthonous source of organic matter supplied the lake with approximately one-third of the total organic matter increment; the remainder was supplied by primary production.

The other approach is by indirect measurements and is feasible only in lakes that thermally stratify. In eutrophic Lake Mikalajki, Poland, Lawacz (1969) trapped seston as it sank from the trophogenic zone to below the epilimnion. The total organic matter production by this method was about half again as great as that of the plankton over a year as measured by the oxygen method. Lawacz attributed the difference in production to unmeasured dissolved organic substances that are produced in the littoral zone. These substances presumably move into the pelagial zone and sink after transformation into particulate form.

Most attempts to quantify the organic sources of tropical freshwaters have been made by measuring the primary productivity of relatively large lakes. The size of these lakes would tend to diminish the importance of an allochthonous organic source, and thus the "lake as a microcosm" view is justified, at least for organic matter production.

As pointed out by Ruttner (1963), the quantity and composition of allochthonous organic matter depends on the ratio of the surface area of the lake to that of the watershed. In general, allochthonous organic sources will be of greater importance to small lakes with large watersheds than to large lakes with small watersheds. Already discussed are the important influencing factors such as climate, the morphological and geological character of the watershed, and plant cover of the watershed.

Considering these factors, the humid tropics are a likely region where lakes may receive flows of significant magnitude from outside their boundaries. These flows can have a marked influence on the limnological characteristics of these lakes. Lakes in which the residence time of the water mass is relatively short are likely candidates for such tightly coupled influences. In the context of ecosystem management, it follows that alteration or perturbation of watersheds could have a profound effect on the activities within such lakes. Similarly, these lakes may be our most sensitive indicators of changes in upstream activity.

Thus, the objectives of this study are to (1) determine the quantity and seasonal distribution of organic matter transfer from the terrestrial to the lacustrine ecosystem, (2) quantitatively compare the allochthonous organic matter source of the lake with the organic matter derived by in situ primary production, (3) evaluate how this one-way regional coupling mechanism influences metabolic activities in the lake, and (4) document the principal energy flows that contribute toward making the watershed a cohesive ecological unit.

REGIONAL SETTING

The Izabal Watershed extends 205 km eastward from the interior of Guatemala to the Caribbean coast. The orientation of this 50-km wide strip of terrain is east-west, located at 88°41' W to 90°34' W and 15°03' N to 15°52' N. The drainage pattern is from the highlands in the western sector, downward to Lake Izabal only a few meters above sea level, and then through the Rio Dulce, finally reaching Amatique Bay in the Gulf of Honduras on the Caribbean. However, for the purpose of this study, the watershed will not include the area downstream from Lake Izabal, but only the region (6,860 km^2) that drains into the lake (Figure 1).

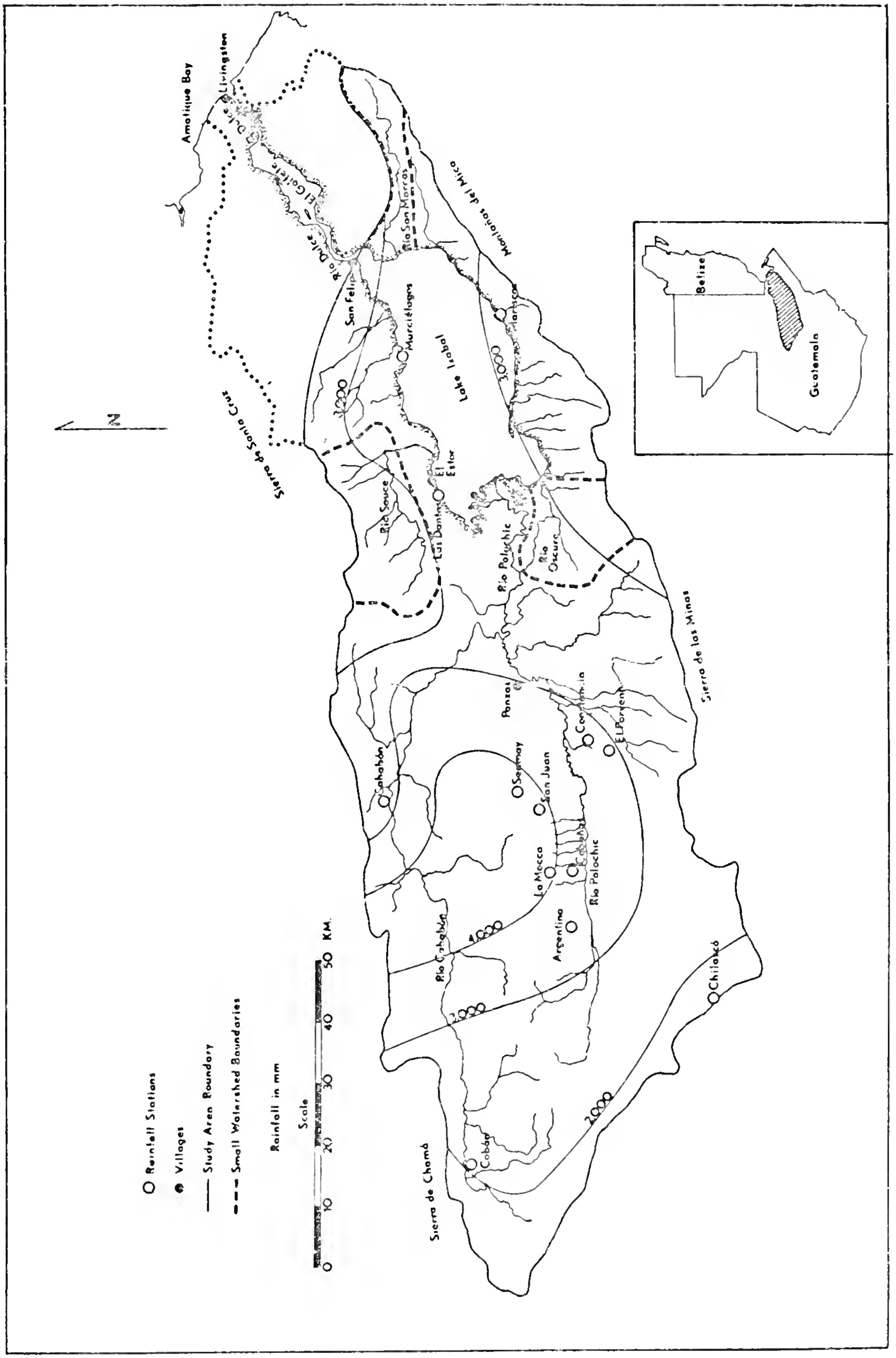
Two mountain ranges delimit the Izabal hydrologic unit; the Sierra de las Minas and the Montañas del Mico lay end-to-end and parallel the southern boundary, while the Sierra de Santa Cruz and Sierra de Chamá create the divide to the north. The major rivers are the Rio Polochic and the Rio Cahabón, which converge into a massive river that is actively building a delta across the end of the lake. Other rivers and small streams, about 40 in all, drain less extensive areas and often are intermittently dry during periods of low rainfall.

Climate

Lakeside Temperature, Rainfall and Solar Radiation

The seasons associated with rainfall and temperature changes near Lake Izabal were described by Snedaker (1970). The wet season begins abruptly

Figure 1.- The Izabal Watershed. Rainfall stations and geographical features of regional importance are labeled.



N
Amatique Bay
Livingston
Rio Dulce
El Golfete
Rio San Marcos
Montañas del Mico
San Felipe
Murciélagos
Lake Izabal
Sierra de Santa Cruz
3,000
El Estor
Rio Sauce
Las Dantas
Rio Polochic
Rio Oscuro
Sierra de las Minas
Panzos
Cahabón
Senahú
San Juan
Teleman
La Mocca
Rio Polochic
Argentina
Rio Cahabón
4,000
3,000
Chilasco
2,000
Cobán
Sierra de Chamá
Rainfall Stations
Villages
Study Area Boundary
Small Watershed Boundaries
Rainfall in mm
Scale
0 10 20 30 40 50 KM.
Belize
Guatemala

sometime in May and tapers off toward the end of the year; the dry season is from December through April. The daily temperature range is greatest during the drier months, reflecting the ameliorating effect of rainfall. The average monthly temperature range is 4.4 C over the year and the annual mean is 25.2 C. The lowest temperatures generally occur in December and January and are associated with cold air masses moving in from the north during the winter.

Finca Murciélagos, located on the north-central shore of the lake, received an annual average of 2,004 mm precipitation over a 6-year period (Snedaker 1970). Rainfall increases to the east and the west of this location. No month is without rainfall, while July is the wettest and February the driest month. August has less precipitation than either of the adjacent months which coincides with the caniculas (dog days), a term that describes a week to 10-day period of dry and cloudless days. Snedaker reports that during his 6-year study, 45.5% of the days experienced at least 1 mm of precipitation, and more precipitation tends to fall at night (ca. 71% of the total).

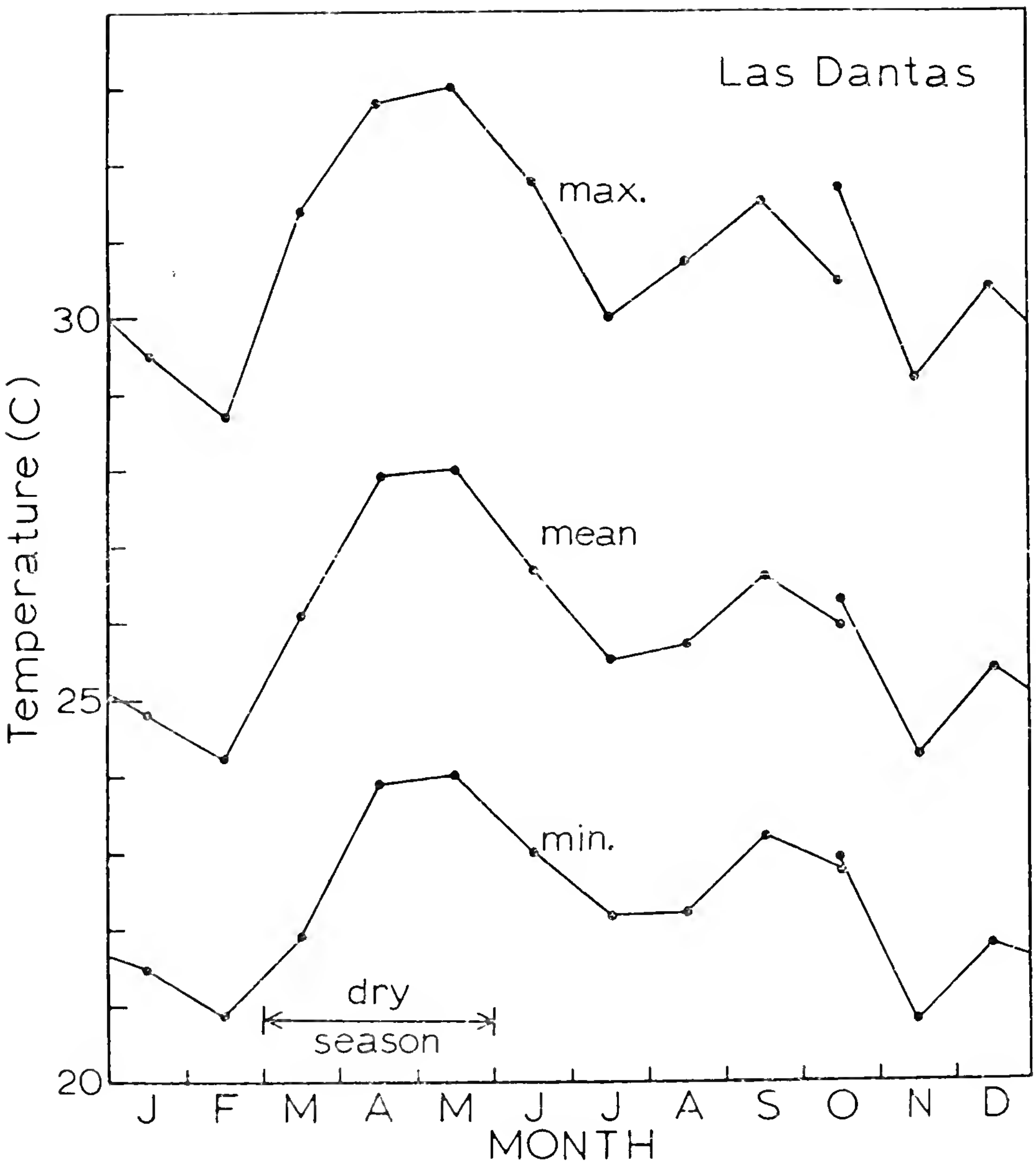
Lake Izabal has a pronounced local effect on the climate, especially the solar radiation. Mornings are generally cloudless in the lowlands, but in the lake area, clouds begin to accumulate over the surrounding terrestrial region from about 10 a.m. to noon. Differential solar heating over the land causes uplifting convective air currents and condensation of the water vapor while the sky above the relatively cooler lake remains clear. About mid to late afternoon these clouds move horizonally across the lake. Snedaker (1970) recorded hourly values of net incident radiation during 1964 and calculated the total daily net radiation received for May and June at 408.1 and 494.1 langleys/day, respectively.

The climate near the lake during the year of study (October 1971-1972) was characterized by examining records maintained by the EXMIBAL mining company on the north and south shores of the lake. The records included daily rainfall and maximum and minimum temperatures from the north shore at Las Dantas, and daily rainfall from the south shore at Mariscos, 32 km to the east-southeast. Average temperatures were calculated from the maximum and minimum temperatures by interpolation using the same relationship that Snedaker (1970) observed from his hourly readings at Finca Murciélagos. Figure 2 shows that the two warmest months were April and May during the dry season. The decrease in temperature after May can be attributed to amelioration by rainfall during the wet season. Temperatures increased until September and thereafter decreased until February. The low November temperature, which interrupts an otherwise continual decrease from September through February, can be attributed to an unseasonably cool, week-long persistence of stormy weather caused by a hurricane on the Atlantic coast.

Mariscos received 3,236 mm rainfall during the year of study, which is considerably more than the 2,210 recorded at Las Dantas (Appendix, Table A). The month of heaviest precipitation for both stations was August (630 mm at Mariscos and 426 mm at Las Dantas). The rainfall at Las Dantas during the year of study is in close agreement with a five-year average (1963-1967) for the same station and slightly higher than the 2,004 mm average from 1961-1967 at Finca Murciélagos (Snedaker 1970).

The climate diagram, which uses the conventions of Walter and Leith (1960-67), illustrates the monthly march of precipitation and average

Figure 2.- Monthly averages of the maximum, minimum, and calculated mean temperatures at Las Dantas for the period of study (October 1971-1972).


Las Dantas
max.
mean
min.
dry
season
30
25
20
Temperature (C)
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

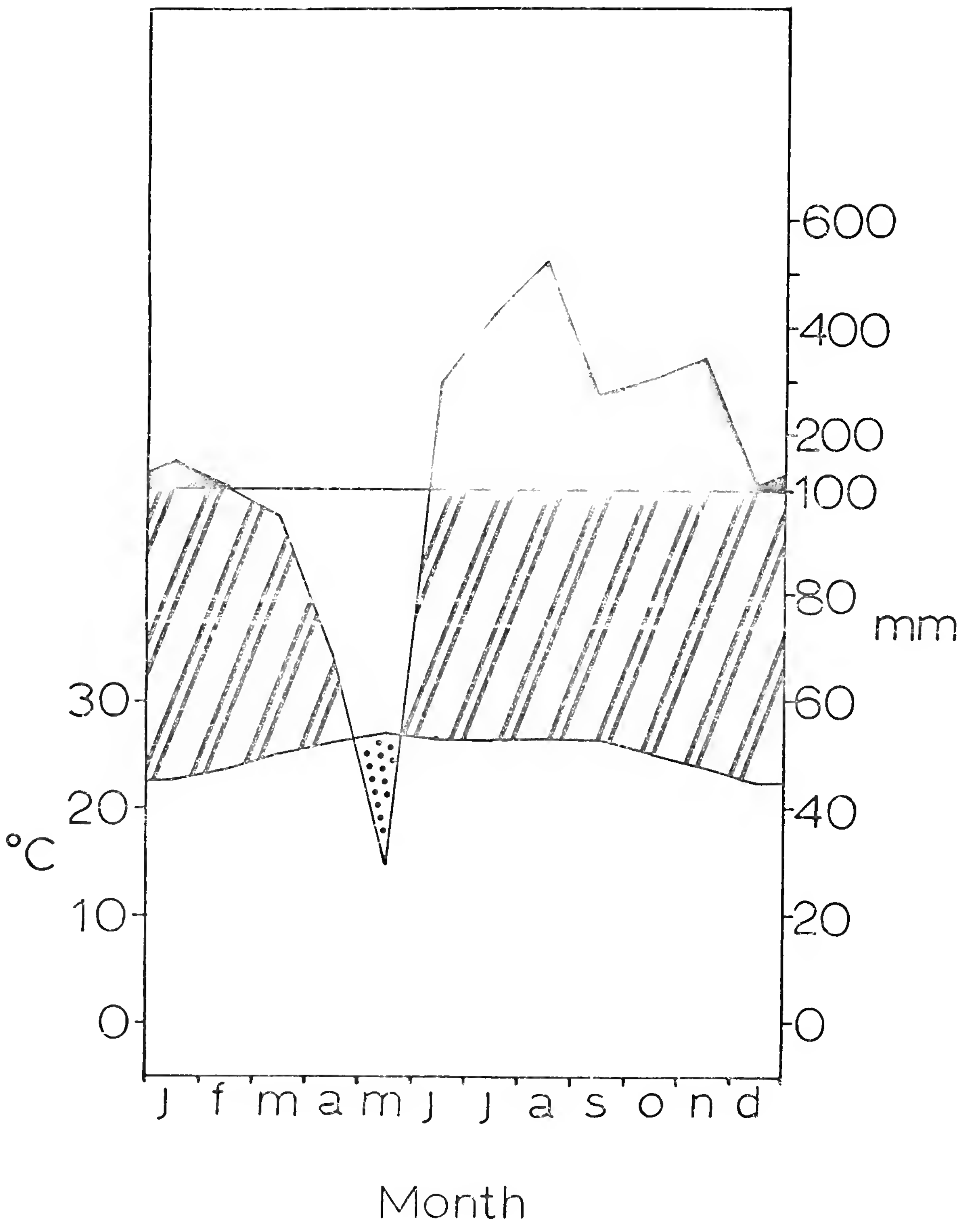
ambient temperature (Figure 3). Rainfall is the average of the records at Mariscos and Las Dantas during the year of study and temperatures are those of Snedaker (1970). The shaded area above 100 mm represents months when rainfall was in excess of evapotranspiration, and is the period when the most surface runoff can be expected. The stippled area represents the period when evaporation is greater than rainfall, implying a water deficit.

Precipitation for the Remainder of the Watershed

The low topography near the eastern part of the lake allows trade winds to pass unobstructed into the basin. Orographic rains occur as the moisture-laden air masses sweep inland from the Caribbean and upward over the Polochic Valley. There is considerable spatial variation in rainfall as illustrated by the isopleths in Figure 1. The data on which these isopleths are based appear in the Appendix, Table B and also include information from the Instituto Geográfico Nacional (1966). Heaviest rainfall, averaging close to 4,000 mm, is concentrated in the north-central region of the Polochic Valley. Radiating from that area, the average decreases to values below 2,000 mm. San Juan received 6,128 mm in 1969, the highest amount recorded for any station in a single year.

To arrive at an estimate of the average rainfall for the Izabal Watershed exclusive of the lake, the areas between the estimated rainfall isopleths (Figure 1) were determined planimetrically. For the year of study, average rainfall for the watershed as a whole was calculated at 2,992 mm.

Figure 3.- Temperature-rainfall climate diagram for Las Dantas and Mariscos during the year of study. Average monthly temperatures were calculated from a 6-year record at Finca Murciélagos.


600
400
200
100
80
mm
60
40
20
0
30
20
°C
10
0
J f m a m J J a s o n d
Month

Geology and Soils

The Izabal Watershed lies in the physiographic province known as the Central American Mountain System, just to the north of the volcanically active Pacific Cordillera (Walper 1960). The orientation of the rivers in the watershed is controlled by the east-west faulting and folding which has produced a series of anticlinal mountains. This major zone of faulting, in which the Polochic Valley lies, is postulated as being tectonically related with the fault zone of the Cayman trench (Bartlett trough) in the northern Caribbean (Walper 1960). The lake occurs in a block fault basin (Dengo and Bohnenberger 1969).

The Rio Polochic originates some 2,100 m above sea level and passes a distance of 100 km before reaching the lake. The headwaters lie between the Sierra de Pansal to the south and the Sierra de Xucaneb and Sierra Tzalamilá to the north (Popenoe 1960). To the north of these two latter confluent ranges, the Rio Cahabón begins its eastwardly flow, finally connecting with the Rio Polochic 53 km downstream. These waters become distributed in the multilobate Polochic Delta before they discharge into the lake. As levees of the distributaries protrude into the lake and deposit alluvium, shallow coves and lagoons become isolated in the delta region, providing interesting ecosystems for the study of seasonal succession and metabolism of the plankton (Brinson 1973).

The structure and stratigraphy of the watershed is complex and incompletely understood (Walper 1960). West of the lake, and at higher elevations, prominent cliffs of sedimentary limestone and interbedded dolomite constitute massive beds of Permian age (Roberts and Irving 1957). Nearby at Cahabón, beds of terrestrial conglomerate and sandstone predominate and are believed to be of Tertiary age. Igneous rocks occur in lenticular arrangement along a fault which parallels the north shore of the lake. This serpentine area is believed to be of late Paleozoic and early Mezozoic age. The mountains that parallel the southern area of the watershed are metamorphic pre-Cambrian rocks consisting of undifferentiated schist, gneiss, phyllite, quartzite, and marble.

The soils of the Izabal Watershed, as all the soils of Guatemala, have been classified and mapped by Simmons et al. 1959. Soils around the north and east perimeter of the lake were examined by Tergas (1965) in relation to the primary production of natural vegetation. Some of these soils have high ratios of calcium to magnesium (1:1.2 to 1:6) as a result of their derivation from serpentine rock. Popenoe (1960) in his remarkable study of the response of soils of the Polochic Valley to shifting cultivation (slash-and-burn), described many of the soil properties. He stated that "Erosion is very slight on the steep lands of the Polochic Valley, probably due to excellent soil physical conditions" imparted by the relatively low bulk densities of the topsoils. Considering the diversity of parent material and the extremes in climatologic regimes of the watershed, a more complete description of the soils would be inappropriate and would necessarily include inaccurate generalizations.

The lithology of the Izabal Watershed is a heterogeneous one, ranging from old metamorphic to relatively young sedimentary rocks. Within this mosaic, one would expect to find significant spatial variation in weathering and differences in the ionic composition of the headwaters of streams. However these local irregularities can be expected to cancel each other as tributaries converge, so that the downstream parts of the rivers will tend to resemble one another.

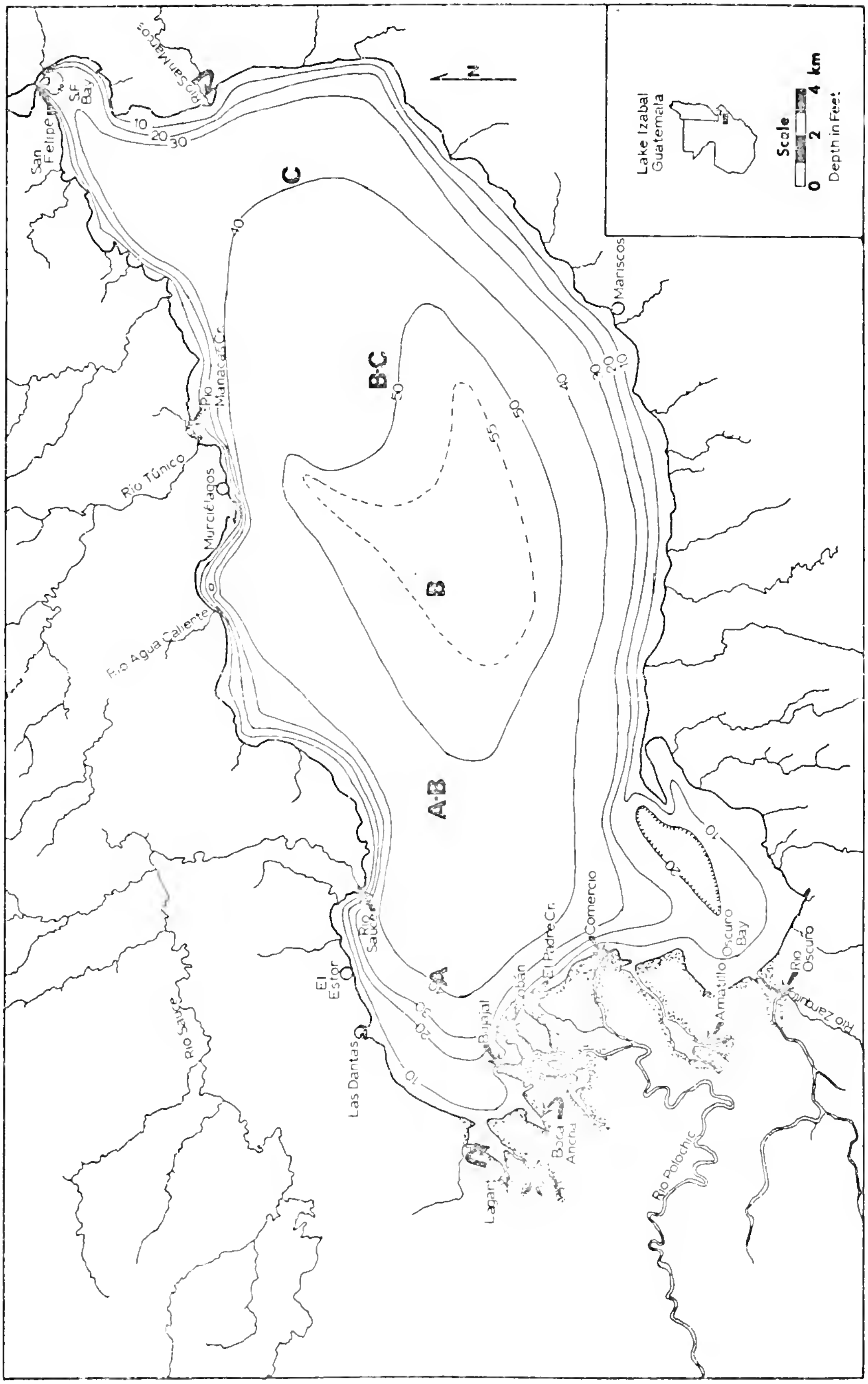
The Lake

Lake Izabal is located between 15°24' N to 15°38' N and 88°58' W to 89°25' W and lies only a few meters above sea level. The central basin of the lake is a broad, nearly flat plain reaching a maximum depth of about 16 m near the center. Thus most of the volume of the lake is below sea level. Most of the shallow areas are the coves and lagoons at the west end of the lake, bordering the delta of the Rio Polochic. According to the bathymetric map (Figure 4) adapted from Brooks (1969) only 9.7% of the area of the 717 km^2 lake is less than 4.6 m (15 feet) deep; 50% of this occurs in the shallow areas near the delta, and the remainder around the perimeter of the lake. The volume of the lake is 8,300 x 10^6 m^3, giving it a mean depth (volume/area) of 11.6 m.

Nearly 50 streams and rivers flow into the lake, and while the greatest number flow into the eastern, northern, and southern edges, the greatest volume is received through the Polochic Delta to the west. The outlet to the lake is at San Felipe, where the lake water enters to Rio Dulce on its flow to Amatique Bay in the Gulf of Honduras on the Caribbean Sea. About midway between San Felipe and the coastal port of Livingston (a distance of 42 km) the Rio Dulce broadens into a large shallow area (4.5 m depth) known as El Golfete.

Tsukada and Deevey (1967) suggested, on the basis of sediment cores that ended in sand and gravel, that lacustrine conditions were established, or reestablished, relatively late during the time of eustatic rise of sea level. Brooks (1969) speculated that the Izabal Basin originated as long ago as the Miocene, and pointed out, on the basis of his inability to

Figure 4.- Bathymetric map of Lake Izabal illustrating sampling stations. A, A-B, B, B-C, and C are the locations of sampling stations on the lake. Adapted from map by Brooks (1969).



Lake Izabal
Guatemala
Scale
0 2 4 km
Depth in Feet
N
San Felipe
S.F. Bay
Rio San Marcos
Mariscos
Rio Manacas Cr.
Rio Túnico
Murciélagos
Rio Agua Caliente
Rio Sauce
El Estor
Las Dantas
Bujajal
Cobán
El Padre Cr.
Comercio
Amatillo
Oscuro Bay
Rio Oscuro
Rio Zarquito
Boca Ancha
Lagart
Rio Polochic
C
B-C
B
A-B
A
10
20
30
40
50
55

find salt traces in the interstitual waters of sediment cores, that marine conditions have been absent in the recent past.

The shallow littoral zone of the lake is narrow and subject to the abrasive action of waves. In some of the protected areas, especially along the north and east shores, the forest grows to the water's edge. The shallow bottom consists of large pebbles where the submerged aquatic macrophyte, Vallisneria, grows in sparce densities. Sandy beaches are more common along the south shore where there is greater exposure to wave action created by prevailing northeasterly winds. Occasionally isolated individuals or aggregates of water lettuce (Pistia stratiotes) washed in from the shallow lagoons and black-water creeks of the delta region can be seen floating on the surface of the lake.

A limnological survey of the lake was made by Nordlie (1970) in August 1969 and March 1970. His most surprising discovery was the relatively high densities of a member of the Tanaidacae, a bottom-dwelling crustacean with marine affinities. Nordlie found the planktonic community to have only moderate primary production. On his March visit he observed extremely low densities of net phytoplankton, whereas in August, they were present in "bloom" densities. Since most of the present study contains detailed seasonal descriptions of the same phenomena that Nordlie observed on his visits, his findings will be discussed in more detail in the chapters that follow.

The Fisheries and People

The Izabal Basin has been, until recently, a region of only modest human activity. The lowlands near the lake were believed to have been settled sparsely during Maya times (Voorhies 1969). Major ceremonial centers were completely absent from this area although there were centers immediately to the south (Copán) and to the north scattered throughout the Petén. During the current century, the population did not increase substantially until malaria control was available and a road was completed from Cobán to El Estor in 1948. This route replaced, at least during the dry season, the older route up the Rio Polochic to Panzós where the Verapaz Railway connected with Pancajche. A road terminating at Pancajche completed the journey to the central highlands of Guatemala. Prior to this, 19th-century ships sailed in from the Caribbean to the colonial town of Izabal on the south shore of the lake. From this location, mule transportation provided an overland access to the central highlands. In the last decade, a spur road was completed, connecting the village of Mariscos on the south shore with the Atlantic Highway that couples Guatemala City with Puerto Barrios and Puerto Santo Tomás de Castilla on the Caribbean. Now the people living around the perimeter of the lake who have access to dugout canoes with outboard motors can reach the road terminating at Mariscos. From there the bus trip to Guatemala's capital city lasts only 4-5 hours. Likewise, the access provided by the lake to its perimeter opened the slopes of the Izabal Basin to agriculture.

Immigration and Labor Alternatives

The influx of Kekchi Indians from the upper Polochic Valley, and of people from other parts of Guatemala, was initiated by the discovery of a rich nickel deposit near the northwestern region of the lake. All the exploratory work for mining the ore has been completed, but the construction of the processing plant for the extraction of the mineral is still pending financial support and legal agreements. The already massive capital outlay, made possible through subsidization by North American firms, has dwarfed other business interests in the valley. In the past 10 years the town of El Estor has grown from a sleepy Indian village to a bustling community.

The labor force required for the initial clearing and exploration of the mining area is now largely unemployed. Although some families have been forced to leave, many remain with the hope that they will again work for the attractive wages paid by the mining company. Some of these desperate people have shifted their means of living to agriculture and fishing. Carter (1969) in an anthropological monograph on the Kekchi cultivators described the problems and successes of these Indians in their efforts to apply highland methods of shifting cultivation to the lowland areas near the lake.

The fishing, which became more effective with the introduction of nylon gill nets in the early 1960's, has since become so unprofitable that it now offers employment and income for only a few dozen individuals around the lake. Holloway (1948) recognized long ago the potential food source of the predominately marine fishes that inhabit the lake, but made no prediction as to what the carrying capacity of this resource might be.

Fishing Regulations and Yields

Current Guatemalan fishing regulations, passed into law in 1936, apply to all inland waters regardless of size or location. One of the restrictions of the law is that gill nets can be no greater than 36 meters in length nor have a mesh size of less than 7 inches. However, gill nets as long as one kilometer with 2 1/2-inch mesh are frequently used during the fishing season. Initially, excellent yields from the relatively virgin fisheries were the incentive for people with capital to invest in this equipment. However, the subsequent decline in yields possibly may have been the result of exceeding the carrying capacity of the fisheries.

The fishermen react to the decreased yield per unit effort in several ways. Some cease fishing altogether, while others send their equipment and hired labor northward to fish in the Rio de la Pasión in the Petén when the demand preceding Easter forces prices upward. Most owners of gill nets have several thousands of dollars invested in equipment, but fishing is usually subsidiary to their main business interests.

The general disregard for the irrelevant and unrealistic laws favors individuals capable of making large capital investments and penalizes to exclusion those individuals fishing at a subsistance level. Dickinson (in press) has discussed in detail the sociological implications of the fisheries as well as thoroughly documenting the geographical features of the region.

Since there is no governmental agency to keep records of inland fish catches, past yields from the lake cannot be estimated. Carr (1971) estimated current yields during a month-long study by observing the weight of catch per unit length of net. He calculated a daily mean fresh-weight of 11.6 pounds per 100 yards (5.75 kg/100 m) of net, and based on other assumptions and measurements, estimated the lakewide yield to be 2,808 kg dry weight per week during the 1970 season.[1] Some fishermen

---

[1] Most of the catch is salted and dried, accounting for 59% loss of fresh weight. They are marketed beyond the Izabal Basin, and only a small percentage of the total catch remains for local consumption.

fish year round while others may be active only when fish prices are high (2 or 3 months of the year). If an average fisherman worked 5 months of the year, then the lake would yield 56,160 kg dry weight annually (0.071 g/m^2 yr).

Fish Behavior and Fisheries Management

No data exist on the standing crop of fish, on growth increments of the population or on recruitment from immigration. Since much of the catch consists of euryhaline marine species, immigration is probably an important factor to consider in fisheries management. If the fisheries resource of the lake is being overexploited, as it presumably is (Carr 1971), then the immigration route through the Rio Dulce--El Golfete region is a logical area for control measures. Disgruntled fishermen that fish only on the lake are aware of this migration route, and of the gill nets set across these routes by their counterparts in the Rio Dulce region.

Fishermen as well as large flocks of cormorants, terns, gulls, and scattered pelicans find another popular fishing region in the shallow coves and black-water lagoons of the Polochic Delta. There the fishing is seasonal for both man and birds. During the dry season, these waters are stagnant and perpetually in bloom with high densities of phytoplankton (Brinson 1973). The increased consumer activity, in response to the highly concentrated food source, coincides with the season when fishing is legal. As law dictates, the fishing ceases in June when heavy rains mark the beginning of the wet season. Ironically, these events coincide with the migration of fish to the open water of the lake where they become more dispersed and harder to catch. Fish-eating birds also disperse, and only a few pelicans remain. The fishing laws thus present a paradox by allowing fish to be caught when they are easiest to catch, and by timing the open season with the high prices preceding Easter which provides incentive for economic gain.

The black anaerobic waters that flush the delta are not completely devoid of fish. Gobies (Gobionellus sp.) which are particularly poor swimmers, can be seen gulping air under the sudd vegetation bordering the lagoons. Vultures and egrets prey upon these fish, but the main predators are schools of large tarpon (Megalops atlantica) that travel the backwaters of the delta. By being facultative air breathers, the tarpon are well adapted to the anaerobic environment.

Marine fish, such as the tarpon, make up the majority of the fish caught in the lake. In order of decreasing yield they include Chloroscombrus sp. (zapatero or leather-jacket jack), several species of catfish including Bagre sp. and Arius spp. (vaca and chunte), and the prized Centropomus undecimalis (robalo or snook). The presence of schools of sardines, anchovies (Anchoviella), and other small herbivorous fish apparently provide much of the food for the larger carnivores. The important fresh-water fishes include Cichlasoma gutulatum (mojarra) and Brycon guatemalensis (machaca).

Some other predominately marine animals, although not directly important to the fishing economy, are conspicuous components of the fauna. Blue crabs (Callinectes sp.) are occasionally caught in nets, and the barnacle, Balanus improvisus, attached to pilings in the eastern end of the lake are testimony of the seasonally brackish water in that area. Porpoises (Tursiops truncatus) apparently do not enter the lake, but do follow the front of high-salinity water as far as the upper Rio Dulce.

Man has noticably reduced the abundance of some of the large aquatic vertebrates which probably has altered aquatic food chains. Both shark (Carcharhinus leucas) and sawfish (Pristis perotteti and P. pectinatus) are reported to inhabit the lake (Thorson et al. 1966) although their presence has gone unnoticed for the past 8 to 10 years. Fishermen assert that nets frighten sharks, and that they have been absent from the lake since gill nets became prevalent. Crocodiles (Crocodylus acutus), once conspicuous carnivores of the aquatic community, have suffered considerable reduction of their populations as a result of hunting pressure. Hunting may have also been responsible for reducing the manatee, a large herbivore, to its present day low population density. Two species of turtles, Dermatemys mawi and Pseudemys scripta ornata, are occasionally caught by baited hook or by gill nets. However, they seem to be relatively abundant and could serve as a potential source of food for the local human population (Carr 1971). Based on the consequences of exploitation of other components of the aquatic community, the "potential food source" offered by turtles would be short-lived, at best. Undoubtedly, the boney fishes will continue to be the principal aquatic resource for human exploitation.

Considering the migration routes and seasonal activity of the fishes, it is doubtful if enforcement of the law during the veda, or prohibition period, would significantly relax fishing below its present intensity. Complete enforcement of the law, which would limit the length of gill nets to 36 meters, would paralyze the fisheries completely and be socially disfunctional (Dickinson, in press). There is an urgent need for fisheries management on Lake Izabal. Any management, however, must demonstrate an understanding of the role of the fishes in the ecosystem as well as the needs of the commercial and subsistance-level fishermen.

Undoubtedly some sacrifices in the habits of the fishermen would be necessary before the fisheries could reach a steady-state level of maximum sustained yield. Proper management of the fisheries may necessarily extend beyond the boundaries of the aquatic ecosystem if regional coupling mechanisms are operative as hypothesized in the Introduction.

HYDROLOGY AND WATER CHARACTERISTICS

The principal objective of monitoring the hydrological regime of the Izabal Watershed was to enable the calculation of rates of inflow and outflow of organic matter to and from the lake. Subsidiary to this purpose was the need to characterize the hydrologic properties of a lake that historically has received almost no limnological attention until recently (Brooks 1969; Nordlie 1970). Even these recent studies lack the perspective of a long-term study necessary for a fuller understanding of the ecological implications of a seasonal hydrological regime. For example, Brooks (1969) labeled the likelihood of brackish water penetration into the lake as a "common misconception" although its occurrence is common knowledge among the non-scientific local inhabitants. Other "anomalies" of the hydrology and water characteristics might be of ecological significance, and their occurrence, if undetected, would unknowingly detract from a more complete understanding of the Izabal Watershed ecosystem.

Information on runoff characteristics of watersheds in the humid tropics has been approached mainly by calculating the excess of precipitation over evapotranspiration from empirical formulae applied to rainfall and ambient temperature. Direct measurements of runoff are few, and the information presented in the following chapter should be valuable for comparison with studies that do exist.

Methods

General Methodology--Field Stations, Logistics, and Schedule

The sampling stations are indicated in Figure 4 and encompass nine river-mouth stations, three main lake stations, and the outflow station at San Felipe. To achieve the objective of the study of estimating the lake's organic matter budget as modified by seasonal changes, samples were collected during both the dry and wet seasons. The dry-season data were collected during the months of March, April, and May. The clear, cloudless days during the warmer dry season helped to distinguish it from the wet season. January, February, and June through October were considered wet-season months because the average local precipitation was greater than 100 mm per month.

The river-mouth stations were sampled to determine the quality and quantity of water entering the lake and the outflow station was sampled to determine the quality and quantity of exports. Lake stations A, B, and C were sampled for chemical oxygen demand (COD) and biological oxygen demand (BOD) as well as for light and dark bottle primary production determinations (Table 1). Concurrently with COD collections, the following data were recorded from surface and bottom samples: dissolved oxygen concentration, pH, total alkalinity, and temperature.

Net plankton was collected from Stations A, B, and C at approximately three-to four-week intervals. On these collection trips temperature profiles and Secchi disk transparencies were determined at the three stations as well as at stations midway between them. These intermediate stations are referred to in the text as A-B and B-C.

The large size of Lake Izabal and the long distances between sampling stations required the use of a relatively fast and reliable mode of

Table 1.- Sampling dates for chemical oxygen demand (COD), biological oxygen demand (BOD), and primary productivity experiments (Prod). Numbers represent day of month

	WET SEASON						DRY SEASON					
	January			February			March			April		
Location	COD	BOD	Prod	COD	BOD	Prod	COD	BOD	Prod	COD	BOD	Prod
Station A	3		11,29[a]			2[a]	28	4[a]		21	10	24
Station B	3						28			21		
Station C							28			21		
San Felipe	3			8			28			21		
Rio Oscuro	25						10			11	1	
Amatillo	25						10			11	10	
El Padre Cr.	17						10			11		
Rio Polochic												
Comercio	25						10			11	1	
Cobán	17						10	14		11		
Bujajal	17						10	14		11	1	
Rio San Marcos							28			21		
Rio Manacas Cr.							28			21		
Rio Sauce							28			21	10	
Rio Túnico							-	-		-		
Largartos							-	-		-		

[a] Primary productivity experiments were not duplicated.

[b] Date during month of September.

Table 1.- extended

May			June			July			August			October		
			WET SEASON											
COD	BOD	Prod	COD	BOD	Prod	COD	BOD	Prod	COD	BOD	Prod	COD	BOD	Prod
19	10,19	28	9		20	29			21		9	5,23	8	27,[b]27
19	19	3	9		5,19	29			21		8	5	8	26[b]
19	19	5,29	9		18	29			21		7	5	5	25[b]
19			-			29	29		21			5		
16			7	7		11			4	2		1,23		
16			7			11			4	2		1		
16			7			11			4			1		
16			7			11			4			1		
16			7			11			4			1,23		
16	10		7	7		11			4	2		1		
19	19		9	9		29	29		21			5		
19	19		9			29			21			5	5	
19			9	9		29	29		4			1		
-	-		-			-			21			-		
-	10		-			-			-			-		

transportation. For this a 25-hp outboard motor was brought from the USA and a 24-foot dugout canoe (25 hundredweight capacity) was purchased at the lake. Routine sample collection required approximately seven hours for stations at the western end of the lake in the Polochic delta. For the remaining stations to the east of El Estor, the samples were collected on another day as ten hours were required due to the longer distances involved.

Ice could be purchased for storing samples during collection trips except during July and August when the ice plant closed for a minor repair. Several weeks of research time were lost due to breakdowns of the outboard motor and the car, which was used to transport equipment to the dock. At least monthly trips to Guatemala City were necessary to purchase repair parts and laboratory supplies.

A room of a concrete-floored house approximately 1/2 km from the dock site was used for the laboratory. Electricity was available three or four hours a day after dusk from a privately owned diesel generator whose output ranged between 85-105 volts A.C. The low and variable voltage was insufficient to operate the spectrophotometer in spite of the constant voltage supply transformer. For this reason, chlorophyll determinations were not made.

Hydrologic Measurements

Discharge rates of several of the major rivers entering the lake were measured at monthly (occasionally twice-monthly) intervals from November 1971-October 1972. The float-and-dye method (Welch 1948) was used to determine the velocity by sprinkling fluorescein dye powder on the water surface and recording the time elapsed in traveling between two floats 50 m apart.

When the velocity was slow (less than 0.3 m/sec) a 25-m distance was used. This procedure was repeated three times and the velocity was estimated to be the mean of the three readings. Measurements were determined far enough upstream from the river's mouth to avoid backforce from the river entering the lake. The cross-sectional areas of the rivers were measured by determining the width and five depths (two near the banks, one in the middle, and two halfway between these). A nail was driven into a tree trunk on the river bank at each station to provide a permanent point of reference for measuring changes of level in the river. Discharge rates (cross-sectional area multiplied by velocity) for all rivers, with the exception of the San Felipe outflow, were multiplied by a factor of 0.8 in order to correct for frictional resistance of the stream bed and banks (Welch 1948). At the San Felipe outlet where frictional resistance is small because of the large cross-sectional area, a factor of 0.9 was used.

Lake levels were recorded at frequent but variable intervals throughout the study year on the municipal dock at El Estor. Two other stations served as level markers on the lake: one on the western end at the mouth of Rio El Padre Creek, and the other at the eastern outlet at San Felipe. The EXMIBAL mining company also recorded lake levels at the plant site 2 km west of Las Dantas.

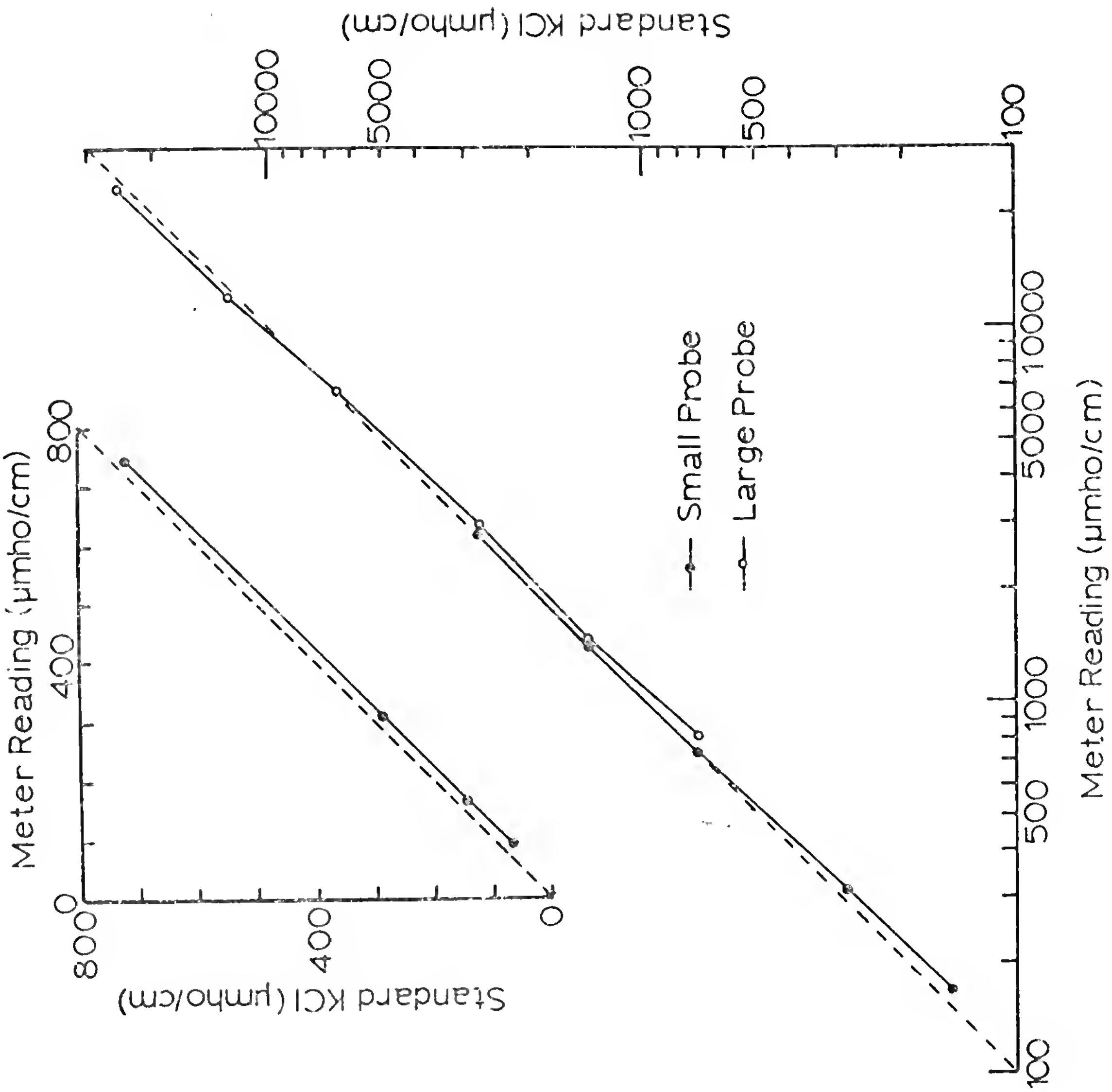
Temperature profiles were recorded with a YSI Model 51A oxygen meter and a YSI 5419 oxygen/temperature pressure-compensated probe with a 50-foot lead. Calibration was performed in the field for each profile, using a mercury thermometer as the standard.

Analyses of Water Characteristics

Samples collected for analyses of pH, total alkalinity, and specific conductance were usually the same as those used for COD analyses. Methods of collection are described in the section - "Metabolism and Organic Matter." Samples for O_2 determinations were collected with a 2- or 3-liter Van Dorn bottle, transferred to 300-ml BOD bottles, and fixed in the field. Temperature was recorded with a mercury thermometer while the water was in the Van Dorn bottle. All other procedures and determinations were made in the laboratory, usually within seven to ten hours from the time the first sample was collected. Total alkalinity and pH were determined first using a Beckman Model N2 pH meter and Beckman glass electrodes. Calibration was performed with factory-prepared buffer solutions (pH 7.0 and pH 4.5). Total alkalinity (carbonate plus bicarbonate) was determined by titration of duplicate 100-ml aliquots to pH 4.5 with a 0.02N HCl solution. The pH meter scale could be read to an accuracy of 0.5 pH unit.

Specific conductance was determined with a Beckman Model RB3 Solu-Bridge and readings were adjusted to 25 C. Two probes were necessary for the range of conductivities encountered. A small, more sensitive probe was used in the range of 50-800 μmho/cm and a large probe, one-tenth as sensitive, was used in the range of 700-40,000 μmho/cm. Figure 5 illustrates the calibration curves determined with dilutions of a standard KCl solution of known specific conductance (Golterman 1969). Readings of lake water, all within the sensitivity range of the small probe, were corrected by adding 20 μmho/cm, based on the calibration curve. Higher conductivity readings, accomplished with the large probe,

Figure 5.- Calibration curves for the small and large probes used for specific conductance measurements between 100 and 30,000 µmho/cm at 25 C. Small probe readings (magnified on insert) were corrected by adding 20 µmho/cm to the meter readings between 50 and 700 µmho/cm. Large probe readings were left uncorrected.


Standard KCl (µmho/cm)
10000
5000
1000
500
100
Small Probe
Large Probe
Meter Reading (µmho/cm)
100
500
1000
5000
10000
Meter Reading (µmho/cm)
0
400
800
Standard KCl (µmho/cm)
0
400
800

required less precision since detecting differences in the salinity gradients was more important than acquiring absolute values. Nevertheless, the calibration curve is in close agreement with the standard KCl solutions (Figure 5).

Samples for mineral analysis were collected April 14 and October 23, 1972. The samples were prepared by filtering the water through membrane filters (47 mm-diameter, 0.60-μ nominal pore size) to remove the seston. The samples were transferred to 0.5-liter bottles and 1% formalin was added as a preservative. The April samples were stored in polyethylene bottles and the October samples in amber glass bottles. Both groups were flown to Gainesville and mineral analyses were performed during March 1973. An atomic absorption spectrophotometer (Perkin-Elmer 303) was used for determination of Ca, Mn, Mg, Si, Fe, Ni, Zn, and Al. Potassium and Na were analyzed with a flame emission spectrophotometer (Beckman DU), phosphorus by colorimetric determination with molybdate (Golterman 1969), NO_3 and Cl with specific ion electrodes in conjunction with an Orion Potentiometer Model 801.

Results and Discussion

River Discharge and Runoff

Discharge rates from six rivers were used to estimate runoff from the Izabal Watershed. All values were calculated from velocities and cross-sectional area measurements of the rivers (Appendix, Table C) except for the values recorded for the Rio Polochic distributaries and the Rio San Marcos in August. These low August values are noteworthy since they occurred during the month of heaviest rainfall. During this period the level of the lake had risen to as high as 1.15 m (August 21) above the lowest level recorded during the preceding dry season (Figure 6) and resulted in flooding of the delta areas. During flooding the rivers were not confined to channel flow, but moved as a sheet across the deltas. If August discharges had been calculated from velocity measurements in the river channels, gross underestimates of runoff would have resulted. To estimate the August runoff, linear regression formulae were calculated from the other measurements using rainfall at Las Dantas as the independent variable and monthly discharge as the dependent variable. In this way August discharges could be calculated by extrapolation from rainfall, assuming a linear relationship between discharge and rainfall. Values for other months were similarly calculated where data were missing (e.g. February). These extiapolated values appear as open circles in Figure 7 and were used for the August values in Figure 8.

Discharge rates at the mouths of the Rio San Marcos and Rio Sauce were low compared to the other rivers measured (Figure 8). The similar patterns of discharge for the Rio Polochic distributaries (Comercio, Cobán, and Bujajal) can be attributed to their common origin. Whereas the Polochic distributaries demonstrated a sharp increase in discharge during June, an increase of similar magnitude for Rio Oscuro did not occur until July. This can be attributed to differences in local rainfall regimes. During the year of study the wet season in the area of the lake began in June,which accounted for the July increase in Rio Oscuro's discharge (Figure 8). The wet season in some regions of the Polochic Valley began in May,which may have accounted for the June increases in the discharges of the Polochic distributaries.

Figure 6.- Monthly estimates of all inputs to the lake (runoff and direct rainfall) and the monthly averages of lake water levels. Lake levels are the number of meters above the lowest recorded week which occurred during the second week of March 1972.

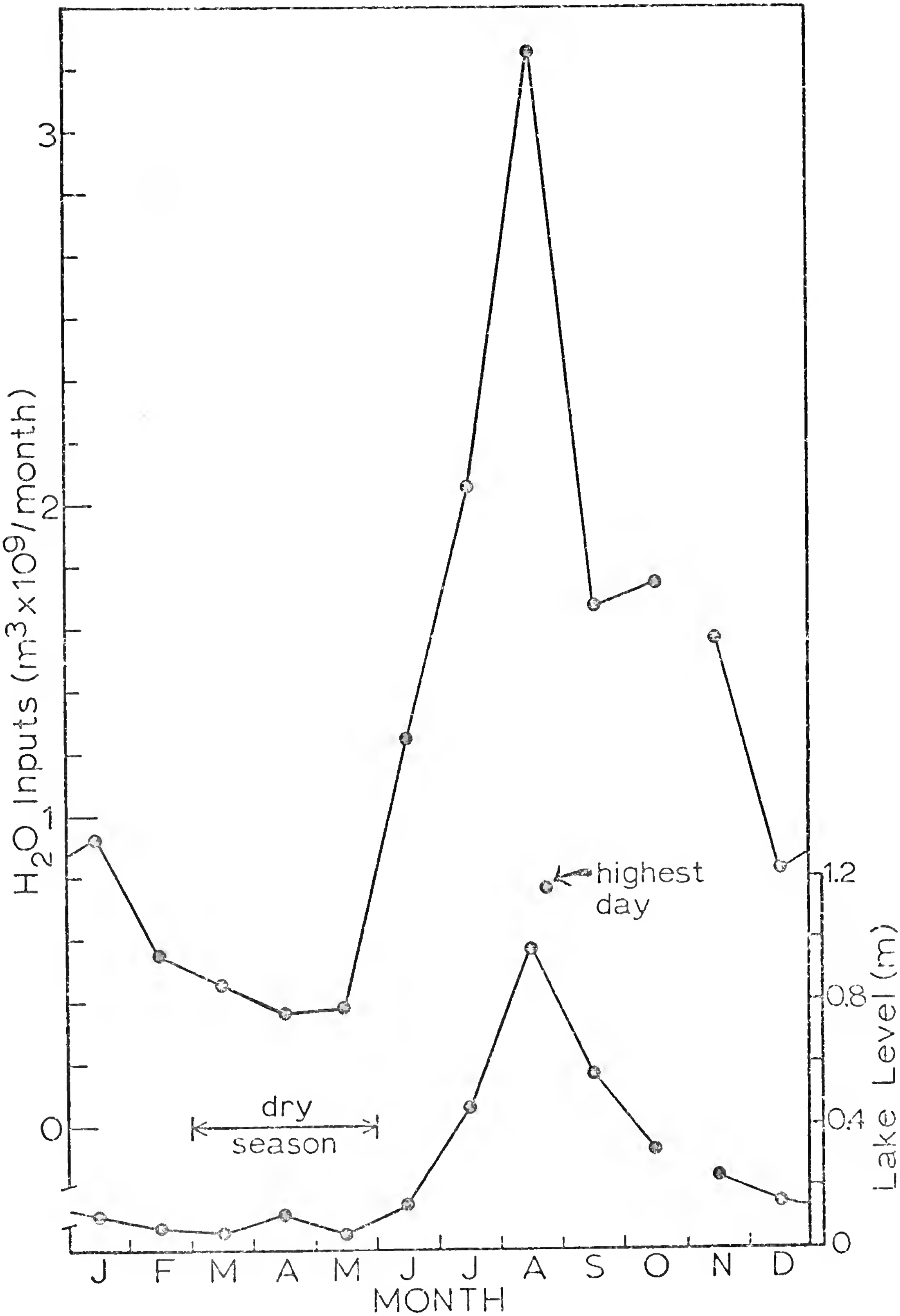

3
2
1
0
H_2O Inputs ($m^3 \times 10^9$/month)
highest
day
dry
season
1.2
0.8
0.4
0
Lake Level (m)
J F M A M J J A S O N D
MONTH

Figure 7.- Linear relationship between monthly rainfall and monthly discharge of rivers emptying into Lake Izabal. The open circles represent extrapolated values for February and August for which discharge data were missing or required correction.

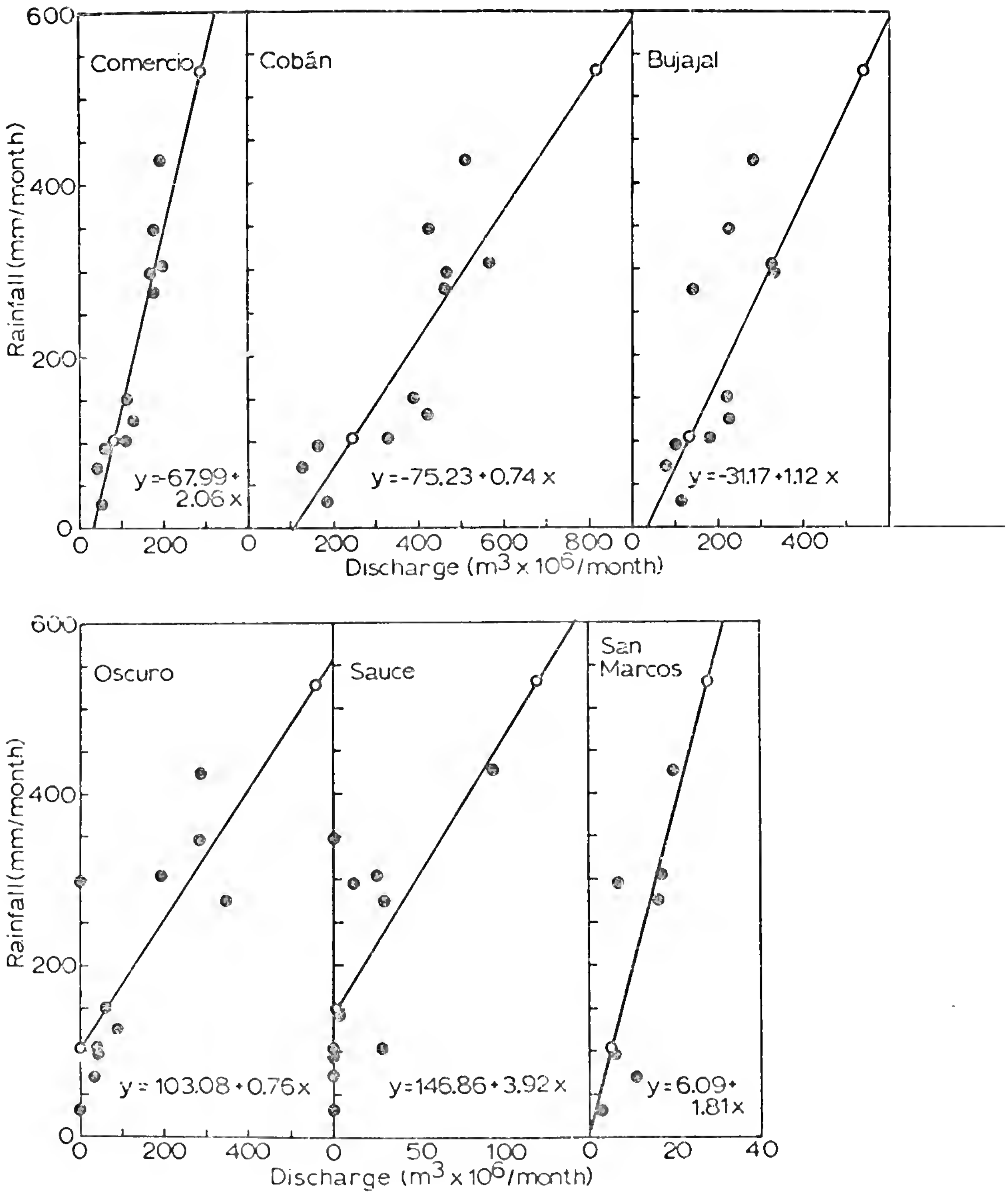

Comercio
y = -67.99 + 2.06 x
Cobán
y = -75.23 + 0.74 x
Bujajal
y = -31.17 + 1.12 x
Rainfall (mm/month)
Discharge (m3 x 106/month)
Oscuro
y = 103.08 + 0.76 x
Sauce
y = 146.86 + 3.92 x
San Marcos
y = 6.09 + 1.81 x
Rainfall (mm/month)
Discharge (m3 x 106/month)

Figure 8.- The seasonal march of monthly discharge rates for some major rivers emptying into Lake Izabal.

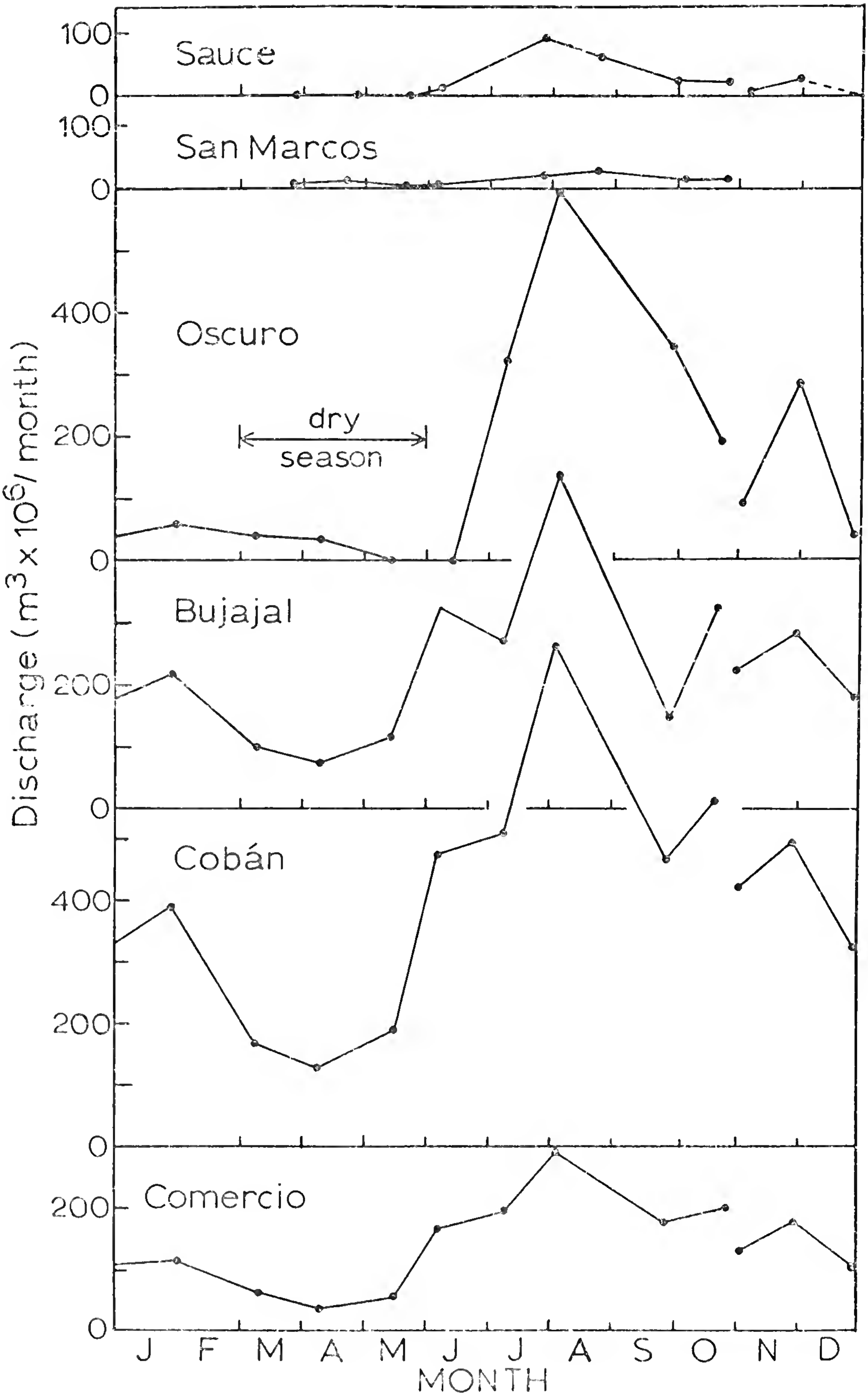

Sauce
San Marcos
Oscuro
Bujajal
Cobán
Comercio
dry season
Discharge (m3 x 10^6/ month)
100
0
100
0
400
200
0
200
0
400
200
0
200
0
J F M A M J J A S O N D
MONTH

Table 2 summarizes the discharge rates of all rivers and watersheds draining into Lake Izabal. Included is runoff from the watersheds to the north and south of the lake which was estimated from the runoff of the Rio Sauce and Rio San Marcos watersheds. The annual discharge from rivers emptying into the extreme western end of the lake was greater than ten times the contribution of the remaining watersheds. The total runoff volume of all watershed areas into Lake Izabal was estimated to be 13,290.9 $m^3 \times 10^6$ during the year of study.

Instead of expressing runoff as a volume, it can be compared directly to rainfall by conversion to equivalent units. This was accomplished by dividing the known runoff volume (m^3) by the area of the watershed (m^2) (Table 3). The annual runoff value of 8,253 mm calculated for the Rio Oscuro watershed was much too high since it is unlikely that rainfall ever reached this value in any part of the watershed. The reason for this overestimate was that at flood stage, the Rio Polochic apparently overflowed into the southern branch of the Rio Oscuro headwaters (Riachuelo Suncal). This resulted in high discharge rates for the Rio Oscuro due partly to water originating from the Polochic watershed. By combining the Rio Polochic and the Rio Oscuro areas (5,480 km^2) and their annual runoff volumes (12,112 $m^3 \times 10^6$), the combined runoff would be 2,210 mm, a more realistic value.

Runoff for all watersheds averaged 1,937 mm. Since the average rainfall for the Izabal Watershed was 2,992 mm, the portion of the precipitation lost as runoff was 65%. This is in close agreement with the watershed of Lake Lanao, Phillipines (Frey 1969) which loses 67% of the 2,873 mm rainfall it receives. Other tropical watersheds receiving

Table 2.- Monthly discharges ($m^3 \times 10^6$) of rivers and watersheds draining into Lake Izabal. Direct rainfall of the lake surface is excluded

	Comercio (1)	Cobán (2)	Bujajal (3)	Oscuro (4)	Amatillo (5)	Total (1-5)	Sauce (6)	San Marcos (7)	North[b] Water-shed (8)	South[c] Water-shed (9)	Total (6-9)	Total (1-9)
Oct 71	132.8	422.1	226.4	89.9	-	-	0.0[a]	6.1[a]	-	-	-	-
Nov	179.7	497.0	284.8	287.4	-	1,248.9	0.8	18.0[a]	1.2	46.4	66.4	1,315.3
Dec	110.3	325.2	179.1	40.5	-	655.1	28.4	5.2[a]	44.7	13.4	91.7	746.8
Jan 72	114.0	386.4	218.7	59.2	-	778.3	1.5[a]	7.6[a]	2.4	19.7	31.2	809.5
Feb[a]	83.0	243.0	128.0	0.0	-	454.0	0.0	5.2	0.0	13.4	18.6	472.6
Mar	62.2	167.3	101.9	41.3	-	372.7	0.0	5.7	0.0	14.8	20.5	393.2
Apr	41.4	124.5	78.7	34.1	-	278.7	0.0	10.9	0.0	28.2	39.1	317.8
May	53.4	187.4	114.8	0.0	-	355.6	0.0	3.2	0.0	8.2	11.4	367.0
Jun	170.5	473.8	330.6	0.0	-	974.9	12.7	6.9	19.9	17.8	57.3	1,032.2
Jul	193.8	507.0	276.2	324.9	153.5	1,455.4	90.3	20.0	142.7	51.6	304.6	1,760.0
Aug[a]	290.0	815.0	538.0	596.2	571.3	2,810.5	67.5	27.9	106.5	72.0	273.9	3,084.4
Sep	178.7	464.3	144.9	347.6	204.6	1,340.1	29.9	16.4	47.2	42.3	135.8	1,475.9
Oct	200.0	564.2	323.3	191.7	108.5	1,387.7	26.2	17.0	41.5	43.8	128.5	1,516.2
Total[d]	1,677.0	4,755.1	2,719.0	1,922.9	1,037.9	12,111.9	257.3	144.0	406.1	371.6	1,179.0	13,290.9

[a] Values extrapolated from regression formula of rainfall vs. runoff. Field readings either underestimated discharge or were not recorded.

[b] North watershed values calculated from runoff of Rio Sauce.

[c] South watershed values calculated from runoff of Rio San Marcos.

[d] Twelve-month total from November 1971 through October 1972.

Table 3.- Summary of hydrologic data for the major watersheds draining into Lake Izabal

Watershed	Area (km^2)	Volume of Annual Runoff ($m^3 \times 10^6$)	Annual Runoff (mm)
Rio Polochic	5,247	10,189	1,942
Rio Oscuro	233	1,923	8,253
Rio Sauce	300	257	857
Rio San Marcos	170	144	847
North Watershed	474	406	857
South Watershed	438	372	847
All Watersheds	6,862	13,291	1,937

less precipitation lose between 40-50% of the rainfall as runoff (Golley et al. 1971).

Snedaker (1970) calculated runoff for Finca Murciélagos by a simple method devised by Holdridge (1967) which requires knowledge of only mean annual biotemperature and annual rainfall. Using this method, Snedaker's runoff estimate was 902 mm or 45% of the rainfall. This is in close agreement with my value for the Rio Sauce watershed (Table 3) which is located on the north shore of the lake near Murciélagos. During the period of study, runoff was 857 mm or 39% of the rainfall (Las Dantas records).

Water Budget

The water budget of the lake was calculated at monthly intervals from inputs by river runoff (already discussed) and by direct precipitation, in addition to the outputs by evaporation and losses though the San Felipe outlet. The monthly contribution by direct precipitation was calculated from the average rainfall at Las Dantas and Mariscos.

Since evaporation from the free water surface of the lake was not measured, a literature search was made to arrive at a reasonable estimate. Free surface evaporation estimates from tropical latitudes appear to be few and the data presented in Table 4 include values for more northern latitudes. However, summer climate regimes, especially in Florida, approximate the year-round climate of the Lake Izabal region. The value of 161 mm/month was chosen as the representative evaporation by averaging the estimates from the humid areas of Lake Helene, Anderson Cue, Lake Michie, Lake Chad, and the Caribbean Lowlands (Table 4). This

Table 4.- Monthly free water surface evaporation measurements for selected warm climates and warm seasons

Region or Lake	Monthly Evaporation (mm)	Year	Source
Lake Helene, Florida[a]	128	1962	Pride et al. 1966
Anderson Cue Lake, Florida[a]	155	1966-68	Brezonik et al. 1969
Lake Elsinore, Calif.[a]	231	-	Szeicz & Endrödi 1969
Lake Tiberias, Israel[a]	193	1949	Reiser 1969
Polish Lakes[b]	140-180	several	Debski 1966
Lake Chad, Africa[c]	188	-	Grove 1972
Caribbean Lowlands	174-254	-	Ray 1931
Lake Michie, N.C.[a]	118	1962-64	Turner 1966
Lake Colorado City, Texas[a]	221-251	1955	Harbeck et al. 1959
East Africa (Nile Region)	90-120	-	Talling 1966

[a] Based on an average of 5 warmest months (May-September).
[b] Based on an average of 4 warmest months (May-August).
[c] Annual total divided by 12.

is equivalent to 115 x 10^6 m^3/month for a surface the size of Lake Izabal and will be considered constant throughout the year.

Changes in lake level (Appendix, Table D, see also Figure 6) represented integrated results of both inputs and outputs. The volume of the lake was calculated from the bathymetric map prepared by Brooks (1969) and was estimated to be 8,300 x 10^6 m^3. Changes in volume were calculated by multiplying changes between mean monthly lake levels by the surface area of the lake.

Table 5 is a summary of the monthly contributions and losses for Lake Izabal. Adding the inputs from runoff and direct precipitation, subtracting the evaporation, and subtracting the positive or negative change in volume resulted in the final value which estimates the monthly loss through the San Felipe outlet. Direct measurement of discharge from the San Felipe outlet was inadequate due to extreme variations in surface velocity. On one day I even observed that the flow had reversed, and further inquiry led to the conclusion that this was a common, if not daily phenomenon. Apparently prevailing northeasterly winds are capable of shifting the leeward level of El Golfete above the level of the lake, thus generating the variation in discharge or reversal of flow at San Felipe. In spite of this difficulty, there was sufficient agreement between the velocities measured in the field and those calculated (Figure 9) to regard the latter values as good estimates of discharge at San Felipe. The direct field measurements were multiplied by a factor of 0.9 to correct for frictional resistance of the banks and bottom (Welch 1948).

The annual water budget for the lake and the watershed is summarized in Figure 10. The average residence time of the water in the lake was

Table 5.- Summary of water budget for Lake Izabal (November 1971-October 1972)

			$m^3 \times 10^6$/month		
Month	Runoff[a]	Direct Rainfall[b]	Evaporation[c]	Change Lake Volume[d]	Loss at Outlet (San Felipe)[e]
Nov 71	1,315.3	246.7	-115	+122.6	1,324.4
Dec 71	746.8	74.2	-115	-171.4	877.4
Jan 72	809.5	106.5	-115	+11.5	789.5
Feb 72	472.6	74.2	-115	-88.9	520.7
Mar 72	393.2	67.8	-115	+23.7	322.3
Apr 72	317.8	49.1	-115	+15.1	236.8
May 72	367.0	20.8	-115	-38.7	311.5
Jun 72	1,032.2	212.6	-115	+67.4	1,062.4
Jul 72	1,760.0	305.8	-115	+302.6	1,648.2
Aug 72	3,084.4	378.6	-115	+253.8	3,094.2
Sep 72	1,475.9	194.5	-115	-249.5	1,804.9
Oct 72	1,516.2	218.7	-115	-151.3	1,771.2
Total	13,290.9	1,949.5	-1,380	+96.9	13,763.5

[a] All watershed areas.

[b] Calculated from the average rainfall of two lakeside stations, Mariscos and Las Dantas.

[c] Estimated from pan evaporation from other localities (Table 4).

[d] Calculated from level changes of lake (Table D, Appendix).

[c] The sum of columns a, b, and c, and the opposite sign of values in column d.

Figure 9.- Relationship between velocities at the San Felipe outlet from direct field measurements and those calculated by balancing the water budget. Perfect agreement between the two estimates would fall on the dashed line. Direct field measurements were multiplied by a factor of 0.9 to correct for frictional resistance of the banks and bottom.

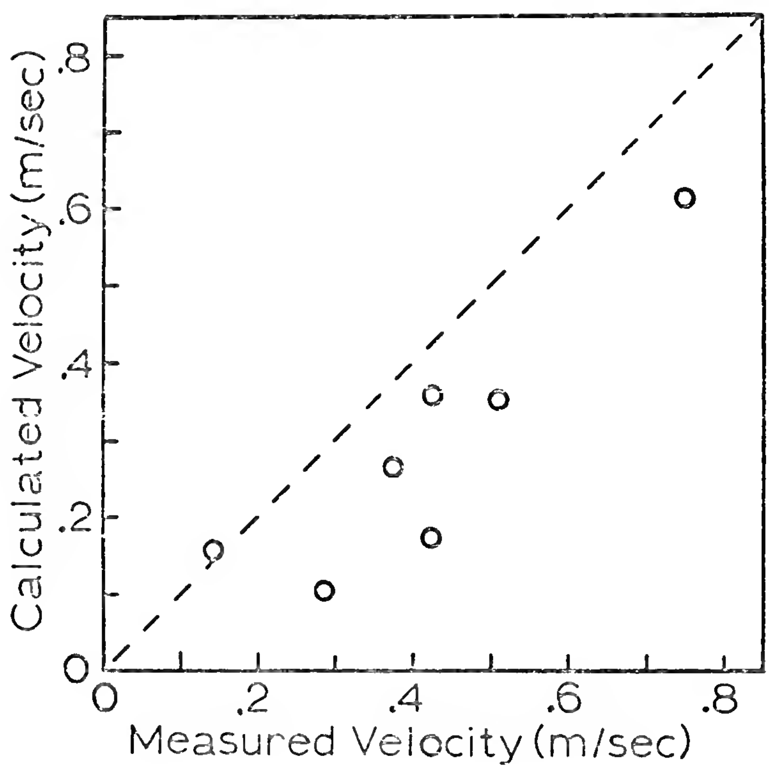
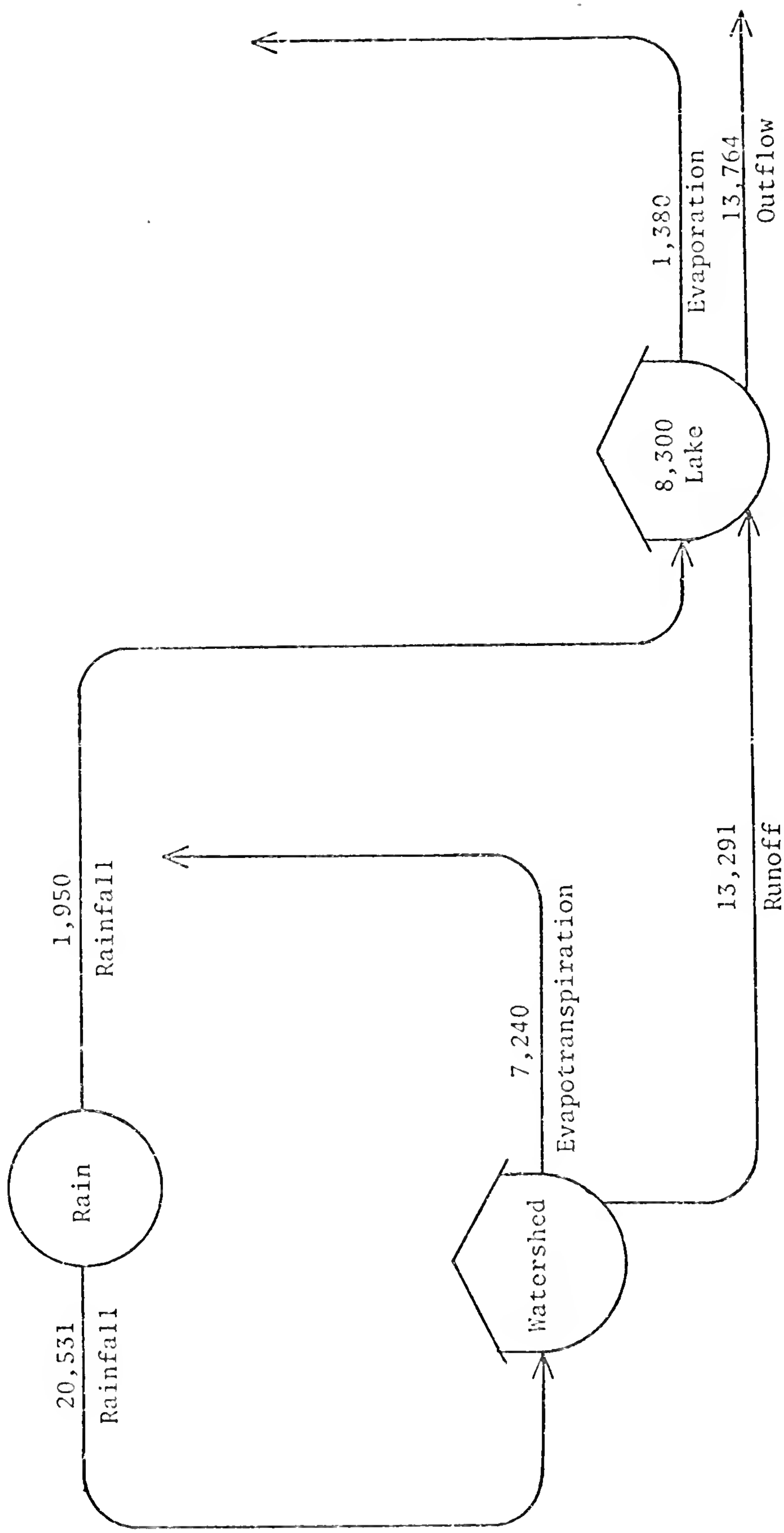

Calculated Velocity (m/sec)
0
.2
.4
.6
.8
0
.2
.4
.6
.8
Measured Velocity (m/sec)

Figure 10.- Summary diagram of water storages and annual flows. All units are expressed in $m^3 \times 10^6$.


Rain
20,531
Rainfall
1,950
Rainfall
Watershed
7,240
Evapotranspiration
13,291
Runoff
8,300
Lake
1,380
Evaporation
13,764
Outflow

calculated by dividing its volume (8,300 x 10^6 m^3) by the 12-month loss by direct evaporation from the surface and the outflow at san Felipe 15,143.5 x 10^6 m^3). This estimated the residence time of the water to be 6.6 months or 0.55 year.

Water Characteristics

Lake Izabal, like other lakes that lack sufficient depth to develop a hypolimnion, would be classified as a third-class lake (Hutchinson 1957) and could fall, functionally at least, into the class of polymictic which is usually reserved for lakes of high mountain regions in equatorial latitudes. Because of Lake Izabal's large area, shallow depth, and high influx of relatively colder waters from rivers, some anomalous and interesting temperature patterns develop.

The Izabal Watershed lies in an area of diverse geological formations, and as a result, receives a variety of water types. Partly because of the large drainage area of a single influent river, the Rio Polochic, much of the water from the various rock types has already mixed before discharging into the lake. Regardless, the large deltaic swamp at the western end of the lake has distinct modifying effects on some of these waters. The proximity of the lake to the sea coast and its connection with a marine environment cannot be overlooked as a potential factor that could influence the ionic composition of this freshwater lake.

Thermal properties and circulation patterns in the lake

Temperature profiles were recorded at approximately monthly intervals at five equidistantly spaced stations along the length of the lake (Figure

4). Figures 11 and 12 illustrate the temperature profiles for each of the five stations (A, A-B, B, B-C, and C). For most stations and dates of sampling, the profiles were isothermal for the first 10-12 m, with the exception of the upper 2-3 m which were heated directly by solar radiation. This surface stratification was only temporary and disappeared rapidly either at sundown or with windy conditions during the day.

More persistant thermal stratification often occurred in the bottom 1-2 m. This was most pronounced at Station A after June when the colder waters from the nearby Rio Polochic created a density current resulting in a cooler layer along the bottom. At Station A-B this seasonal change was more noticable, as the profile is isothermal until June, the beginning of the wet season. Stations B and B-C showed the same characteristics but the thermoclines were not as sharp as the more westerly stations.

Station C was located 30 km east of the Rio Polochic and little influence from the density layers was expected. The stratified layer found on April 8 can only be explained if the 2 C increase in temperature of the upper column (since March 16) failed to circulate with the bottom meter. More interesting was the noticeable increase in bottom water temperature on June 13, due to the arrival of a warmer but denser water mass of high specific conductance (465 μmho/cm at 13 m and only 248 μmho/cm at the surface). This warmer water originated from the brackish conditions that developed at the San Felipe outlet during the preceeding dry season (p. 89).

A dry-season increase in temperatures was recorded for all stations from a low in February to a maximum in June. For most of the

Figure 11.- Vertical temperature profiles of Lake Stations A, A-B, and B recorded at approximately monthly intervals.

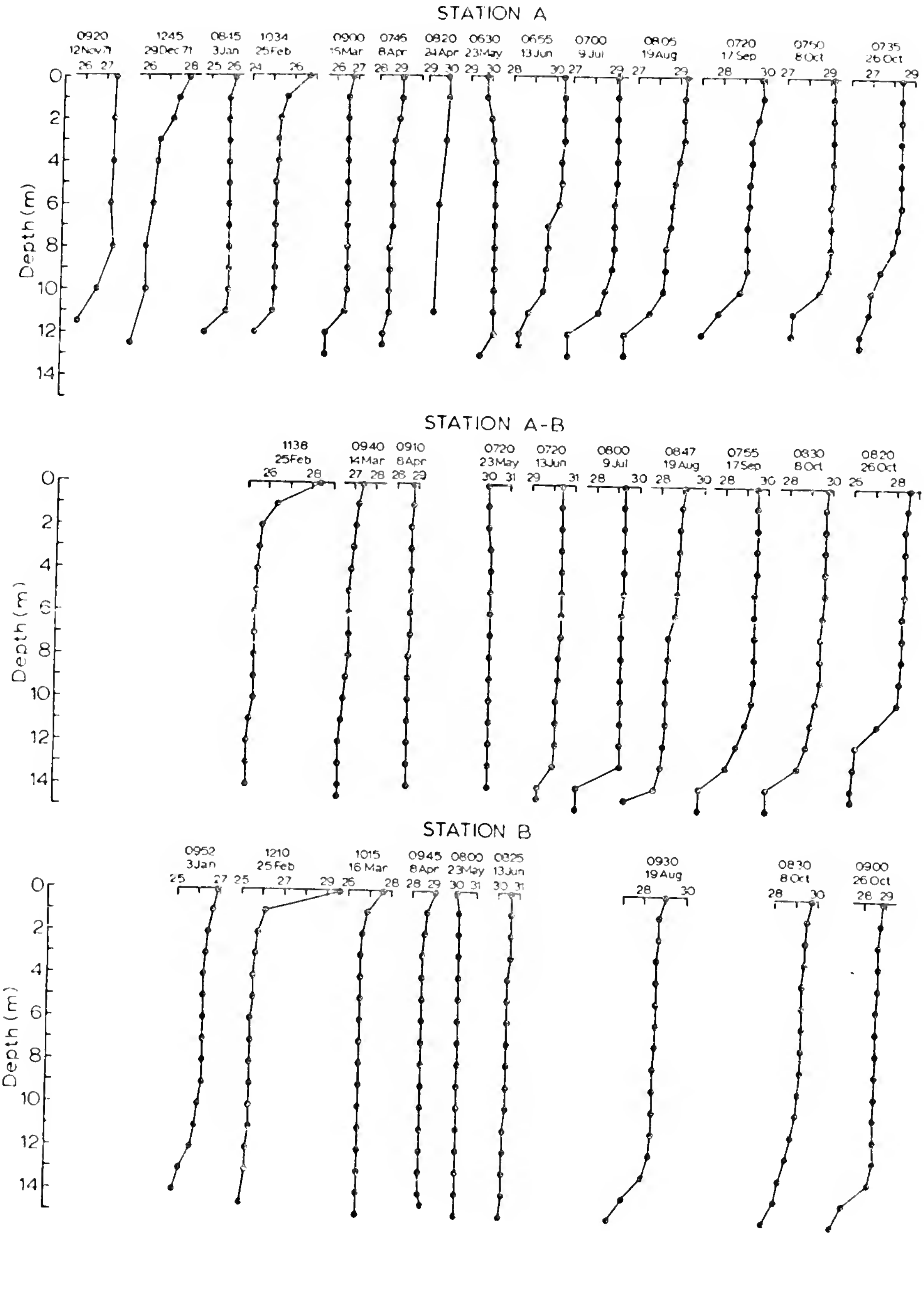
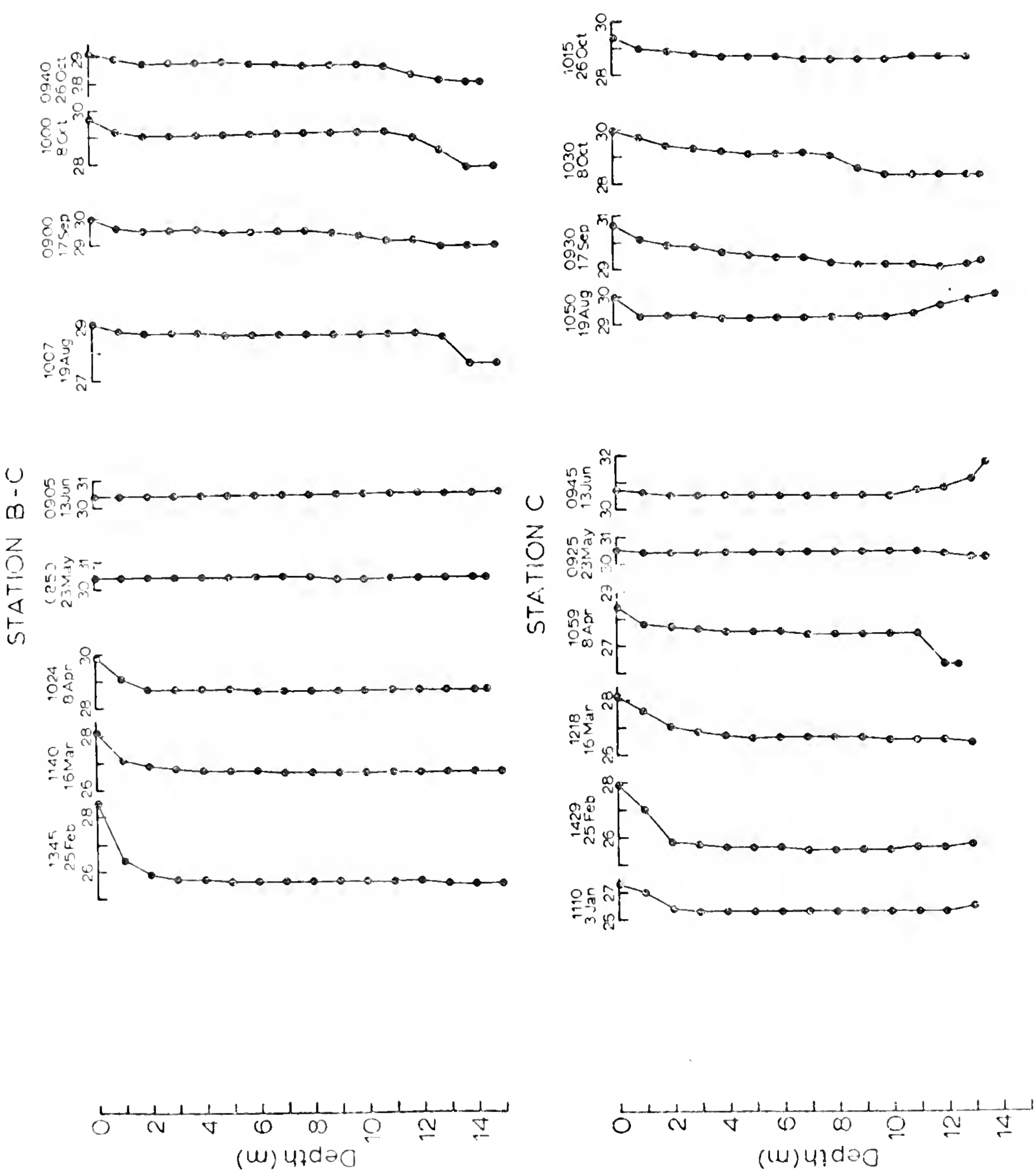

STATION A
Depth (m)
STATION A-B
STATION B

Figure 12.- Vertical temperature profiles of Lake Stations B-C and C recorded at approximately monthly intervals.


STATION B-C
STATION C
Depth (m)
Depth (m)
1345 25 Feb
1140 16 Mar
1024 8 Apr
23 May
0905 13 Jun
1007 19 Aug
0900 17 Sep
1000 8 Oct
0940 26 Oct
1110 3 Jan
1429 25 Feb
1218 16 Mar
1059 8 Apr
0925 23 May
0945 13 Jun
1050 19 Aug
0930 17 Sep
1030 8 Oct
1015 26 Oct

water mass, the minimum was approximately 25.5 C and the maximum 30.4 C, a difference of 4.9 C.

The seasonal pattern of water characteristics

The water samples were arbitrarily divided into four groups--lake stations (A, B, C and San Felipe), swamp waters (Oscuro, Amatillo, El Padre), Polochic distributaries (Comercio, Cobán, Bujajal), and small rivers (Sauce, San Marcos, Manacas Creek, Túnico). These groups are based not on water characteristics per se, but on the origin and locality of the water. The same divisions will be recognized in the treatment of the organic matter data. The results of measurements of pH, total alkalinity, specific conductance, dissolved oxygen concentration, and temperature are presented graphically by station to illustrate the magnitude of seasonal changes (Figure 13-16). Table 6 summarizes the ranges of the extremes measured as well as the approximate ranges for more representative values.

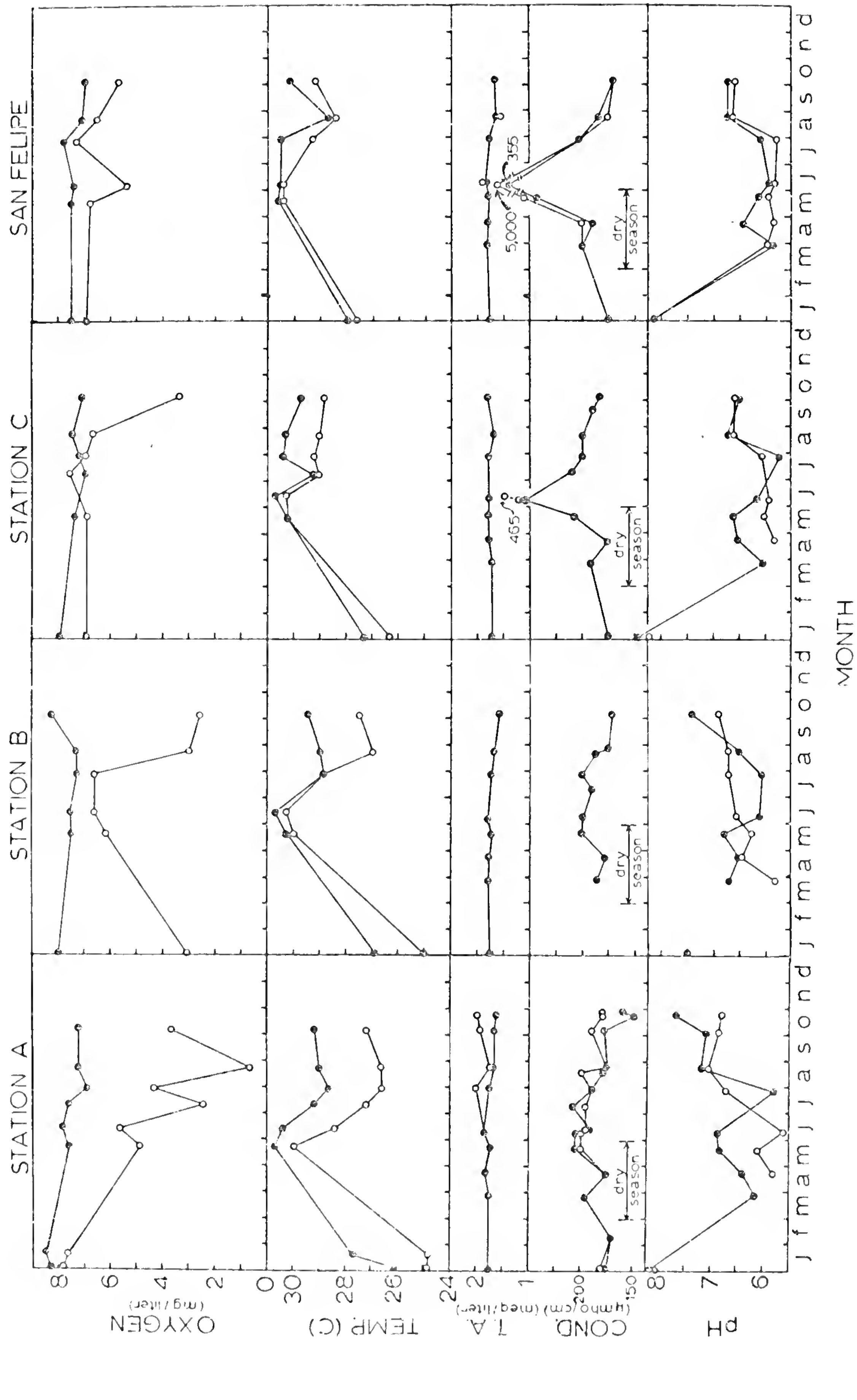
Compared with the other groups, the lake stations (Figure 13) were least variable seasonally for all parameters except specific conductance. This exception was due to the upstream movement of brackish water from the Rio Dulce, through the San Felipe outlet, and into the lake. Total alkalinity showed little seasonal change. Some stratification was noted at Station A due to the density current created by the Rio Polochic waters of slightly higher total alkalinity. A decrease occurred from above pH 8 in January to below pH 7 in March, and then showed a trend toward increase after July. Temperatures increased during the dry season and began to decrease after June. Dissolved oxygen concentrations at the surface probably varied daily as much as they did seasonally.

Table 6.- Ranges of temperature, pH, total alkalinity (T.A.), specific conductance, and dissolved oxygen saturation for all stations sampled at Lake Izabal

		Most Values	Extremes Measured
Lake Stations (A, B, C, & San Felipe)	Temp. (C)	26.0-30.0	24.1-31.4
	pH	6.00-7.00	5.60-8.25
	T.A. (meq/liter)	1.70-1.80	1.60-2.00
	Cond. (μmho/cm)	175-200	150-465[a]
	O_2 (% Sat.)	80-105	8-107
Swamp Waters (Oscuro, Amatillo, El Padre Cr.)	Temp. (C)	25.0-31.0	23.8-31.3
	pH	5.50-7.00	5.20-7.30
	T.A. (meq/liter)	1.00-2.10	0.82-2.37
	Cond. (μmho/cm)	100-200	65-230
	O_2 (% Sat.)	0-100	0-113
Rio Polochic (Comercio, Cobán, Bujajal)	Temp. (C)	23.5-30.5	23.0-30.9
	pH	5.50-6.75	5.20-8.00
	T.A. (meq/liter)	1.50-2.00	1.59-2.19
	Cond. (μmho/cm)	170-225	157-260
	O_2 (% Sat.)	75-95	47-101
Small Rivers (Sauce, San Marcos Manacas Cr., Túnico)	Temp. (C)	25.0-29.0	24.2-32.8
	pH	6.00-7.00	5.75-8.20
	T.A. (meq/liter)	1.00-2.75	0.80-2.82
	Cond. (μmho/cm)	100-250	79-268
	O_2 (% Sat.)	90-100	84-105

[a] The highest conductivity was recorded at San Felipe (5,000 μmho/cm) due to a localized brackish water mass.

Figure 13.- Seasonal changes in dissolved oxygen concentration, temperature, total alkalinity (T.A.), conductivity, and pH for lake stations. Solid circles represent surface readings and clear circles the bottom readings at 11.5 m (Station A), 15 m (Station B), 12 m (Station C), and 10 m (San Felipe).


STATION A
STATION B
STATION C
SAN FELIPE
OXYGEN (mg/liter)
TEMP (C)
T.A. (meq/liter)
COND. (μmho/cm)
pH
dry season
465
5,000
355
MONTH
j f m a m j j a s o n d

Stratification of oxygen is highly variable depending on the frequency and the depth to which vertical circulation occurred.

The swamp waters (Figure 14) became diluted at the beginning of the wet season as reflected by the decreases below dry-season values in conductivity and total alkalinity after June. The pH was variable, but tended to decrease during the dry season. Both temperature and dissolved oxygen concentration decreased dramatically at the beginning of the wet season. The flushing of these rivers by the colder and poorly oxygenated waters originating in the surrounding swamp forest also destroyed the stratification that had been established during the dry season.

The water of the Rio Polochic distributaries (Figure 15) was characterized by dry-season decreases in pH, increases in conductivity and temperature, little change in total alkalinity, and absence of low dissolved oxygen concentrations.

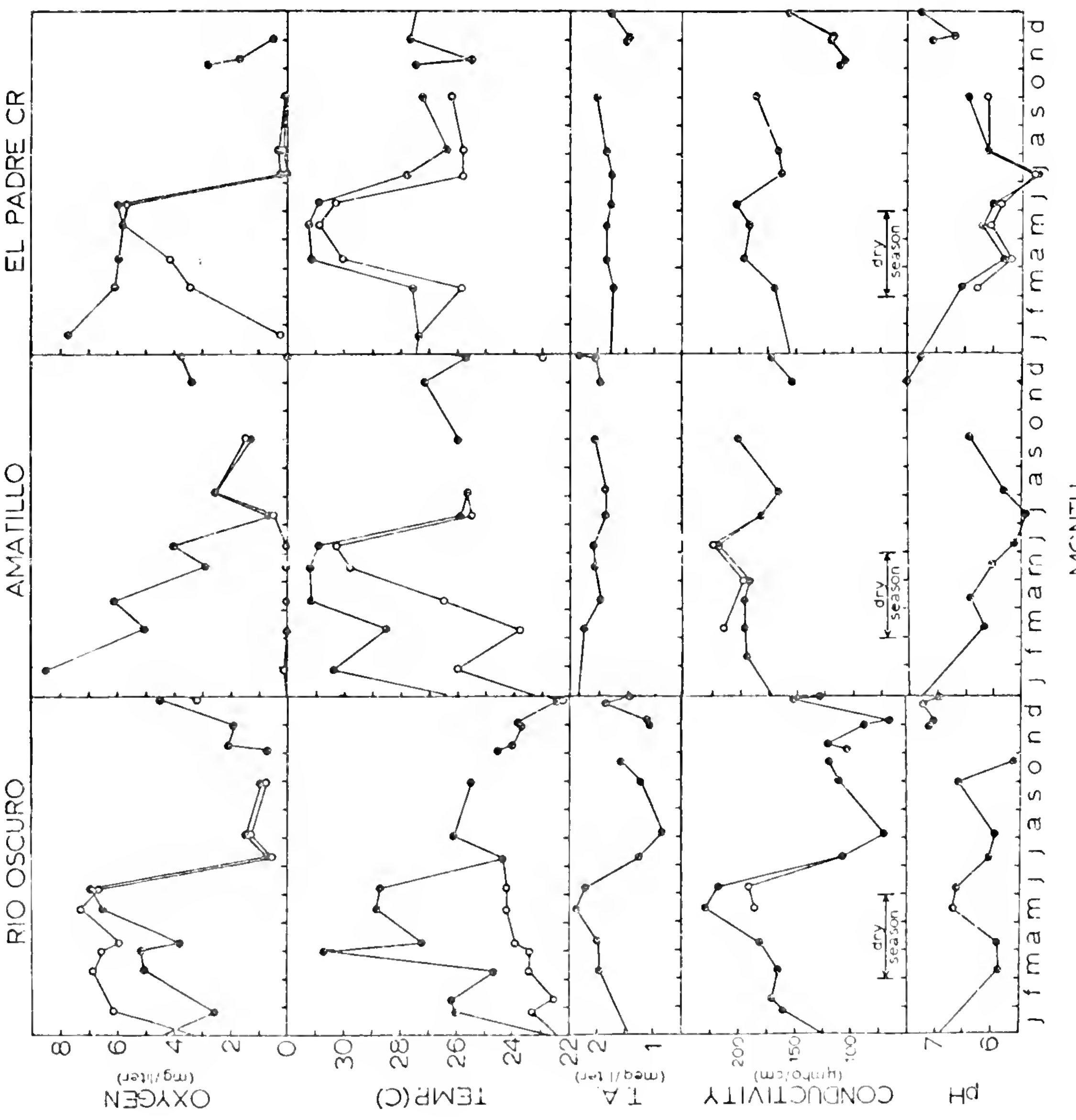
All the small rivers (Figure 16), except for the Rio San Marcos, ceased flowing during the dry season. Thus changes at the beginning of the wet season are less marked in the San Marcos water than in the other small rivers. The seasonal trends were similar to those of the Rio Polochic distributaries described above.

The implications of these seasonal changes in water quality for metabolic activity of the lake and plankton abundance will be discussed in the following sections.

Mineral analyses and the Na:Cl ratio

Samples of lake and river water that were analyzed for dissolved minerals were collected during the dry season (April 14, 1972) and the wet season (October 23, 1972). The results (Appendix, Table E) show

Figure 14.- Seasonal changes in dissolved oxygen concentration, temperature, total alkalinity (T.A.), conductivity, and pH for swamp waters. Solid circles represent surface readings and clear circles the bottom readings at 5 m (Rio Oscuro), 3 m (Amatillo), and 2 m (El Padre Creek).



RIO OSCURO
AMATILLO
EL PADRE CR
OXYGEN
(mg/liter)
TEMP (C)
T.A.
(meq/liter)
CONDUCTIVITY
(μmho/cm)
pH
dry season
j f m a m j j a s o n d
MONTH

Figure 15.- Seasonal changes in dissolved oxygen concentration, temperature, total alkalinity (T.A.), conductivity and pH for distributaries of the Rio Polochic (Comercio, Cobán and Bujajal).

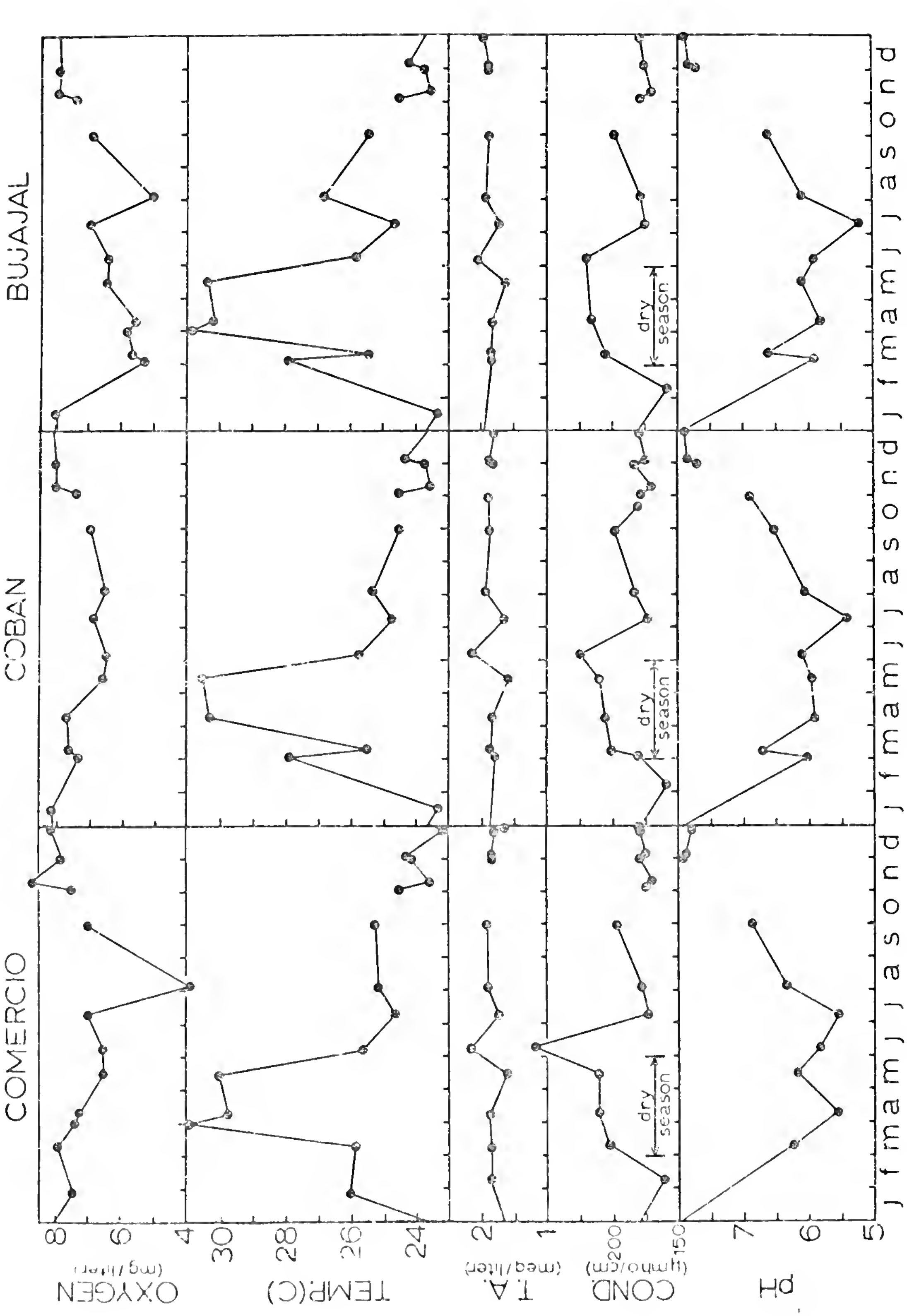
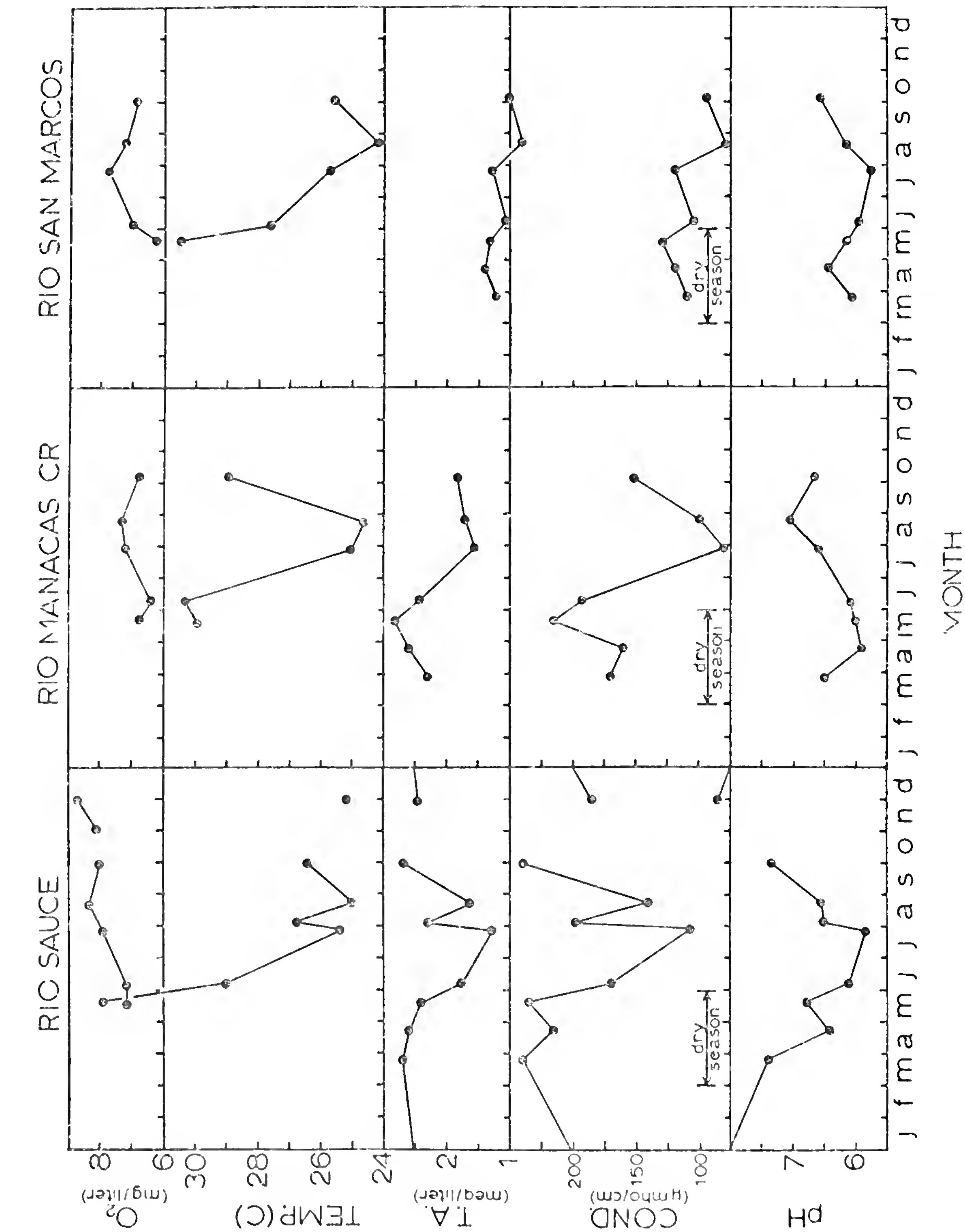

COMERCIO
COBAN
BUJAJAL
OXYGEN (mg/liter)
TEMP(C)
T.A. (meq/liter)
COND. (μmho/cm)
pH
dry season
j f m a m j j a s o n d
MONTH

Figure 16.- Seasonal changes in dissolved oxygen concentration, temperature, total alkalinity (T.A.), conductivity, and pH for small rivers (Sauce, San Marcos, and Manacas Creek).



RIO SAUCE
RIO MANACAS CR
RIO SAN MARCOS
O_2 (mg/liter)
TEMP.(C)
T.A. (meq/liter)
COND. (μ mho/cm)
pH
dry season
MONTH
j f m a m j j a s o n d

that Mn, Fe, Zn, and Ni were detected only occasionally, and always at the lower range of the sensitivity of the tests. Attributing significance to these results would be unwarranted.

The presence of chloride apparently interfered with the measurement of nitrate for the brackish waters of the Rio Dulce Salt Spring and Amatique Bay (October 23) yielding suspiciously high values of 2.7 and 8.5 mg/liter, respectively. Except for the Rio Agua Caliente and Rio Sauce during the wet season, nitrate was near the limit of detection (0.62 mg/liter) of the specific ion electrode. Dry-season concentrations of nitrate were greater than 1 mg/liter in some of the swamp waters (Oscuro Bay, Amatillo, El Padre Creek, and Ensenada El Padre) as well as the Comercio and Cobán distributaries of the Rio Polochic. Dissolved phosphate concentrations ranged between 0.04-0.175 mg/liter and in this range of sensitivity the significance of the results is subject to question.

The high concentrations of Ca, Mg, and Si in the Rio Agua Caliente can be attributed to the hot spring at its origin. However, the low discharge of this river would have resulted in less contribution to the lake of these ions than less concentrated rivers with higher discharges. The Rio Sauce drained a limestone area (probably dolomite) and differed from the lake water by its higher Mg and Si concentration and lower Ca. Rio Manacas Creek during the dry season had a Mg:Ca ratio greater than one. The Rio San Marcos was notably more dilute than the lake water as suggested by the consistantly lower specific conductance of the river throughout the year (Figure 16). Silica concentrations for the October 23 samples may be high due to storage for three months in glass bottles.

The analyses for sodium and chloride in the lake and Rio Polochic waters, however, have some interesting implications for understanding circulatory patterns of the lake water. These data and the ratios of sodium to chloride are presented in Table 7. On April 14 both Na and Cl were higher at San Felipe and Station C at 12.5-m depth than in the rest of the lake. The appearance of slightly brackish water was noted also with conductivity determinations at San Felipe in April but not until June at Station C (Figure 13). Thus the mineral analyses of Na and Cl provided a more sensitive method than conductivity measurements for detection of brackish water as it entered the lake from the Rio Dulce.

The average Na:Cl ratio for the April 14 lake station samples (excluding San Felipe and Station C, 12.5) was 0.52. This value is slightly lower than the ratio 0.56 for sea water (Remane and Schlieper 1971). On October 23 the high ratios of 1.33 at Station A (11.5 m) and 1.69 at Station B (15 m) distinguished them from the ratios of the remaining lake stations. The origin of these high Na:Cl ratios is apparent by comparing them with the October 23 average of the Polochic samples which was 1.76. This provides a conclusive check for the existance of the density current implied by the O_2, alkalinity and specific conductivity stratification at Station A (Figure 13) after the initiation of the wet season.

If the Rio Polochic had been the only source of water for the lake, then the lake water would have been more dilute than it was. Even on April 14, when Na and Cl concentrations were higher in the Rio Polochic, they were not as high as the more dilute lake water on October 23

Table 7.- Sodium and chloride concentrations (mg/liter) and Na:Cl ratios for lake stations and distributaries of the Rio Polochic. Averages are calculated for selected stations

	14 April 1972			23 October 1972		
	mg/liter		Na:Cl	mg/liter		Na:Cl
	Na	Cl	ratio	Na	Cl	ratio
Lake Stations						
Station A - Surf	4.5	7.8	.58	3.3	4.1	.80
Station A - 11.5 m	4.3	8.2	.52	3.2	2.4	(1.33)
Station B - Surf	4.3	8.8	.49	3.5	6.0	.58
Station B - 15 m	4.3	8.8	.49	2.7	1.6	(1.69)
Station C - Surf	4.3	8.2	.52	3.6	5.5	.65
Station C - 12 m	8.2	10.5	-	3.6	6.4	.56
San Felipe - Surf & 10 m	7.7	15.6	-	3.7	4.6	.80
Average			.52			.68[a]
Rio Polochic						
Comercio	3.1	4.9	.63	1.9	1.0	1.90
Coban	3.1	4.5	.69	2.2	1.0	2.20
Bujajal	3.1	1.9[b]	-	2.0	1.7	1.18
Average			.66			1.76

[a] Numbers in parentheses not calculated in average.

[b] Accuracy of determination questionable.

(excluding Station A-11.5 m, and Station B-15 m). By examining Table E of the Appendix, there is no evidence for possible sources of high Na or Cl from the rivers sampled, except Rio Agua Caliente. However, its wet-season discharge was low and the river did not flow at all throughout most of the dry season. Further confirmation is available from August 1969, when Brooks (1969) detected Na and Cl concentrations in the Rio Polochic to be 3.2 and 2.2 mg/liter respectively. Higher concentrations (4.8 mg Na/liter and 7.5 mg Cl/liter) were reported by Brooks for lake water samples.

Brackish water movement into Lake Izabal

To determine the seasonality and extent of movement of the saline-fresh water interface between Lake Izabal and Amatique Bay, several sampling trips were made into the Rio Dulce-El Golfete region (Figure 17). Two of these trips traversed the area between the San Felipe outlet and the coastal port of Livingston; one was made during the dry season (March 22-23, 1972) and the other during the wet season (October 26, 1972). A third transect (May 13) included only Stations 1-8. The sampling stations are numbered from 1 to 11 in Figure 17.

On the first transect (March 22-23) a salt-water wedge was observed extending from Station 11 at Livingston to El Golfete between Stations 5 and 6 (Figure 18). The deep high-salinity water was nearly isothermal (29.4-29.6 C) and slightly warmer than the surface waters (Figure 19). A strong (ca. 0.6 m/sec) outgoing current in the upper 1-2 m of the Rio Dulce below El Golfete marked the interface with the relatively motionless deep layers. An increase in conductivity at Station 8 over a 17-hour period was attributed to downstream tidal forces (Figure 20). This

Figure 17.- Map of the Rio Dulce-El Golfete system. Sampling stations (1-11) on the Rio Dulce and El Golfete are represented with triangles. Lake stations (lower left-hand corner) are not shown.

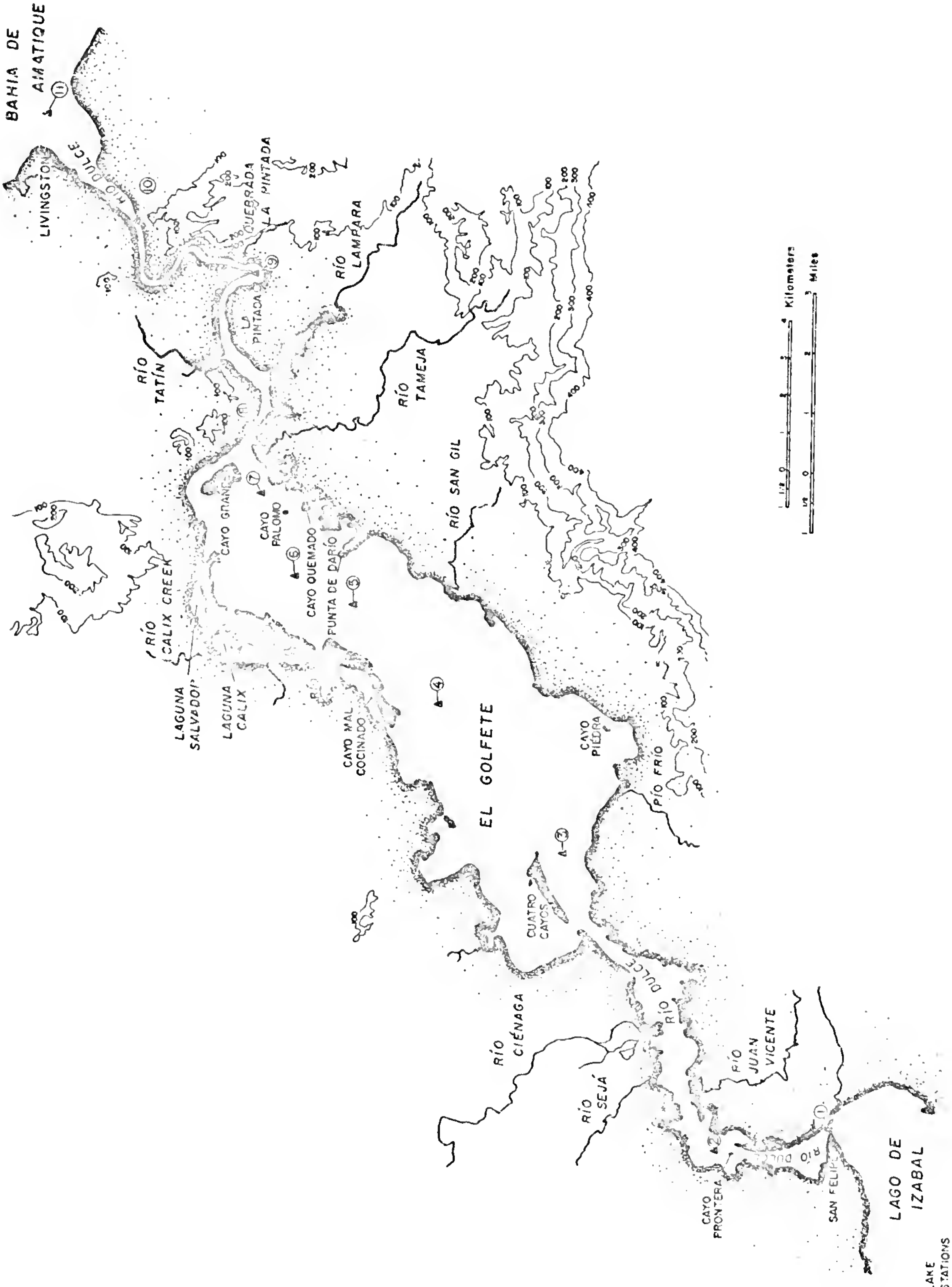

BAHIA DE AMATIQUE
LIVINGSTON
RÍO DULCE
QUEBRADA LA PINTADA
RÍO LAMPARA
LA PINTADA
RÍO TATÍN
RÍO TAMEJA
RÍO SAN GIL
CAYO GRANDE
CAYO PALOMO
CAYO QUEMADO
PUNTA DE DARÍO
RÍO CALIX CREEK
LAGUNA SALVADOR
LAGUNA CALIX
CAYO MAL COCINADO
EL GOLFETE
CAYO PIEDRA
RÍO FRÍO
CUATRO CAYOS
RÍO DULCE
RÍO CIÉNAGA
RÍO SEJÁ
RÍO JUAN VICENTE
CAYO FRONTERA
SAN FELIPE
RÍO DULCE
LAGO DE IZABAL
← LAKE STATIONS
Kilometers
Miles

Figure 18.- Conductivity profiles (March 22-23, 1972) along the Rio Dulce from San Felipe (Station 1) to Amatique Bay (Station 11).

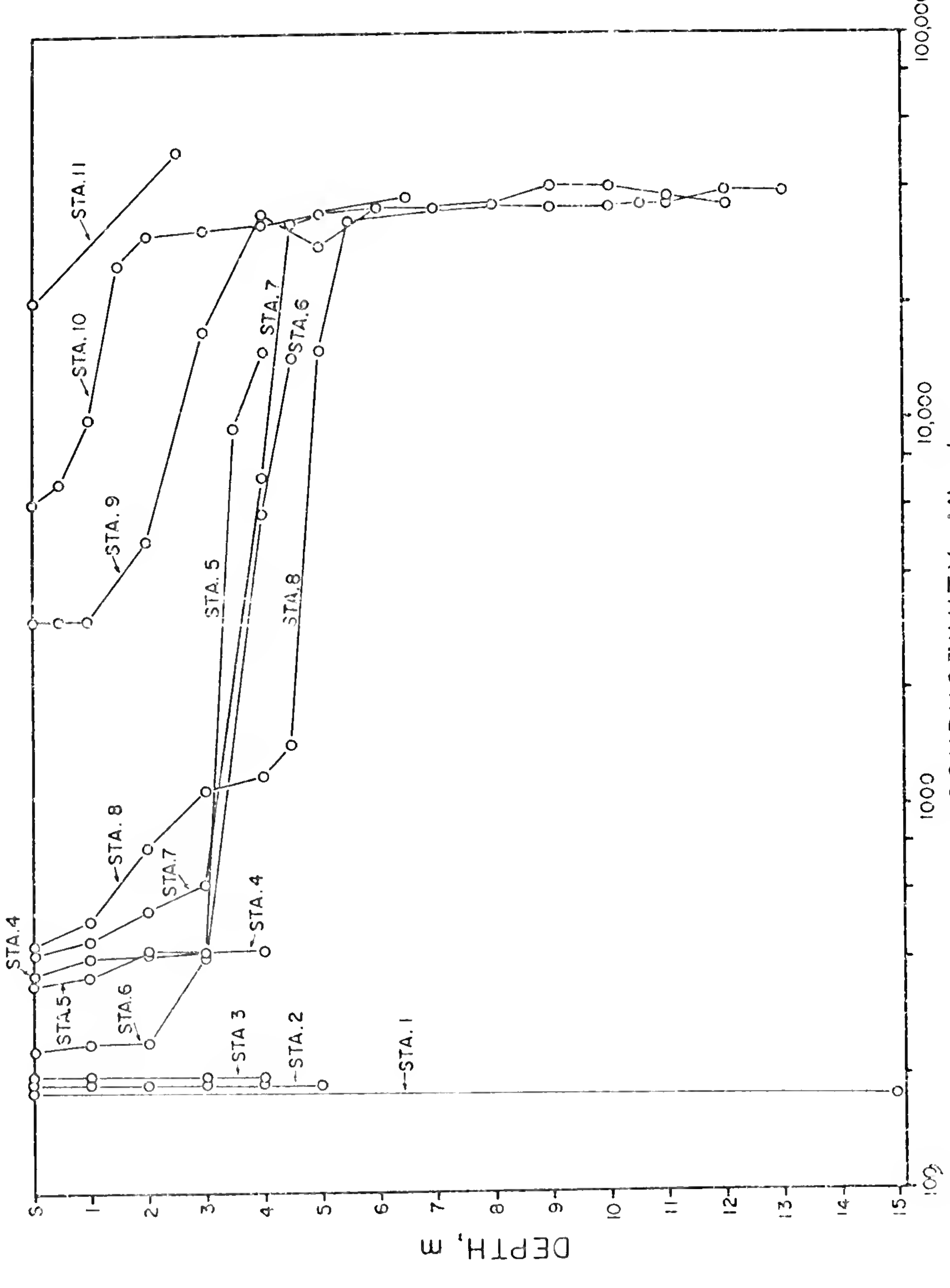

DEPTH, m
CONDUCTIVITY, μMho/cm
100
1000
10,000
100,000
S
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
STA.1
STA.2
STA 3
STA.4
STA.5
STA.6
STA.7
STA.8
STA.9
STA.10
STA.11

Figure 19.- Temperature profiles at two stations illustrating a slight temperature increase associated with the halocline. On Station 8, the halocline occurs at 5 m, on Station 9, at 3.5 m.

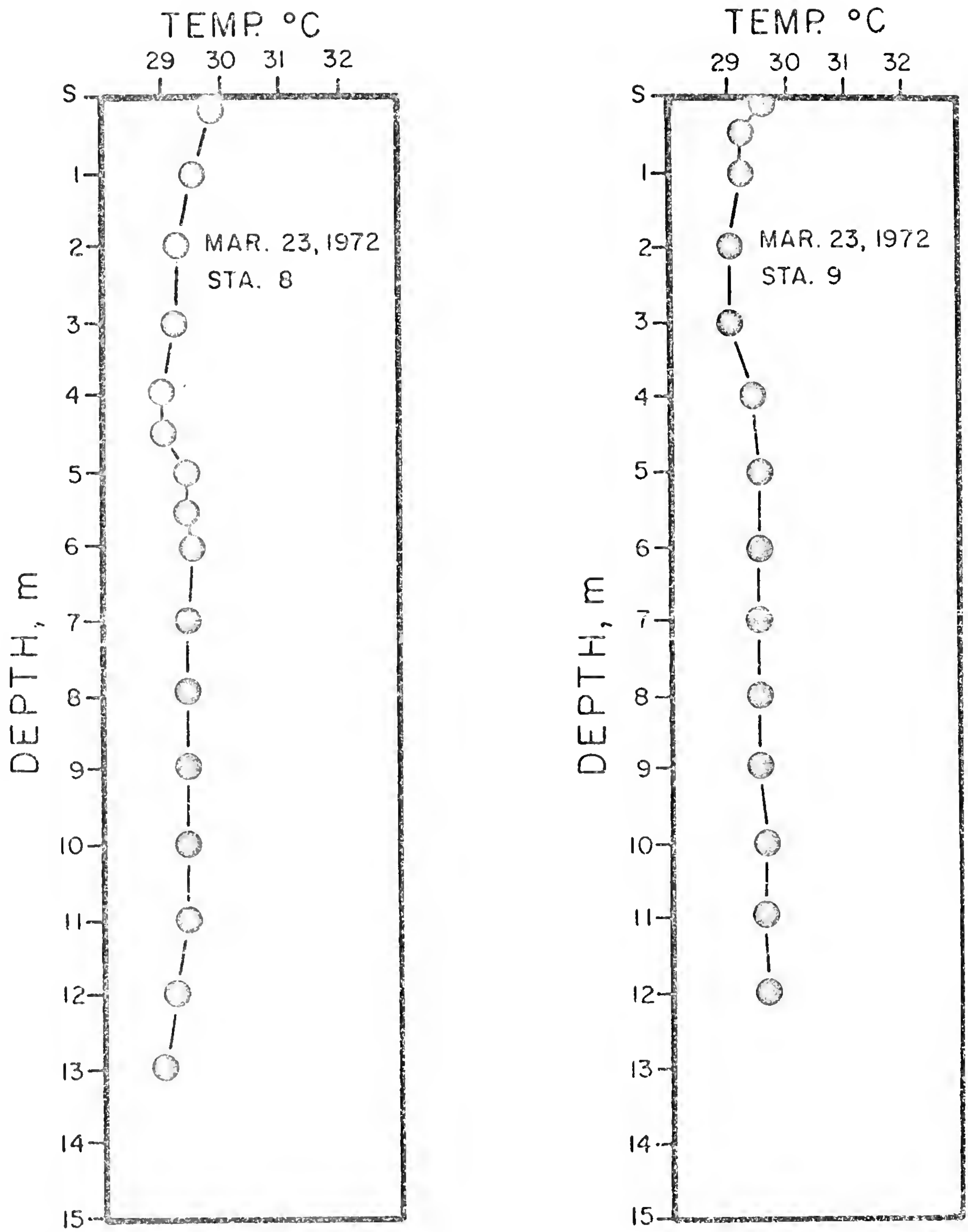
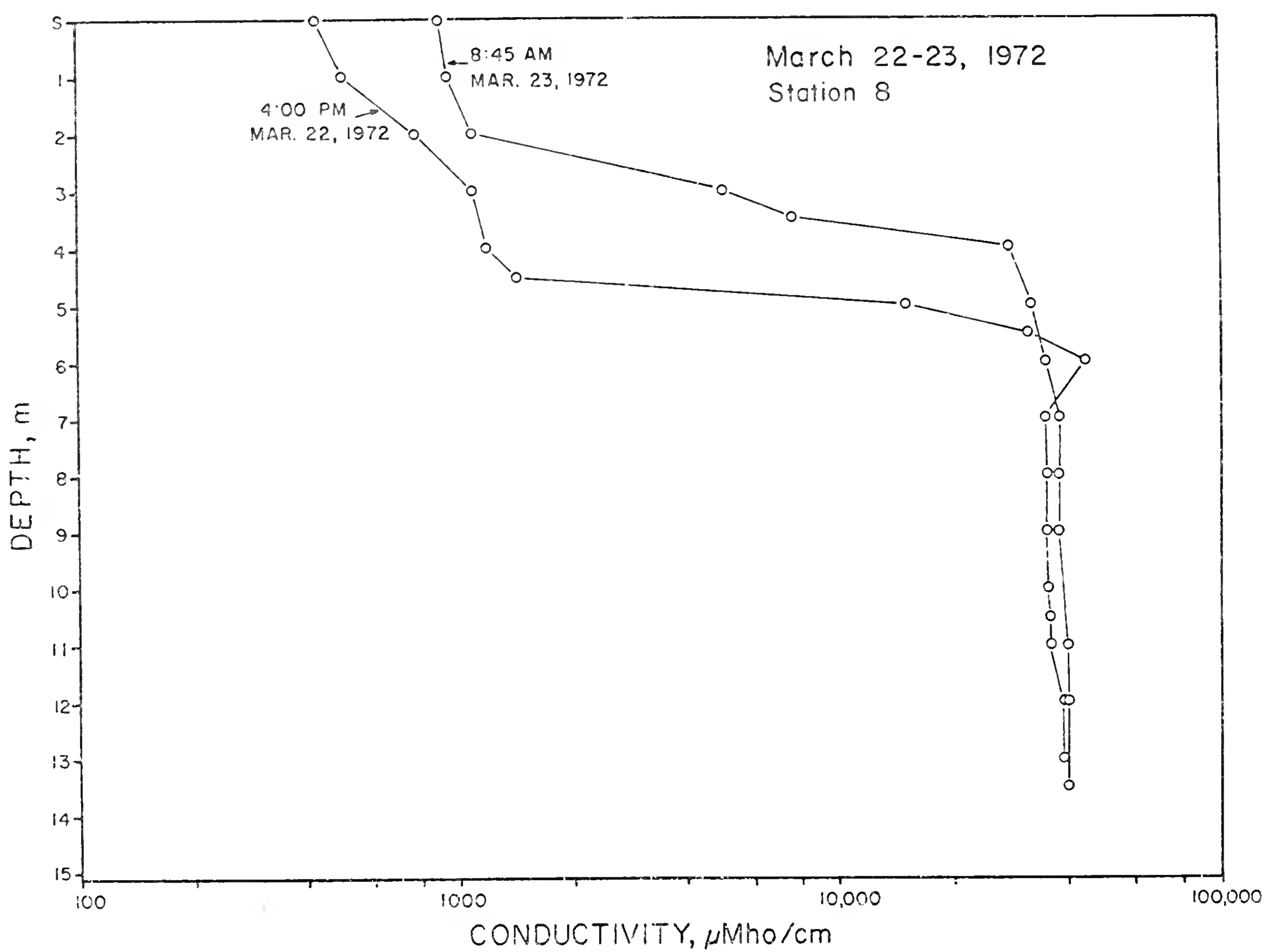

TEMP. °C
29
30
31
32
DEPTH, m
S
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
MAR. 23, 1972
STA. 8
TEMP. °C
29
30
31
32
DEPTH, m
S
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
MAR. 23, 1972
STA. 9

Figure 20.- Observed diurnal change in the conductivity profile of the waters at the lower reaches of El Golfete (Station 8). The diurnal variation is due to tidal movements.


March 22-23, 1972
Station 8
8:45 AM
MAR. 23, 1972
4:00 PM
MAR. 22, 1972
DEPTH, m
S
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
100
1000
10,000
100,000
CONDUCTIVITY, μMho/cm

resulted in an upward displacement of the halocline by approximately 2 m, demonstrating the mechanism for upstream movement of the high-salinity water mass.

On March 22 the specific conductance of the ground water (ca. 30-cm depth) of the swamp forest at Cuatro Cayos in the southwestern end of El Golfete was measured. The conductivity increased from the edge of the island to 5-m distance from the shore, and then decreased gradually to a distance of 35 m where the ground-water salinity was still higher than the surrounding El Golfete water (Figure 21). The presence of this higher salinity water indicated that salt-water intrusion had occurred during dry seasons prior to 1972 and that the swamp forest, where some red mangroves were present, maintained the brackish condition throughout the wet season.

On May 13 brackish water was detected as far upstream as Station 1 at San Felipe (Figure 22) on a transect which was conducted downstream to the upper end of the lower Rio Dulce at Station 8. The main mass of the salt-water wedge, determined at ca. 14,000 μmho/cm on March 22 at Station 7, had moved 7.6 km across the Golfete to Station 4 in 22 days, or an average of 345 m/day.

The last dry-season measurements on June 13 included lake stations whose conductivities were measurably higher than previously recorded. At Station C the reading of 465 μmho/cm at the bottom (Figure 13) and other measurements above 200 μmho/cm were detected between San Felipe and Station C (Figure 23). I failed to detect a continuously declining gradient of conductivity between San Felipe and Station C on June 13. The presence of high conductivity water at San Felipe (Station 1, 10 m)

Figure 21.- Conductivity of the ground water in a swamp forest at Cuatro Cayos. Readings were taken at a depth of 30 cm.

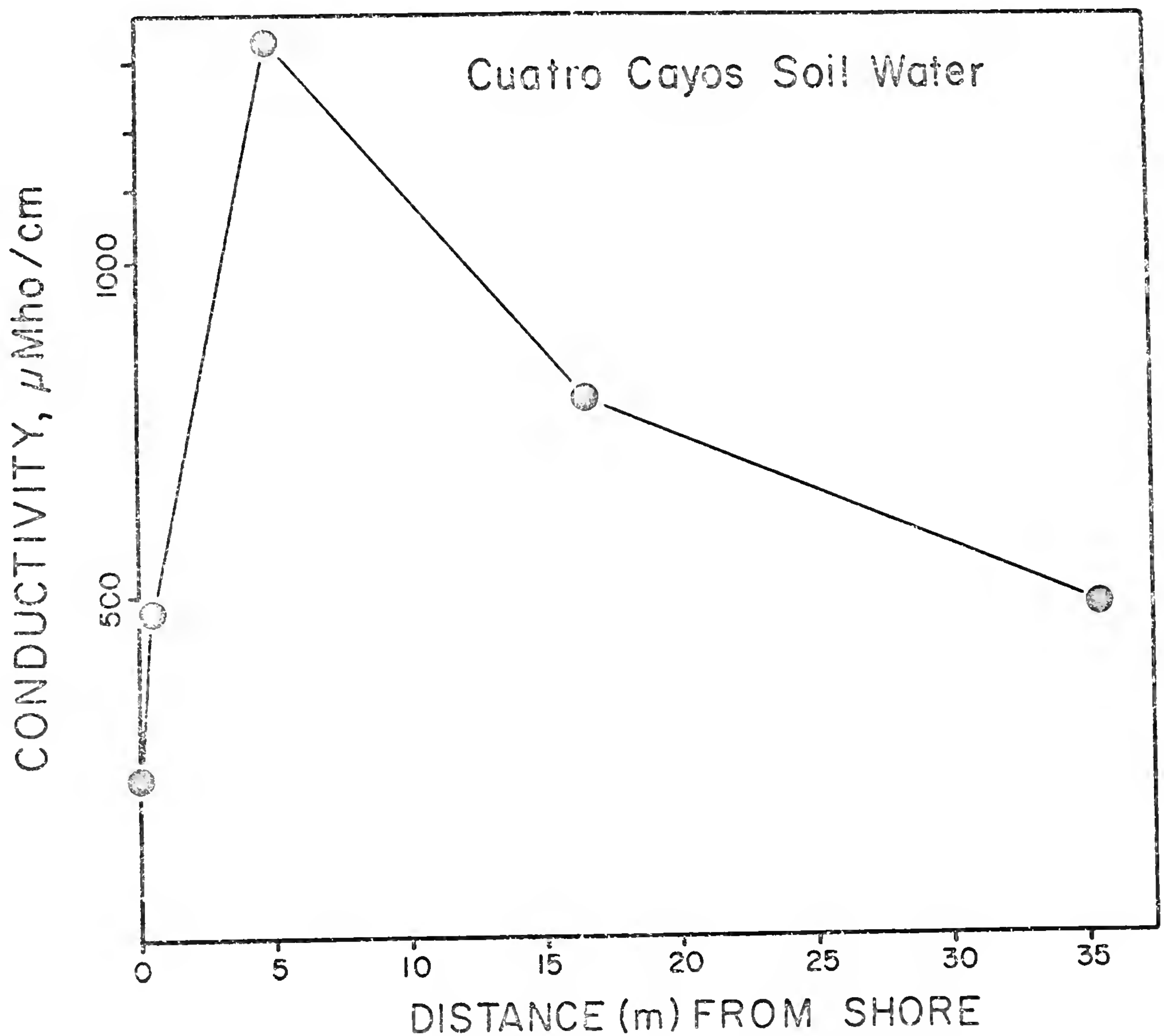

Cuatro Cayos Soil Water
CONDUCTIVITY, μMho/cm
1000
500
0
5
10
15
20
25
30
35
DISTANCE (m) FROM SHORE

Figure 22.- Conductivity profiles along the Rio Dulce from San Felipe (Station 1) to the lower reaches of El Golfete (Station 8).

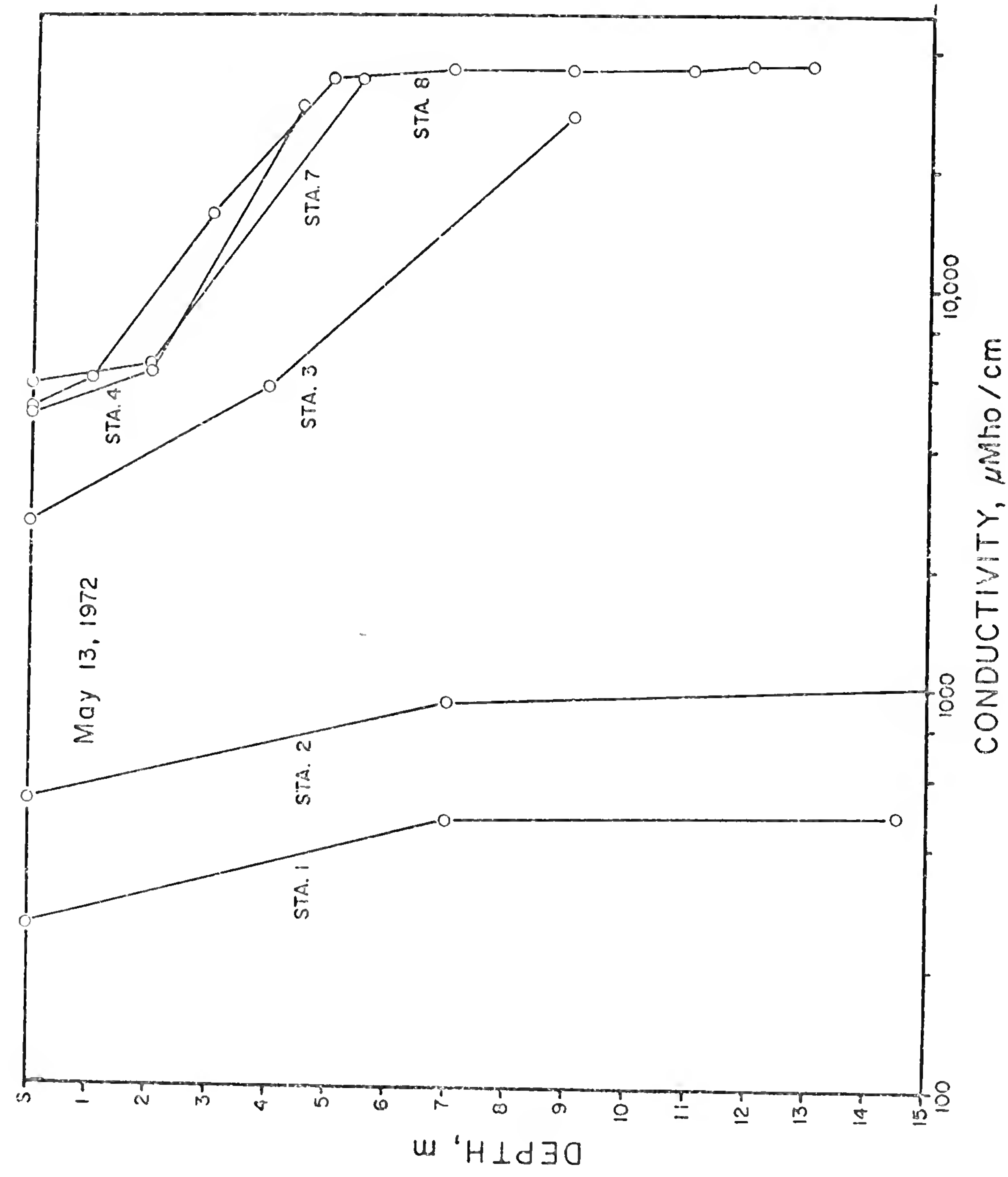
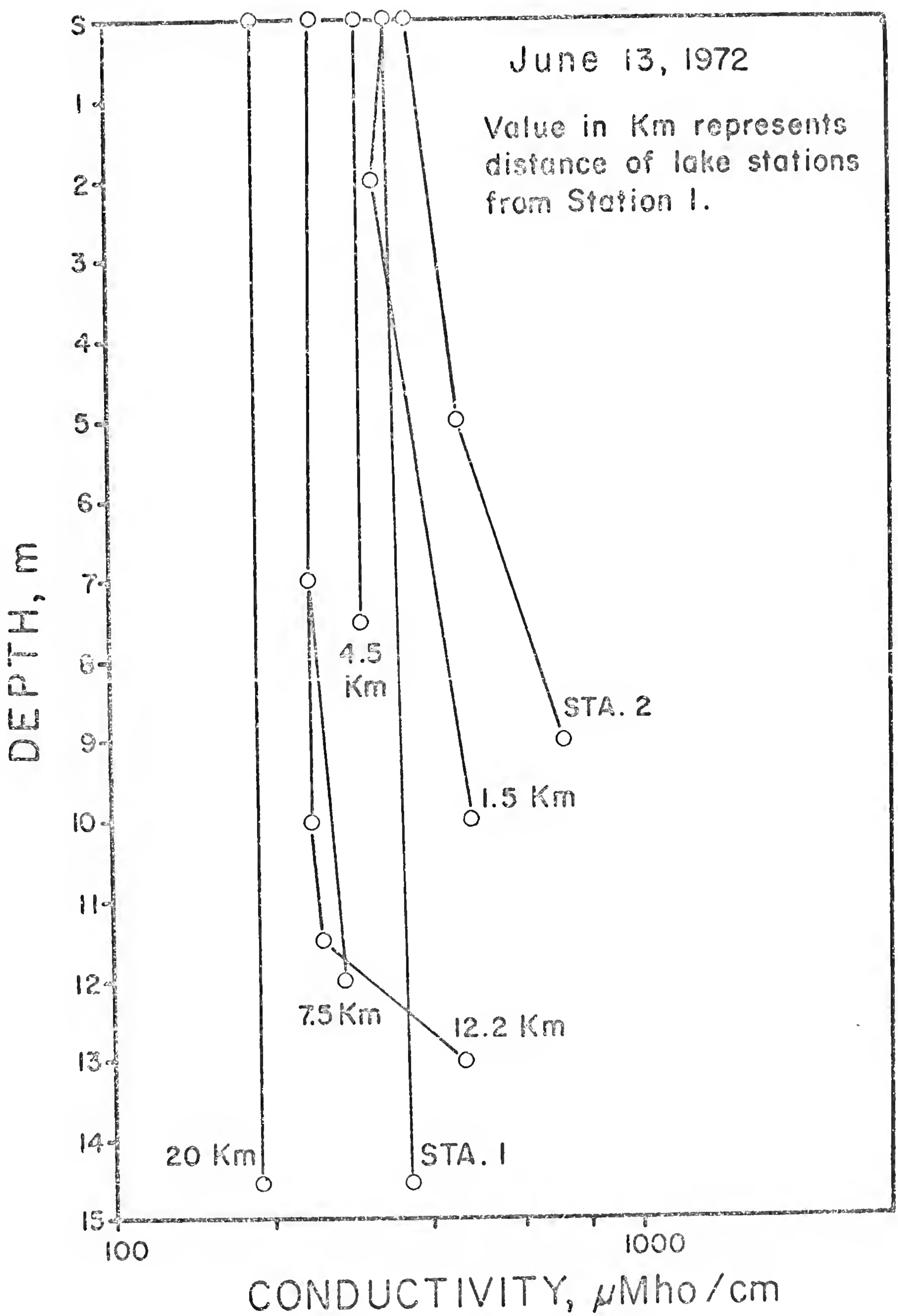

May 13, 1972
STA. 1
STA. 2
STA. 3
STA. 4
STA. 7
STA. 8
DEPTH, m
S
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
100
1000
10,000
CONDUCTIVITY, μMho / cm

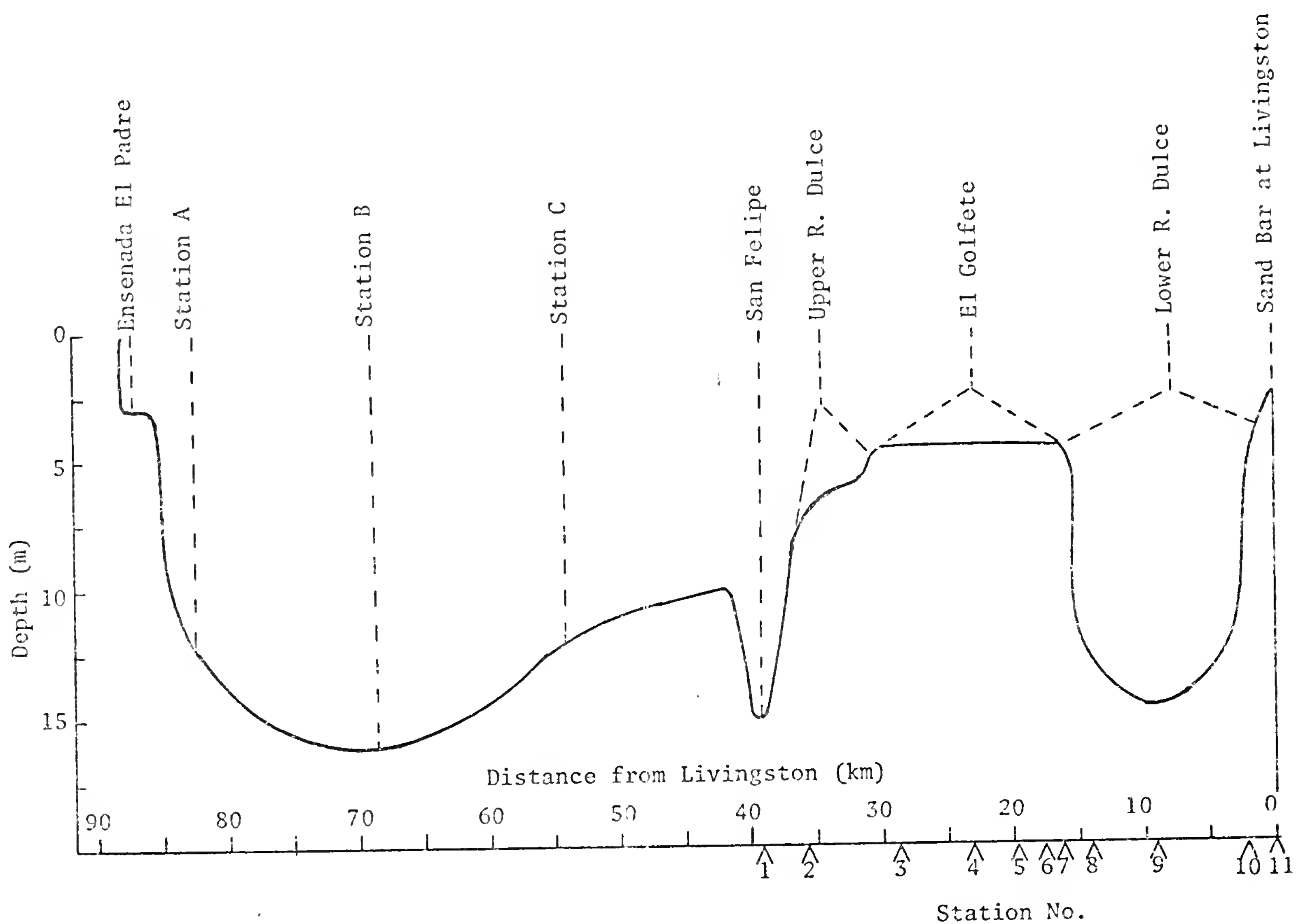
Figure 23.- Conductivity profiles taken at several stations in Lake Izabal and the upper reaches of Rio Dulce (Stations 1 and 2). Notice that a detectable increase in conductivity occurs as far as 12.2 km inside the lake at a time corresponding to the end of the dry season.


June 13, 1972
Value in Km represents distance of lake stations from Station I.
S
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
DEPTH, m
4.5 Km
STA. 2
1.5 Km
7.5 Km
12.2 Km
20 Km
STA. I
100
1000
CONDUCTIVITY, µMho/cm

on June 9 and its absence on June 13 (only 365 μmho/cm) emphasized the haline discontinuity in this region. This can be attributed to the movement of discrete water masses and their eventual mixing with lake water which diluted them, thus dispersing the denser high-salinity layers.

The movement of brackish water into the lake was probably not a continual flow, but an occasional spill-over depending on wind-generated currents and tidal forces. Gravitational force also may have caused denser masses of high-conductivity water to sink to deeper regions of the bottom profile. The dry-season current at San Felipe shifts with the prevailing winds, lending support to the belief that the level of El Golfete and the lake were approximately the same. El Golfete (4.5-m depth) served as only a temporary barrier for the upstream movement of the salt-water wedge. San Felipe Bay constituted another barrier (10 m) between the deeper region of the San Felipe narrows (15 m) and the deeper lake (Figure 24). On a given year, the amount of brackish water that crosses these barriers probably depends on the intensity and length of the dry season. Two local inhabitants informed me that on some years they have noted brackish surface water (by taste) as far into the lake as Finca Jocoló on the north shore (ca. 7 km from San Felipe) and Finca Icacal (ca. 8 km from San Felipe). Popenoe (personal communication) has detected a brackish taste in surface water as far westward as Zapotillo near El Estor. An even more widespread occurrence of brackish water is implicit in these observations based on the stratification patterns that developed during the year of study. This would suggest that during some years the lake receives much larger quantities of brackish water than was observed during the 1972 dry season. This may

Figure 24.- Bottom profile of the Lake Izabal-Rio Dulce system, showing locations of sampling stations. The vertical scale is exaggerated 2,000 times.


Ensenada El Padre
Station A
Station B
Station C
San Felipe
Upper R. Dulce
El Golfete
Lower R. Dulce
Sand Bar at Livingston
Depth (m)
0
5
10
15
Distance from Livingston (km)
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
Station No.

explain why Tsukada and Deevey (1967) reported conductivities of 300-400 µmho/cm for the lake in 1964, approximately twice that of normal lake values measured in 1971-72.

Bottom water samples in July from Station C and San Felipe failed to show haline discontinuities due to higher salinity deep water. The rise in lake level at the beginning of the wet season resulted in an increased outflow at San Felipe, thereby forcing the brackish water downstream. Tributaries emptying into the Rio Dulce and El Golfete contributed to the overall dilution and flushing of the waterway.

No attempt was made to follow the movement of brackish water downstream during the wet season. However, another transect was made of sampling Stations 1-11 on October 18. No evidence of saline water could be detected except at Station 11 where the surface reading was 440 µmho/cm and the bottom (1 m) was 2,500 µmho/cm. Attempts to find residual pockets of denser saline water in El Golfete were unsuccessful, even in the black-water lagoons of the mangrove fringe on the north shore.

Summary Statement

The hydrologic regime of the Izabal Watershed imposes a marked influence on the seasonal water flows and circulation patterns of the lake. The year of study can be characterized as abnormally wet as evidenced by the flooding of inflowing rivers and the occurrence of an unusually high water level of the lake. The dry season, during which monthly rainfall was less than 100 mm, is usually of five months duration (Snedaker 1970), but lasted only three months--March, April, and May--

during 1972. Over 90% of the runoff volume entered the lake through the Rio Polochic Delta at the western end of the lake, and was largely responsible for the relatively short residence time of 6.6 months for the water mass of the lake. These colder river waters created profile-bound density currents that spread over the broad basin of the lake, causing temporary thermal stratification of the lower 1-2 m. The inflow of colder waters and the decreased insolation later in the wet season, resulted in a decrease of the temperature of the water column to ca. 5 C below the dry-season temperature maximum. Stratification was usually absent in the lower layers during the dry season, but present in the surface layers on calm days due to localized heating of the upper 2-3 m. Thus the lake could be classified as warm polymictic.

Whereas wet-season influences originated at the western end of the lake, dry-season influences were noticed at the opposite end. At the lake's outlet to the sea, where dry-season outflow was low and sometimes absent, high-conductivity water worked its way up from the lower Rio Dulce and over the barriers imposed by the shallow El Golfete and San Felipe Bay. This penetration of high-conductivity water was low during the year of study, apparently due to the brief dry season. However, during other years, the penetration may be much greater, and there is evidence that the concentration of Na and Cl ions in the lake water, although more dilute than in most hard waters, is regulated by the seasonal influx of water of marine origin. Other than this, the ionic composition of the water showed no interesting anomalies, except for the high Mg:Ca ratios of some of the smaller rivers that apparently drain serpentine and dolomite formations.

River discharge was greatest in August, the wettest month, just three months after the beginning of the wet season. Runoff waters were most dilute during July and August. Although conductivity, alkalinity and temperature of the lake waters roughly paralleled the seasonal changes of the rivers, the magnitude of change was much smaller, owing to the buffering effect of the large water mass of the lake.

NET PLANKTON AND BENTHIC COMMUNITIES

An understanding of the seasonal changes in plankton abundance would require not only a constant monitoring of many environmental parameters, but also a knowledge of the requirements of each species and their influence on one another. Even under the controlled conditions of chemostats, this problem is formidable. The objective of following the seasonal changes in net-plankton abundance was not to acquire precise information on the population dynamics of individual species, but to gain insight on the gross seasonal periodicity of the biotic component of the lacustrine ecosystem.

Only part of the plankton community is sampled when collected with a net, and some important plankters are probably unrepresented in the samples, while others, that may vary in size, could be underestimated due to selection for larger individuals. Thus, the net plankton does not represent a natural assemblage of organisms, but rather an artificially selected community whose lower limit in size is determined by the mesh aperture of the plankton net.

By using vertical tows, the collection method integrates the numbers of organisms in the water column by sampling most of its length, but ignores vertical stratification which probably would be of less interest in a shallow lake than a deep one.

Methods

Phytoplankton and zooplankton were sampled 15 times from January 6 to October 26, 1972, at three- to four-week intervals at Stations A, B, and C (Figure 4). Three vertical tows were made at each station with a No. 20 plankton net (25-cm diameter) and the tows approximated the depth of the stations. At Stations A, B, and C, the tow lengths were 12.5 m, 14.65 m, and 11.80 m, respectively. The three tows were combined at each station and anesthetized with absolute ethyl alcohol at about 5% by volume. Upon return to the laboratory, the samples were diluted so they could be counted and were fixed with a buffered formalin solution (40% formaldehyde) at 2% concentration by volume.

The volumes of the plankton tows were calculated as the length of the tows multiplied by the area of the net (0.049 m^2). Counts were made of three one-ml subsamples of the thoroughly mixed samples. Most of the larger plankton were counted with a dissecting microscope at 45x magnification and a binocular compound microscope was used for counting rotifers (100x magnification). Identifications were made with the aid of Ward and Whipple's Fresh-Water Biology (Edmondson 1959), Fresh-Water Algae of the United States (Smith 1950), and the Fresh-Water Invertebrates of the United States (Pennak 1953).

Pennate diatoms were counted as one unit per cell, and no attempt was made to distinguish species. Each *Melesira granulata* filament was counted as one unit as were *Pediastrum simplex* colonies, *Anacystis cyanea* gelatinous masses, and *Eudorina* sp. colonies. Calanoid and cylopoid copepods were counted as two groups; each individual was counted as one unit. Adults and copepodids were not distinguished from each other, but the nauplii were counted seperately. Cladocera were identified and counted to species except for the Bosminids; no distinction was made between Eubosmina tubiscen and Bosmina longirostris. Cladoceran eggs were counted as one group. Rotifers were identified and counted to genus or species. Individuals within the colonial forms were counted as discrete units.

Collections of bottom fauna were made between October 10-16, 1972 with a 9 x 9 in (522.6 cm^2) Ekman sampler. The contents of two grabs at each station were sieved through a No. 40 mesh screen to retain the organisms.

Results and Discussion

Phytoplankton and Zooplankton Communities

The algae were represented by several diatoms of the pennate type and one centric, 3 blue-green algae, 3 desmids, 3 other species of green alage, and 1 dinoflagellate. Nineteen species of zooplankton were counted which included 2 calanoid and 2 cyclopoid copepods, 5 cladocerans, and 9 rotifers. Table 8 is a partial list of species.

Diatoms

Diatom populations, represented by the dominant Synedra ulna and other less numerous unidentified species, were generally abundant throughout the sampling period (Figure 25). A noteworthy feature of the seasonal change was that increases and decreases followed the same general trend for all stations. The maximum density was on July 29 when 421.5 organisms/liter were present at Station C. The early high density at Station A (April 30) coincided with the presence of extremely high numbers of Melosira granulata at that station (Figure 25).

Table 8.- Species list of net plankton frequently collected from Lake Izabal

Algae

Diatoms

Melosira granulata (Ehrenberg) Ralfs
Synedra ulna (Nitzsch) Ehrenberg

Blue-green Algae

Anacystis cyanea (Kützing) Drouet & Daily
Anabaena flos-aquae (Lyngby) Brébisson
Lyngbya sp.

Green Algae

Staurastrum pingue Teiling
S. leptocladum Nordst. var. *denticulatum*
S. tohopekaligense Wolle
Cosmarium sp.
Pediastrum simplex var. *duodenarium* (Bailey) Rabenhorst
Eudorina sp.
Coelastrum sp.

Pyrrophyta

Ceratium hirundinella (O.F. Müeller) Schrank

Cladocera

Bosmina longirostris (O.F. Müeller)
Eubosmina tubicen (Brehm)
Moina micrura Kurz
Ceriodaphnia lacustris Birge
Diaphanosoma brachyurum

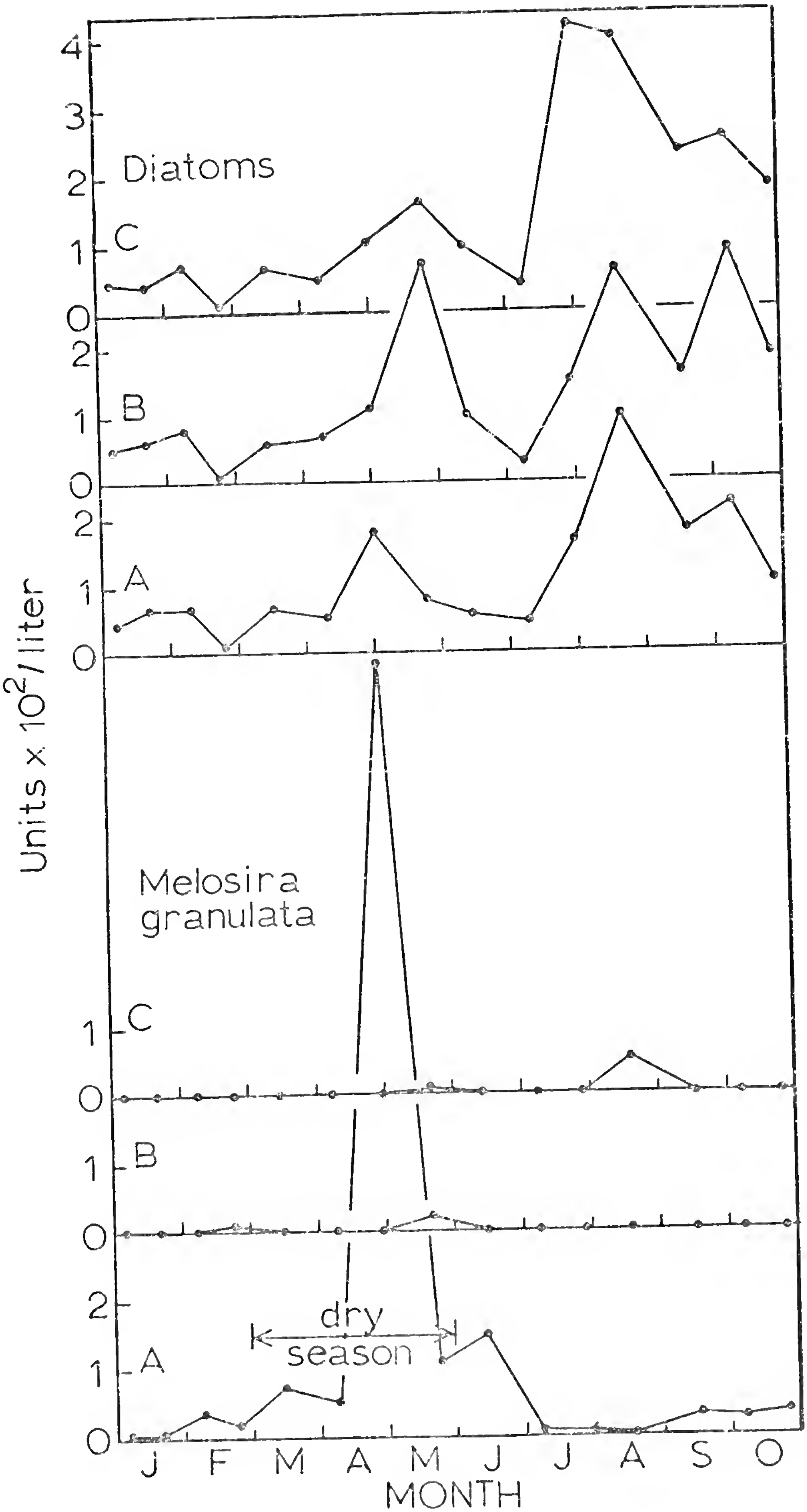
Copepoda

Diaptomus dorsalis Marsh
Pseudodiaptomus culebrensis Marsh
Mesocyclops edax (E.A. Forbes)
Mesocyclops (Thermocyclops) inversus Kiefer

Rotifera

Brachionus falcatus Zacharias
B. havanaensis Rousselet
Keratella cochlearis (Gosse)
Filinia pejleri Hutchinson
Conochilus unicornis Rousselet
Conochiloides dossuarius (Hudson)
Sinantherina sp.
Hexarthra sp.
Platyias sp.

Figure 25.- Seasonal changes in abundance of pennate diatoms and *Melosira granulata*.


Diatoms
C
B
A
Melosira
granulata
C
B
A
dry
season
Units x 10²/liter
0
1
2
3
4
J
F
M
A
M
J
J
A
S
O
MONTH

M. granulata filaments were present in high densities only at Station A but occasionally appeared in smaller numbers at Stations B and C. The origin of the *Melosira* at Station A was from horizontal displacement rather than in situ growth. It is a common dry-season occurrence for a steady breeze to blow every morning from the Polochic Valley, over the delta, and across the lake. On one morning I observed this phenomenon from a hill at Las Dantas overlooking the lake. A large plume of water whose color differed from lake water, moved out from Ensenada Los Lagartos and into the offshore area of the lake.

M. granulata is of widespread occurrence in the summer plankton of eutrophic temperate lakes. It characteristically occurs in lakes with blue-green algae blooms, particularly *Anacystis cyanea*, but their maxima do not necessarily coincide (Hutchinson 1967).

Green algae

Staurastrum spp. were found only in low concentrations at the beginning of the sampling period (Figure 26 and 27). Thereafter a bloom of *Staurastrum pingue* occurred at Station A on April 30 when 2,348 organisms/liter were present. This was followed on the next sampling date by a less abrupt increase at Station B. Part of this abundance at Station B could have been a result of horizontal redistribution from Station A rather than in situ growth. If that were so, then the horizontal currents did not carry plankton to Station C as there was no evidence for an increase there. *S. pingue* generally occurs in hard, productive waters and is often associated with blue-green algae and diatoms (Hutchinson 1967).

Figure 26.- Seasonal changes in abundance of *Staurastrum leptocladum* and *S. pingue*.

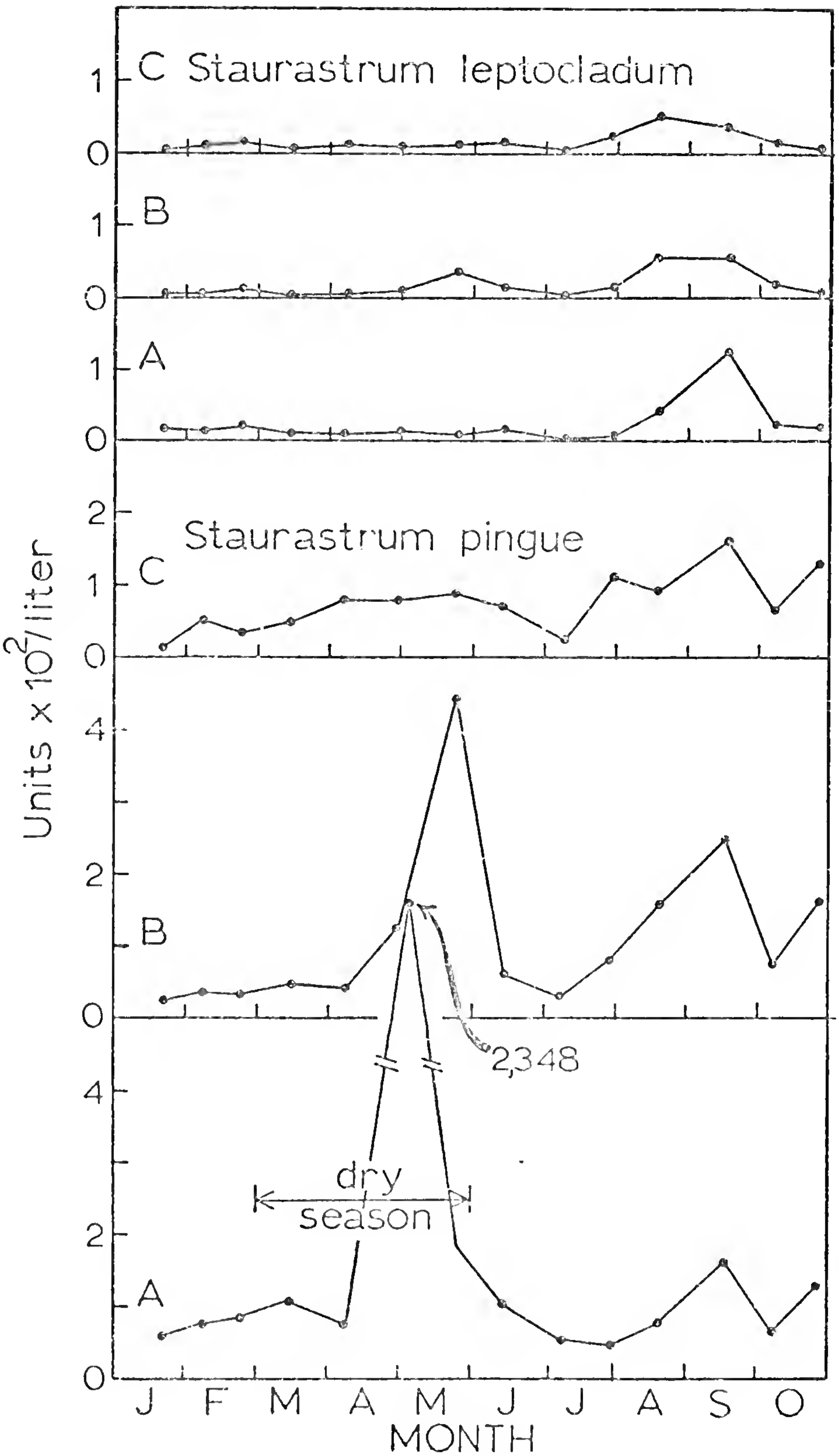
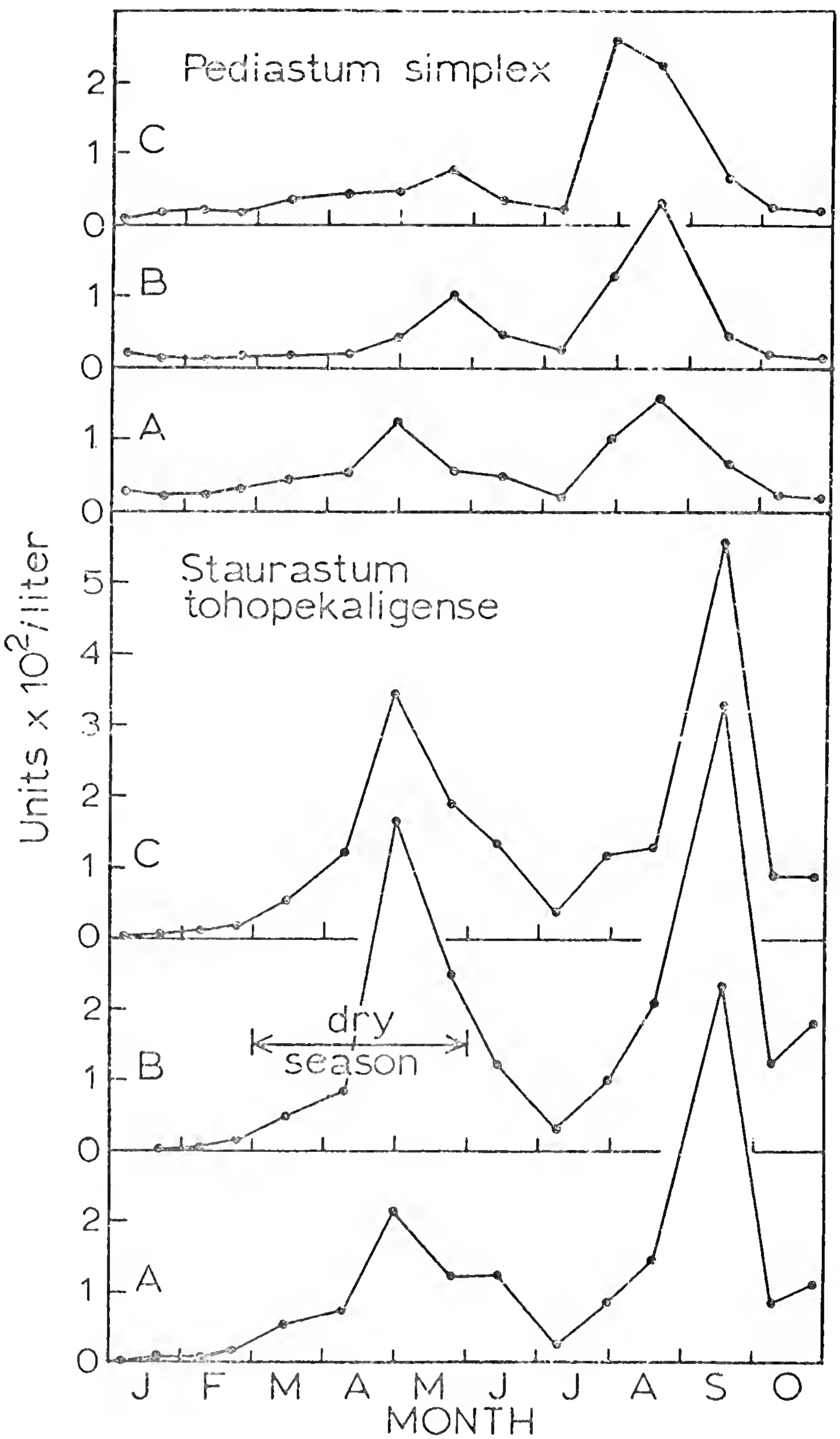

C Staurastrum leptocladum
B
A
Staurastrum pingue
C
B
A
2,348
dry season
Units x 10^2/liter
J F M A M J J A S O
MONTH

Figure 27.- Seasonal changes in abundance of *Pediastrum simplex* and *Staurastrum tohopekaligense*.


Pediastum simplex
C
B
A
Staurastum
tohopekaligense
C
B
A
dry
season
Units x 10²/liter
J F M A M J J A S O
MONTH
0
1
2
3
4
5

S. leptocladum var. *denticulatum* was the least abundant species of desmid and no large increases occurred until September when a maximum of 124.3 organisms/liter was reached at Station A (Figure 26). *S. tohopekaligense* pulsed twice during the study period, simultaneously reaching high densities at all three stations (Figure 27). The April 30 high (466 organisms/liter at Station B) occurred when *S. pingue* bloomed at Station A and the increase before September 19 coincided with the increases of *S. pingue* (particularly Stations A and B).

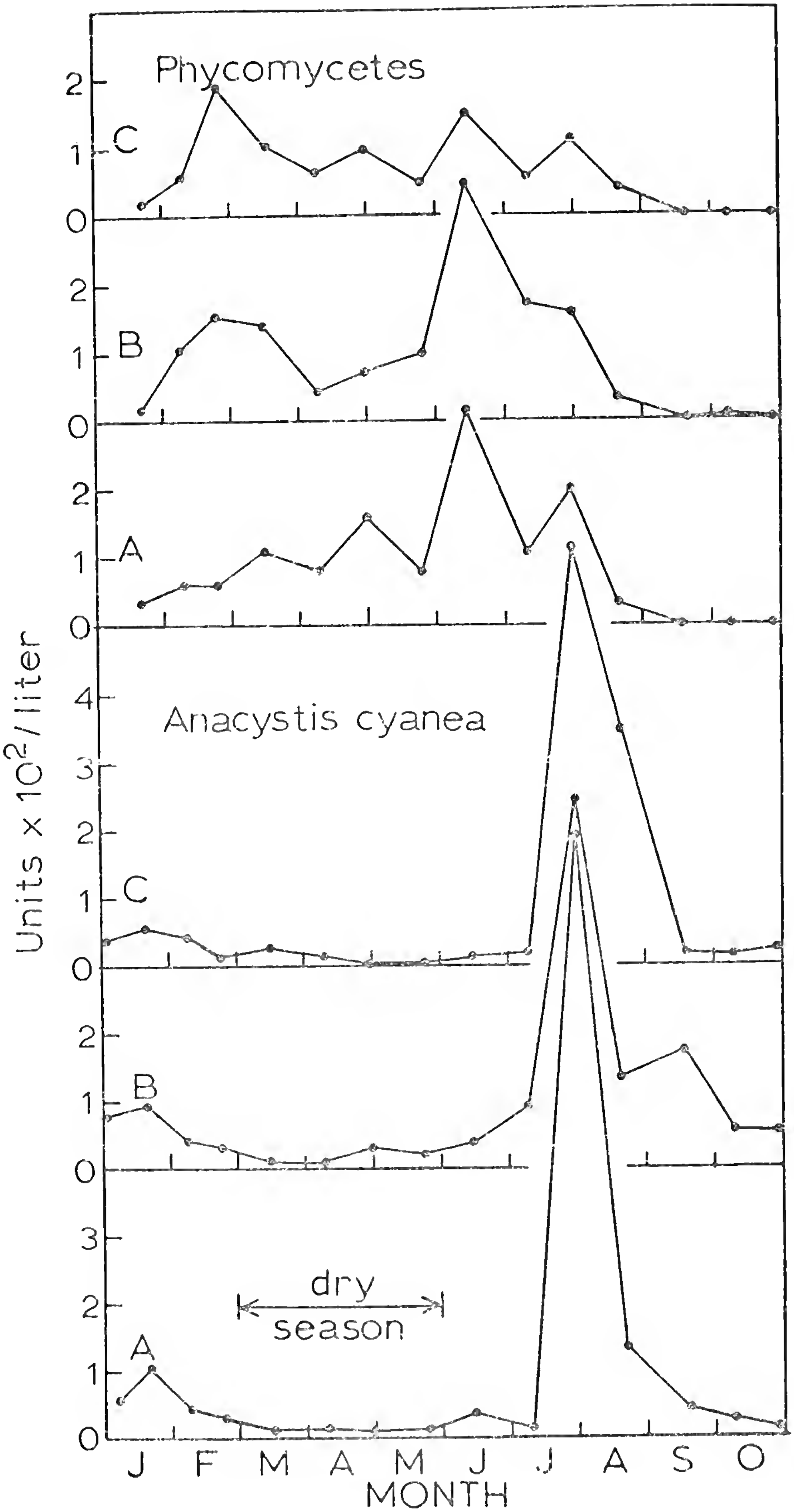
Pediastrum simplex var. *duodenarium* showed an overall increase from the beginning of the sampling period until May (Figure 27). At Station A the density began to decrease prior to the decrease at Stations B and C, a similar pattern to that of *S. pingue*. The subsequent decline was followed by a higher peak in late July and August, reaching a maximum of 262 organisms/liter on July 29 at Station C.

The most striking feature of the seasonal changes in the green algae was the prevalence of two periods of increase for the majority of species and stations, the first during April-May and the second during August-September.

Blue-green algae

Anacystis cyanea was the only species of blue-green algae present at all times of the year and in quantities worthy of reporting. Modest densities were present in January, but subsequent lower densities persisted until July (Figure 28). The extremely high densities encountered on July 29 at all three stations (543-899 organisms/liter) was such an abrupt increase that its occurrence could not have been predicted on the basis of increases prior to that date (except perhaps Station B). At the

Figure 28.- Seasonal changes in abundance of phycomycetes and *Anacystis cyanea*.


Phycomycetes
C
B
A
Anacystis cyanea
C
B
A
dry
season
Units x 10^2/liter
J F M A M J J A S O
MONTH
0
1
2
3
4

time of this pulse, green algae and diatoms were present in low densities relative to other sampling periods.

Other algae

Ceratium hirundinella was present in low numbers (up to 19 organisms/liter) during some periods and completely absent from the plankton at other times. Some forms of *C. hirundinella* are eurytopic, but the species is most characteristic of eutrophic warm waters with a slightly alkaline pH. It is present in the epilimnion of many temperate lakes in the summer, but also was found in the small lakes of Java (Ruttner 1952, in Hutchinson 1967). *Eudorina* sp. was never more abundant than 1 colony/liter and was often absent, while *Coelastrum* sp. was nearly always present and reached a maximum density of 17 colonies/liter.

Phycomycetes

One of the most interesting observations was the occurrence of an organism believed to be an aquatic phycomycete. The free-living cottony masses did not appear to be attached to particles or other organisms. It was abundant in nearly all of the plankton samples until its disappearance at the end of the sampling period in September and October (Figure 28). The pulses of abundance did not coincide with pulses of the dominant phytoplankton. The first pulse, evident at Stations B and C, occurred in February and March and preceded the dry-season blooms of phytoplankton. Likewise, the maximum abundance for the year was observed at Stations A and B which preceded wet-season phytoplankton blooms. Failure to find cases where this or similar phycomycetes have been reported previously as a component of lake plankton makes this observation an unusual curiosity.

Copepods

Cyclopoid copepods were represented by Thermocyclops inversus and Mesocyclops edax, the latter being more abundant. Adults and copepodids were grouped together and were more abundant during the first half of the sampling period than the second (Figure 29). No abrupt changes were noted, and the lake appeared to be relatively homogeneous at all sampling stations for any particular sampling date.

Of the calanoid copepods, Diaptomus dorsalis was far more abundant than Pseudodiaptomus culebrensis. Calanoids were generally less abundant than cyclopoids during the beginning of the sampling period, while the opposite was true for July-September (Figure 29). There seemed to be more similarities in changes between Stations A and B than for Station C and the other stations. However, the nauplii (of both calanoids and cyclopoids) had a very homogeneous distribution throughout the lake for any particular collection. Relative to collections preceding and after July 9, densities on that date were markedly low. There was some evidence of decreased egg numbers between May and June before the decrease in nauplii in July, but no comparable explanation exists for the sharp increase in nauplii at the end of July.

Cladocera

Diaphanosoma brachyurum increased throughout the dry-season months (March-May) at all stations (Figure 30). The decrease that followed was most abrupt at Station A, less at Station B, and least at Station C. Moina micrura and Bosmina longirostris showed no evidence of seasonal synchrony in abundance at the sampling stations. Little can be said about

Figure 29.- Seasonal changes in abundance of copepods.

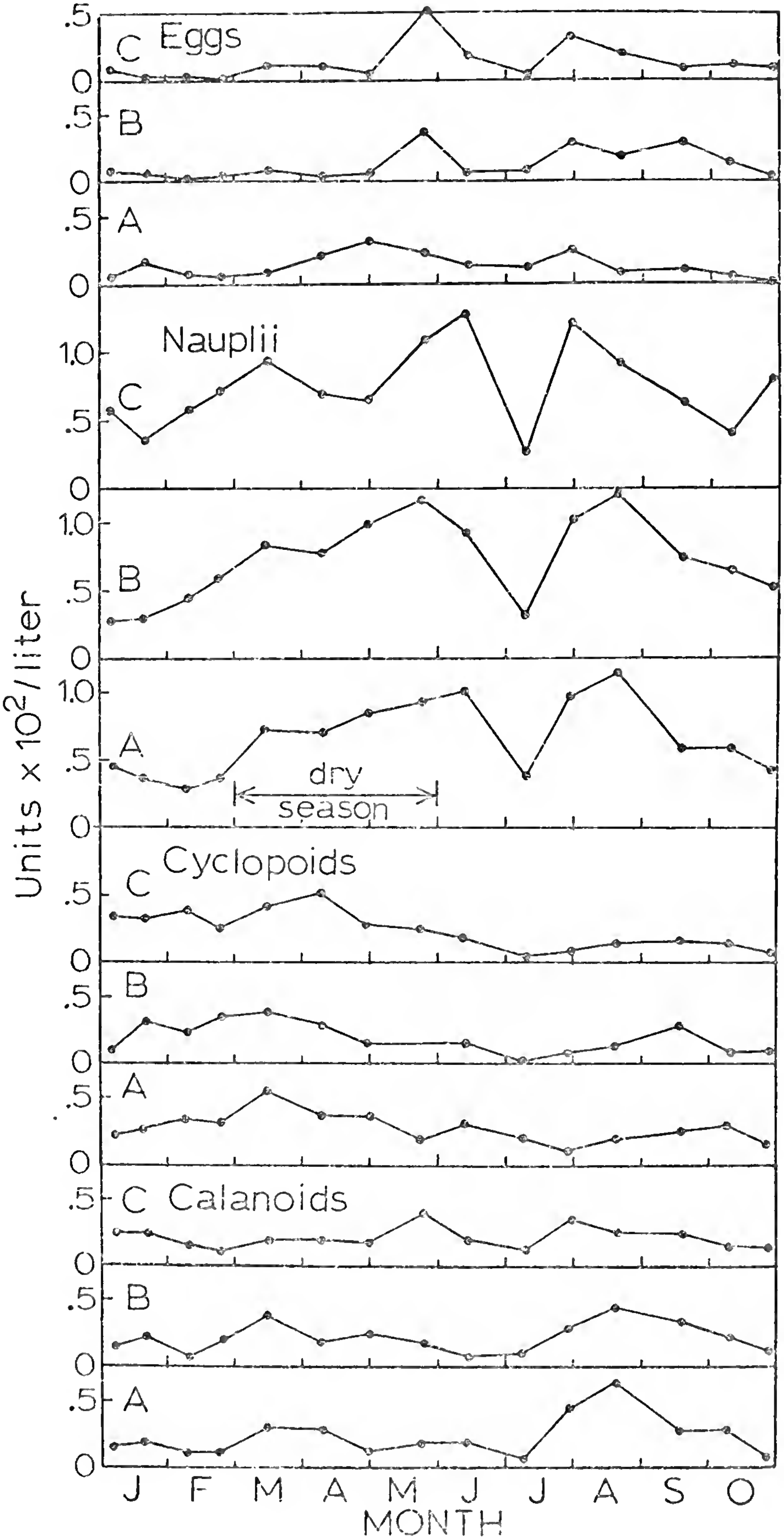
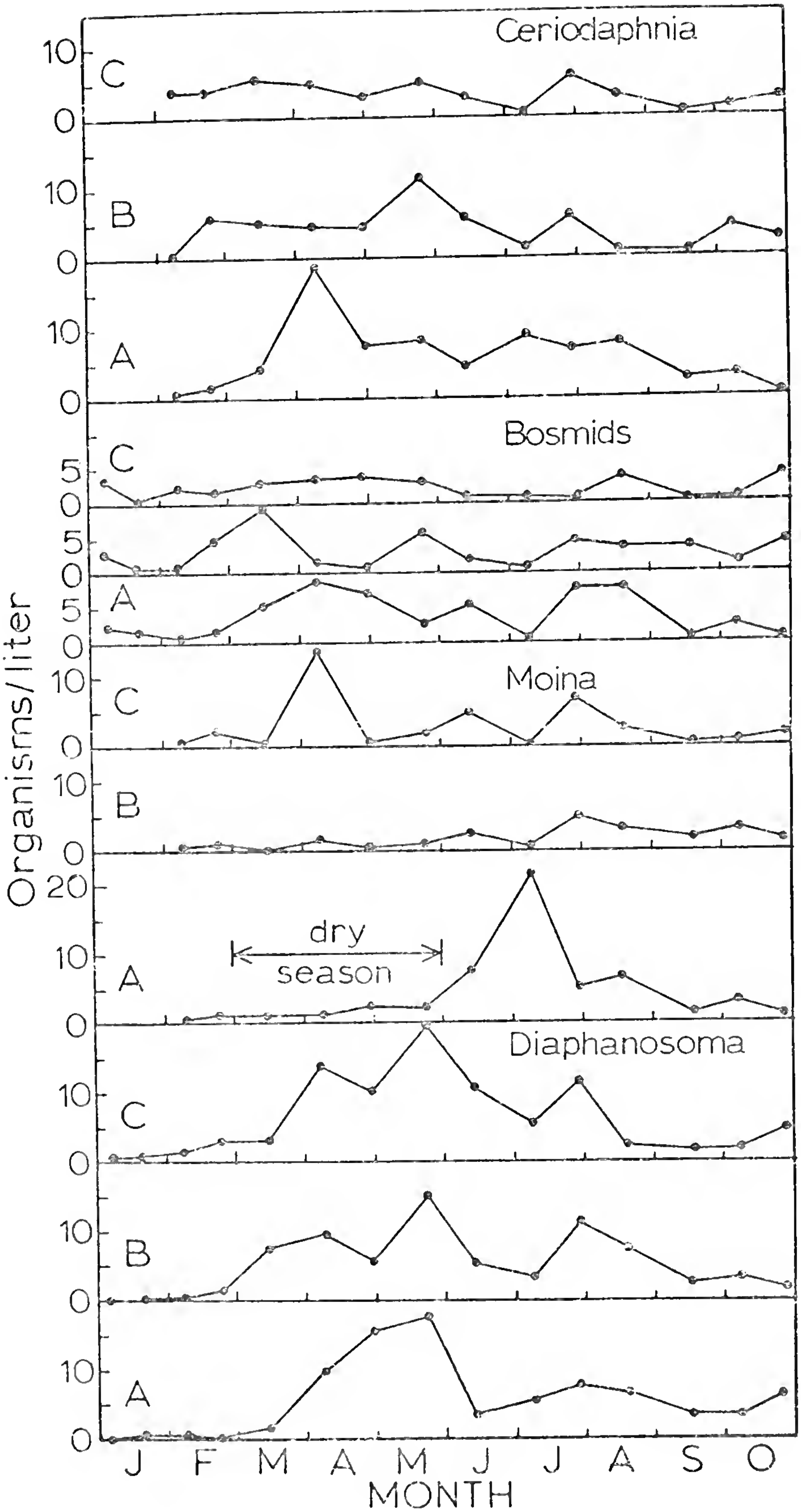

Eggs
C
B
A
Nauplii
C
B
A
dry
season
Cyclopoids
C
B
A
Calanoids
C
B
A
.5
0
1.0
Units x 10²/liter
J F M A M J J A S O
MONTH

Figure 30.- Seasonal changes in abundance of cladocera.


Ceriodaphnia
Bosmids
Moina
Diaphanosoma
dry season
C
B
A
Organisms/liter
J F M A M J J A S O
MONTH

Ceriodaphnia lacustris except that it was present in moderate numbers throughout most of the sampling period.

Rotifers

No distinct seasonal trends in abundance could be detected for rotifers. Where rapid increases did occur, they were more common in colonial rotifers at Station A (Figure 31). For example *Conochilus unicornis* increased to a maximum of 79 organisms/liter at Station A during August, *Conochiloides dossuarius* increased rapidly to 24 organisms/liter at the same station in April, while the greatest increase in *Sinantherina* was between September and October at Station A (to 59 organisms/liter). The non-colonial rotifers showed no distinct seasonal trends (Figure 32). This was likely due to the long interval between collection dates relative to the generation times of most rotifer populations.

Possible Controlling Factors

The most apparent feature of seasonal changes in phytoplankton populations was the late dry-season pulse in April and May and a later wet-season pulse in August and September. Only the dry-season pulse in *Melosira granulata* at Station A can be attributed to horizontal movement rather than in situ growth. The synchrony between stations and between species of algae for the two pulses indicate that the factors controlling growth were present at the same time throughout the lake and had similar effects on most of the species. Environmental factors commonly accepted as regulators of phytoplankton growth are solar radiation, temperature, and nutrients. Of these, only solar radiation and temperature were

Figure 31.- Seasonal changes in abundance of colonial rotifers.

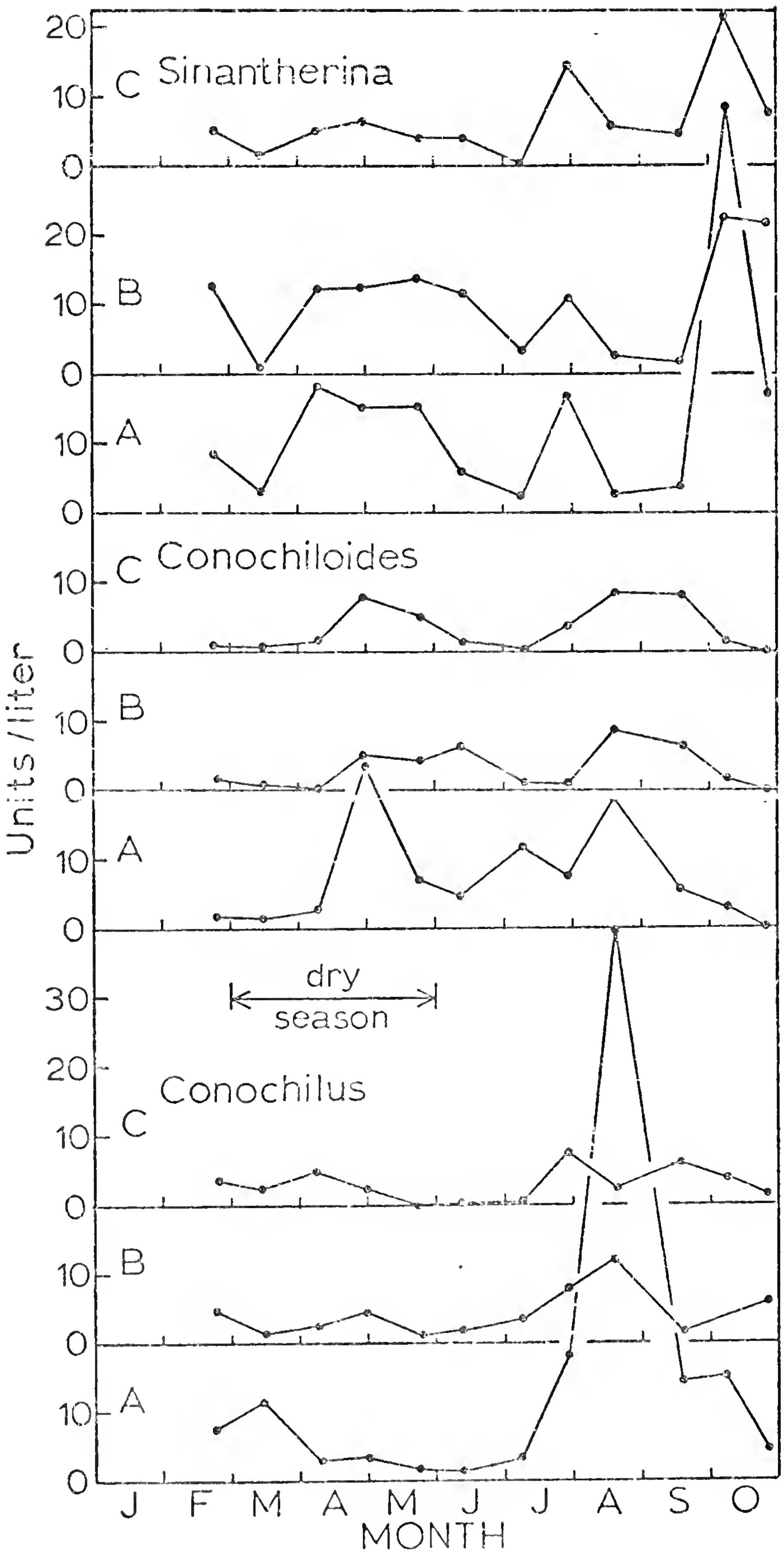
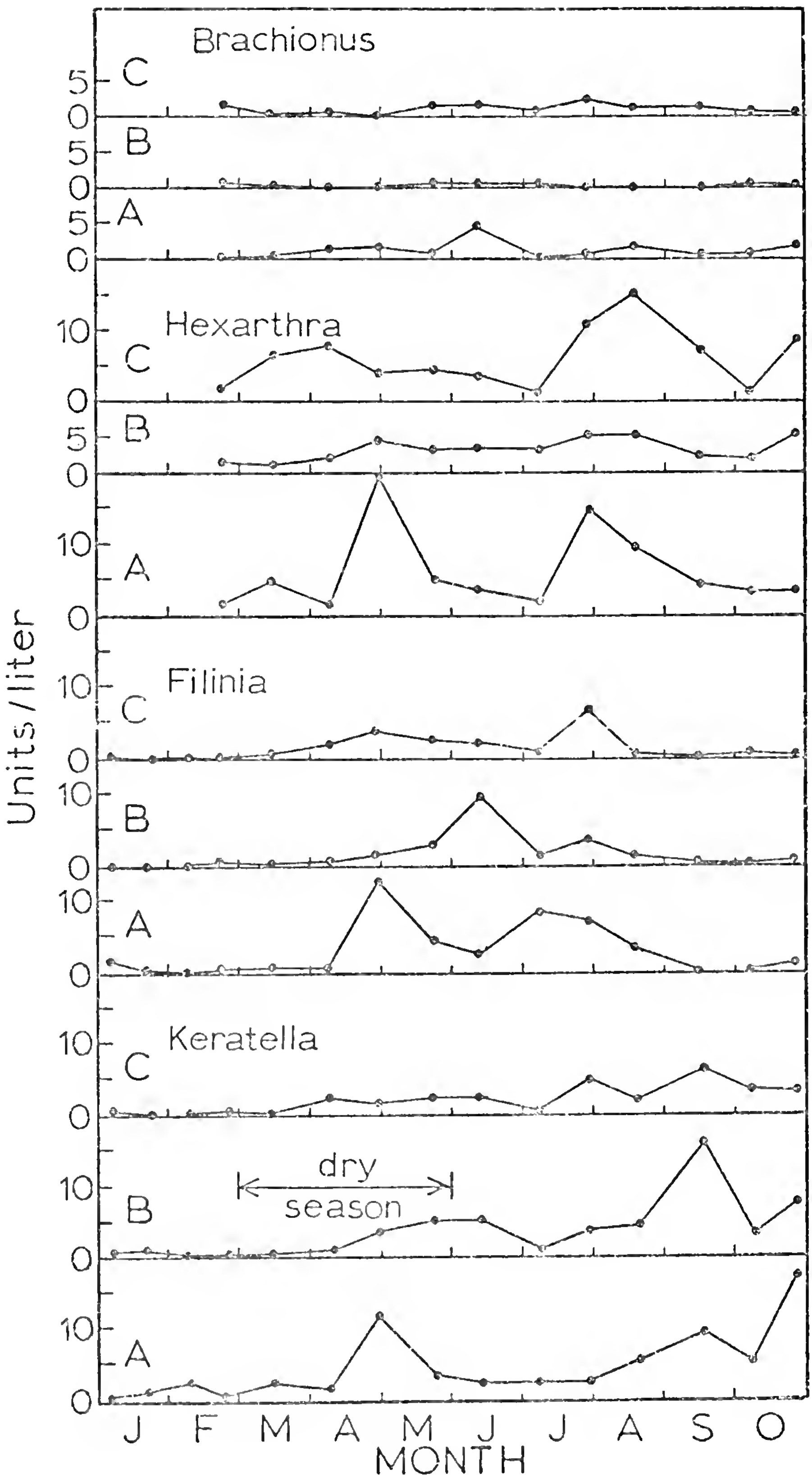

Sinantherina
Conochiloides
Conochilus
C
B
A
dry
season
Units / liter
0
10
20
30
J
F
M
A
M
J
J
A
S
O
MONTH

Figure 32.- Seasonal changes in abundance of solitary rotifers.


Brachionus
C
5
0
B
5
0
A
5
0
Hexarthra
10
C
0
B
5
0
10
A
0
Filinia
10
C
0
10
B
0
10
A
0
Keratella
10
C
0
dry
season
10
B
0
10
A
0
Units / liter
J F M A M J J A S O
MONTH

monitored at sufficient intervals to enable detecting seasonal trends; samples for nutrient analysis were collected only twice (April 14 and October 23). Grazing by zooplankton may be an additional consideration, but it is unlikely that the zooplankton would have effectively grazed some of the larger phytoplankton such as Pediastrum and Anacystis. Diatoms, however, may have been subject to some control by grazing. Anderson (1958) noted a phytoplankton minimum when nutrient deficiency was unlikely in Lake Lenore, Washington, but Moina hutchinsoni were moderately abundant. Thus, it is interesting to note that M. micrura experienced an annual maximum at Station A when diatoms had decreased (Figure 30).

For the lake stations, and particularly Stations A and B, the surface and bottom temperatures were highest during the dry season and decreased in July at the beginning of the wet season (Figure 13). This was a result of an increase in discharge to the lake of river water of lower temperature, noticeable in the deep samples from Stations A and B. The lower insolation in July also could have contributed to the decrease in water temperature. It is possible that the decrease in solar radiation could have been partially responsible for the lower numbers of phytoplankton between the April-May and August-September pulses. Secchi disk transparencies in July for the three stations were among the lowest observed during the year (Figure 44). In the absence of large densities of plankton, the decreased transparency might be attributed to higher turbidity induced by wet-season inputs of silt and detritus-laden waters from the watershed. Floating debris, ranging from leaves to large logs, were especially abundant in the area of Station A, and as a result, navigation was often hazardous.

In the search for an explanation of the decrease during July for many of the planktonic species, the possibility of inhibitory substances cannot be overruled. This was the month of initial flushing of the colored waters of the lagoons (Amatillo, Lagartos) and rivers (El Padre Creek, Rio Oscuro) of the Polochic Delta. The water exported from this area to the lake differed sharply from lake water in its organic matter concentration (Figure 34), dissolved oxygen, pH, total alkalinity, and conductivity (Figure 14). Although a complete list of potentially inhibitory substances from these anaerobic or near-anaerobic waters is not in order here, a few would include hydrogen sulfide, tannins, and heavy metals (Cu, Zn, Al) either in ionic form or present as complexes with organic matter.

In spite of the possibility of inhibitory substances, some of the largest pulses in phytoplankton occurred soon after the July 9 low. It is interesting that some substances, inhibitory to certain species, are apparently stimulatory to others. For example, Lefévre et al. (1952, in Hutchinson 1967) collected pond water at different times of the year to test its effect on plankton cultures. Water collected in October, when there was a great deal of decomposition of higher plants, was stimulatory to two species of *Pediastrum* (*P. boryanum* and *P. clathraturm* var. *punctulatum*) but was inhibitory to two species of *Cosmarium*. Similarly, substances which may be inhibitory at high concentrations may be stimulatory at low concentrations. If the low numbers of phytoplankton sampled at a time coinciding with the initial flushing of the watershed were evidence of inhibition, then subsequent dilution of the lake by wet-season rains could have rendered such substances innocuous or even stimulatory.

Data on critical nutrients are both scanty and unreliable, but it is unlikely that these would have been limiting. For example, silica ranged from 10-14 mg/liter for both sampling periods (Appendix, Table E) well above 0-1 mg/liter, a range for which there is evidence suggesting a limitation of diatom growth in nature (Lund 1950). Because no samples were analyzed for nutrients during the July 9 low in phytoplankton density, no conclusions can be drawn from control by nutrients.

The dramatic increase of Anacystis cyanea on July 29 is noteworthy because it marked the increase of the other phytoplankton populations. Blue-green algae are typically found in waters with high dissolved organic matter and some of the highest concentrations of organic matter in the lake were detected in July (Figure 34). However, no specific organic substance has been found to facilitate their growth (Hutchinson 1967). Nevertheless, the sudden appearance of high densities of A. cyanea on July 29 marked the beginning of conditions apparently favorable to the growth of other phytoplankton. A. cyanea persisted until the end of the sampling period. A. cyanea is one of the greatest problem algae in eutrophic lakes of northern latitudes, particularly when it forms massive summer water blooms. In India, it develops permanent blooms in artificial temple tanks. Maximum numbers occur in July and decrease to a minimum a month later in August. No changes in temperature or phosphate concentration is observed during the bloom reduction (Hutchinson 1967).

Grazing by zooplankton can be discounted as a factor contributing to the July 9 low in phytoplankton not only because it is likely that most of the algae were too large to serve as a direct food source, but also because many species of the zooplankton were present in low numbers on that date. Nauplii underwent a sharp decrease as well. An exception was the pulse in Moina micrura at Station A which reached a maximum of 21 organisms/liter.

In spite of the homogeneous distribution and the distinct bimodal pulse demonstrated by the net plankton during 1972, it would be tenuous, at best, to expect this to be a regular annual occurrence. However, Nordlie (1970) also has evidence of seasonality in the plankton abundance of Lake Izabal. In August 1969 the phytoplankton diversity was approximately the same along the east-west axis of the lake. Presumably it was also relatively abundant. Heaviest zooplankton populations were at the west end and their abundance decreased in the eastern region. This may have been a situation similar to my August 1972 observations.

During March 1970, Nordlie's samples showed the greatest phytoplankton diversity at the east end of the lake, while almost none were present from the middle and west end. Zooplankters were similarly distributed as in 1969 but more dense. Although I found phytoplankton to be much less abundant in March 1972 than August 1972, it was much more abundant than implied by Nordlie for his March 1970 samples. It is possible that Nordlie's sampling in March preceded a dry-season pulse in abundance, such as that observed in April and May 1972.

Benthic Community

The most interesting curiosity of the bottom fauna was the occurrence of Tanaidacea, first reported from the lake by Nordlie (1970). Several species of this family are known from fresh waters, but it is likely that all are dependent on slightly more saline water than is usual far from the coast (Hutchinson 1967). The highest density recorded was 296 organisms/m^2 at San Felipe Bay (Table 9) where the penetration of brackish water from the coast is at least a seasonal event. It is doubtful, however, that the specimens collected from the outfalls of the Rio Polochic distributaries (Comercio and Cobán) ever come in contact with water of conductivity greater than ca. 200 μmho/cm. More sampling, both on a spatial and seasonal basis, would be necessary to adequately establish distributional and temporal patterns. Nordlie (1970) calculated abundances of Tanaidacea as high as 1,378/m^2 in previous collections from the lake.

Members of the family Chaoborinae, presumably Chaoborus, were present in the bottom deposits both in larval and pupal stages. Densities were as high as 77 organisms/m^2 and they were present at all localities sampled except Station 15 (Figure 39) where none were found. They also were collected occasionally in net plankton tows. The Tendipedinae were found at all stations and ranged between 10-77 organisms/m^2. Adults were seen frequently and in massive numbers above the lake. Oligochaeta were present at five of the twelve stations with densities ranging from 19-153 organisms/m^2. The gastropods, most of which were not alive when collected, were present at six of the twelve stations.

The average density of 29 organisms/m^2 for the Chaoborinae was below that found by Deevey (1957) in Lake Amatitlán (40/m^2), and much lower than his mean for Lake Güija (1,278/m^2). Deevey found no Tendipidae at Lake Güija but reported a mean of 673 organisms/m^2 for Lake Amatitlán, an order of magnitude greater than my samples at Lake Izabal (Table 9).

The density of bottom fauna was strikingly low compared to lakes in temperate latitudes (Deevey 1941), but it must be remembered that

Table 9.- Bottom fauna of Lake Izabal expressed in numbers/m^2. Samples were collected October 10-16 1972. Numbers refer to sampling stations illustrated in Figure 39

No.	Station	Depth (m)	Tanaidacea	Chaoborinae Larvae	Chaoborinae Pupae	Tendipedinae	Oligochaeta	Gastropoda	Total Excluding Gastropoda
12	Oscuro Bay	4.0	0	38	0	57	153	0	248
7	Ensenada El Padre	3.1	0	10	10	77	0	67	97
6	Cobán Outfall	10.5	19	10	0	38	115	57	182
9	Comercio Outfall	11.2	239	19	0	48	0	48	306
10	Comercio Outfall	14.0	19	10	10	57	0	0	96
14	Station A	12.5	0	10	0	67	153	20	230
15	Station AA-B	14.2	0	0	0	48	0	0	48
16	Station A-B	14.5	0	19	10	57	0	0	86
17	Station B	15.7	57	77	0	57	19	10	210
18	Station B-C	15.0	0	10	10	29	29	19	78
19	Station C[a]	13.0	0	29	38	77	0	0	144
20	San Felipe Bay	9.5	296	29	10	10	0	0	345
	Average		52.5	21.8	7.3	51.8	39.1	18.4	172.5

[a] Sample partially decomposed due to drying; absence of Oligochaeta uncertain.

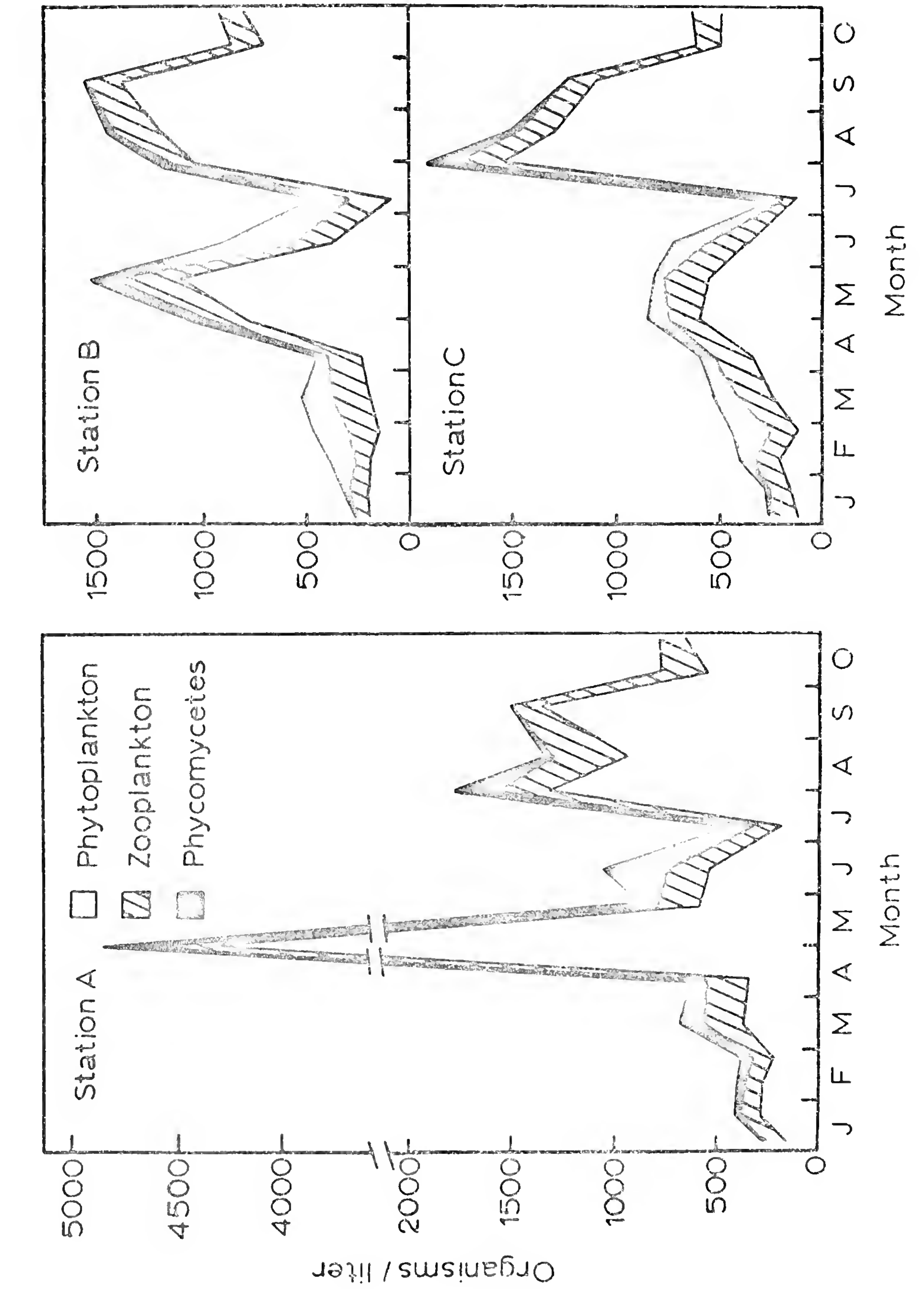
these numbers represent standing crop and not rates of biomass increment. Although the higher year-round temperatures of tropical lakes may result in growth rates of benthic organisms as much as two or three times those of temperate lakes, it is doubtful if this factor would make their production comparable. A plausible explanation for the difference is that the more intense metabolism of the free water would tend to be more complete in tropical lakes, so that less surplus energy reaches the sediments and their fauna (Deevey 1957). This may be true for monomictic lakes (studied by Deevey) which remain stratified throughout most of the year, but for lakes such as Lake Izabal that mix frequently to the bottom, it is unlikely that the benthic organisms would be restricted by energy availability. A more reasonable explanation may be predation by bottom-feeding fishes. Such fishes would have access to benthic organisms in all areas of the lake since they are not restricted by an anaerobic zone in Lake Izabal as they are seasonally, at least, in monomictic lakes. Bottom-feeding fishes are well represented in the lake and include marine catfish and several species of cichlids. The presence of substantial amounts of organic matter in the surface muds will be discussed as a potential source of food for detritus consumers in the section, "Metabolism and Organic Matter."

Summary Statement

The net phytoplankton assemblage of Lake Izabal was characteristic of that found in many other shallow productive lakes with moderately hard waters. Most of these species have a wide latitudinal distribution. The predominant taxonomic groups included diatoms, myxophycetes, desmids, and members of the chlorococcales. The zooplankton composition had a slightly more tropical flavor, especially with regard to the copepods. For example, species of Mesocyclops were present, a genus of predominantly tropical distribution, and Diaptomus dorsalis, also present, is common in countries bordering the Caribbean. Cladocera were less abundant than copepods, and while the rotifers were more diverse than other zooplankton groups, their abundance was much lower. The only surprising feature of the benthic community was the relatively abundant occurrence of a member of the Tanaidacea which is a group characteristic of marine and brackish waters.

The most apparent feature of seasonal change was the late dry-season pulse of phytoplankton in April and May followed by a wet-season pulse in August and September (Figure 33). These pulses did not seem to coincide with rates of gross primary productivity except in late September and October when both phytoplankton abundance and primary productivity rates decreased (see following section, Metabolism and Organic Matter). Apparently differences in the standing crop of net phytoplankton over periods of 3 or 4 weeks were an insensitive indicator of daily rates. This could be attributed to the high variation in rates of turnover possible in a system with low storage capacity. In most cases the pulses could be attributed to in situ growth rather than to distribution by horizontal currents. The interluding low abundance between the two pulses coincided with the inception of the wet season when runoff increased dramatically, discharging large quantities of silt and organic debris into the lake. The resulting decrease in transparency of the lake water may have been partly responsible for the low phytoplankton abundance during

Figure 33.- Total net-plankton abundance (units or organisms per liter) represented by phytoplankton, zooplankton, and phycomycetes.


Station A
Phytoplankton
Zooplankton
Phycomycetes
Organisms / liter
5000
4500
4000
2000
1500
1000
500
0
J F M A M J J A S O
Month
Station B
1500
1000
500
0
Station C
1500
1000
500
0
J F M A M J J A S O
Month

this period. Other controlling factors that cannot be overruled are the influx of inhibitory or toxic substances, moderate decreases in temperature, or changes in nutrient availability. The low abundance in June and July was interrupted by a bloom of *Anacystis cyanea* in late July which shortly preceded an increase in most other species of phytoplankton. Zooplankton populations on the whole were comparatively more stable than phytoplankton populations.

METABOLISM AND ORGANIC MATTER

This chapter, which represents the core of the present study, attempts to estimate the magnitude of the principal energy flows responsible for the metabolism of the lake ecosystem. One of these energy flows, that from allochthonous detritus input, received special attention. In lakes that approximate the surface area of Lake Izabal, allochthonous energy sources are generally regarded as insignificant contributions to total metabolism. This is undoubtedly true for lakes whose replacement time for the water mass is in the tens or hundreds of years. However, by virtue of the relatively small volume of Lake Izabal in relationship to its surface area, as well as it location within a watershed receiving high rainfall, the annual replacement of a large portion of the water mass by runoff could conceivably produce an energy surplus or deficit. This would ultimately depend on the organic matter concentrations of the inflowing and outflowing waters.

Other important metabolic compartments in aquatic ecosystems are the plankton and the bottom muds. In the gradient from deep to shallow lakes, the proportion of total metabolism attributed to the bottom muds becomes greater. Thus some attention was given to the energy flow of the benthos, although the metabolism of the planktonic compartment was expected to be of greater magnitude.

Methods

Chemical Oxygen Demand

The concentration of organic compounds in the lake and river waters was determined by oxidative digestion with potassium dichromate and sulfuric acid, commonly known as "wet oxidation." Several procedures were reviewed and a number of modifications were made before routine analysis was established. Silver sulfate (Ag_2SO_4) used as a catalyst for the oxidation is particularly effective for straight-chain alcohols and acids (Golterman 1969) but certain phenolic compounds are generally resistant to oxidation, even in the presence of a catalyst. In spite of this and other disadvantages, the method was generally useful in the absence of more sophisticated instrumentation.

Fraction definitions and conversion criteria

The limnological application of organic analysis by quantitative dichromate oxidation has been reviewed and tested by Maciolek (1962). To maximize the information that could be extracted from a single test, the samples were separated to distinguish three size fractions. Total COD represents all the organic matter sizes in the sample, dissolved and particulate. Dissolved COD is the fraction remaining after vacuum filtration through a 0.80-μ pore membrane filter and theoretically should contain particles no greater in diameter than the filter's pore size as well as soluble organic matter. Particulate COD refers to organic matter greater than 0.80 μ in diameter, calculated by subtracting the total COD from the dissolved COD concentration. Net Particulate COD is the fraction collected with a No. 20 plankton net whose mesh aperture is 76 μ (Welch 1948).

Theoretically this should represent particles whose diameter is greater than the aperture size (approximately 100 times the size of the particulate COD) and corresponds to the organic matter of the net plankton.

Maciolek (1962) reported COD as Oxygen Consumed (O.C.). He pointed out that a theoretical Oxygen Equivalent (O.E.) must be assumed in order to convert COD (or O.C.) to organic matter. The O.E. is constant for an individual pure compound (e.g., the O.E. of hexose is 1.06). The mg Oxygen Consumed divided by the assumed O.E. for representative organic compounds yields the weight of the organic compound,

$$\frac{\text{mg O.C. (or COD)}}{\text{mg O.E.}} = \text{mg Organic Matter.}$$

Several approaches can be used to determine the O.E., including calculation from elemental composition and from proximate composition determined from proteins, lipids, and carbohydrates. Table 10 lists characteristic O.E.'s that were reported by Maciolek (1962) in approximate order of their limnological importance. In the section-- Balance of the Organic Matter Budget -- where the energy budget of the lake is calculated, a value of 1.44 O.E. was selected to convert COD values to organic matter.

The relationship between combustion calorimetry and oxygen consumed is close enough to permit an accurate caloric estimate by quantitative oxidation (Maciolek 1962). A value of 3.4 gcal per mg of O.C. is suggested, which would be equivalent to approximately 4.86 gcal per mg organic matter.

Collection and treatment of samples

Water samples were collected in the field in clean 500-ml narrow-neck amber glass bottles. When deep samples were collected a 2- or 3-liter Van Dorn bottle was used. Surface waters were generally taken by

Table 10.- Characteristic oxygen equivalents (O.E.) in approximate order of their limnological importance[a]

Sample Type	O.E. Range	Representative O.E.
Dissolved matter	1.42-1.47	1.44
Seston	1.39-1.53	1.40
Organic sediment	-----	1.46
Phytoplankton	1.40-1.47	1.44
Aquatic invertebrates	1.48-1.69	1.54
Net plankton	1.40-1.55	1.52

[a] From Maciolek (1962).

immersing the collection bottle beneath the surface (10-25 cm). The samples were stored on ice during transport to the laboratory. Generally there was a maximum lapse of 7-8 hours between the first field collection and the laboratory treatment of the samples.

The procedure for chemical oxygen demand (American Public Health Association 1965) was modified slightly. Mercuric sulfate ($Hg\ SO_4$) was not added to eliminate interference by chloride because of the low concentration of this ion (<12 ppm). One hundred-ml samples were oven-dried at 95 C in 200 or 250-ml Erlenmeyer flasks requiring approximately 18 hours for complete evaporation of the water. Ten ml of 0.05N $K_2Cr_2O_7$ were added to the flask followed by 25 ml of concentrated H_2SO_4 in which 5 g/liter of Ag_2SO_4 was dissolved as a catalyst. The samples were digested for three hours in boiling rain water in unsealed pressure cookers to facilitate even heat distribution of the samples. The mouths of the flasks were covered with aluminum foil and the necks of the flasks provided a refluxing surface which may have minimized the loss of volatile organics. After digestion, 100 ml of distilled water were added and the flasks were cooled to room temperature in a water bath. Titrations of blanks and samples were made with a 0.025N (approx.) $Fe(NH_4)_2(SO_4)_2 \cdot 6H_2O$ solution and three drops of ferroin solution (G. Frederick Smith Co.) were used as an indicator.

To determine the dissolved fraction of the total organic matter, 100 ml of sample were vacuum filtered through a 0.80-μ pore Metricel GA-4 membrane filter (Gelman Instrument Co.) The filters were first rinsed with distilled water to rid them of possible organic contamination and were then purged before filtration of the sample with approximately 200 ml of of the sample to clear the distilled water. The dissolved organic matter samples were treated as described above and the particulate organic matter was determined by subtraction.

A No. 20 plankton net (25-cm diameter) was used for filtering water and concentrating samples for the determination of large particulate organic matter. River samples were collected by holding the net below the surface in the current (of known velocity) for a known time period (usually less than one minute). When velocities were too great for holding the net in position, a bucket was used to remove samples just below the surface and 200 liters were poured through the plankton net. Samples were stored on ice until they were transported to the laboratory. They were always analyzed the same day as collected.

The procedure for digestion and analysis was modified from the method of Golterman (1969). Samples were concentrated to 50 ml or, if the total sample was too high in organic matter for this procedure, an aliquot (1/2 or 1/4 of the total sample) was used instead. Since the samples were high in organic matter concentration, they were not dried and reagents that were added for digestion were the same as described above except that 1.000$\underline{N}$ $K_2Cr_2O_7$ was the oxidant. The aluminum foil-capped flasks were digested for three hours. After dilution with 80 ml of distilled water, the samples were cooled and titrated with 0.25$\underline{N}$ (approx.) $Fe(NH_4)_2(SO_4)_2 \cdot 6\ H_2O$ in the presence of 3 drops of ferroin indicator solution.

<u>Dissolved Oxygen Concentration Determinations</u>

The precision of methods for the determination of dissolved oxygen in natural waters makes possible the measurement of the metabolic activities of consumers and producers over relatively short periods of time. The method used for dissolved oxygen in this study is a modification of the Winkler method (Golterman 1969). The modification employs a much higher concentration of KI than normally used, thus reducing errors due to volatilization of I_2 and interference by organic matter. Hydroxides dissolve more readily and the starch endpoint is sharper. Nitrite (NO_2) interference was eliminated by use of sodium azide. Approximately 0.010<u>N</u> sodium thiosulfate was used to titrate duplicate 100-ml aliquots from each bottle resulting in a precision of about 0.03 mg O_2/liter.

Ground glass-stoppered BOD bottles of 300-ml capacity were used for nearly all water collections for oxygen determination. The $MnSO_4$ reagent and alkaline iodine-azide solution were added immediately after sampling and acidification was delayed until immediately before titration in the laboratory.

<u>Biological oxygen demand</u>

Large plastic containers (9.5 or 18.9 liters) were used to collect water samples in the field for transport to the laboratory. For the river and lake surface samples, the mouth of the jug was held approximately 20 cm below the surface and allowed to fill. Deeper samples were collected with a 3-liter Van Dorn sampler and the water was drained into the plastic jugs. A subsample was usually collected and fixed at the field site for measuring the in situ dissolved oxygen concentration.

In the afternoon or evening of the day of collection, the oxygen concentrations of the water in the plastic jugs were measured with a YSI oxygen meter (Model 51A). If the concentration was below 5 mg O_2/liter, the samples were aerated until they contained 6-8 mg/liter oxygen.

After thorough mixing of the water to ensure homogeneity of organic matter and oxygen, samples were carefully siphoned into eight darkened BOD bottles. The first and the eighth bottles filled were immediately analyzed for oxygen. The other six BOD bottles were submerged in a darkened water bath to prevent air leaks and to minimize ambient fluctuations in temperature. The bottles were agitated daily to resuspend particulate matter that may have settled to the bottom.

Duplicate bottles were analyzed for dissolved oxygen after one, three and seven days of incubation. Due to the limitation in number of BOD bottles, several trials were incubated for five days only, i.e., duplicates were analyzed on day zero and after five days and respiration rates were averaged on a daily basis. A directly comparable 5-day daily rate can be determined from the other procedure by averaging the 3-day and 7-day oxygen concentrations, subtracting this from the zero-day concentration, and dividing the difference by the number of days (5).

Respiration of bottom muds and their organic content

Samples of bottom mud were collected during October 1972 with an Ekman sampler (522.6 cm^2). When each haul (2 per station) was lifted into the boat, efforts were made to disturb the structure as little as possible. The top leaves of the sampler were folded back to gain access to the mud and a hypodermic syringe was used to remove 5-ml subsamples from the upper 2 cm of the mud in the Ekman sampler. The orifice of the syringe was enlarged to 7-mm diameter to allow the collection of particulate matter. Two 5-ml subsamples were placed in a 300-ml BOD bottle which was stoppered and returned to the laboratory. Three BOD bottles were filled from each haul, for a total of six per station.

In the laboratory, the BOD bottles were carefully filled by slowly siphoning lake water down the side of the bottles to minimize disturbance of the mud. The water was initially turbid, but became clear after one hour with the settling of suspended mud particles. An initial bottle was filled for determination of the O_2 concentration in the lake water as well as three control bottles for determining the respiration of lake water only (without mud). The bottles were incubated in darkness at ambient room temperature (ca. 25 C).

Subsamples from these BOD bottles were drawn from ca. 4 cm above the mud layer into 75-ml bottles with an aspirator. The volume of reagents used for oxygen concentration determination were adjusted to the size of the sample. The initial bottle (lake water) was analyzed immediately after all samples were prepared. Duplicate bottles with mud and one bottle with lake water were analyzed for oxygen after two, four, and eight hours of incubation time.

Respiration rates were calculated from the differences between these determinations. To convert the rate of change of oxygen concentration to respiration rate per unit area of mud, the following calculations were made:

Volume of water mass = 0.300 liter (total) - 0.010 liter (mud)

= 0.290

Inside diameter of BOD bottle = 6.35 cm

Cross sectional area = 31.67 cm^2 or $31.67 \times 10^{-4}\ m^2$

$$\frac{\text{mg } O_2/\text{liter}}{\text{hr}} \times \frac{0.29 \text{ liter}}{31.67 \times 10^{-4}\ m^2} = 91.57 \text{ mg } O_2/m^2 \text{ hr}$$

The respiration rate (mg O_2/liter hr) was multiplied by the constant 91.57 to yield mg O_2/m^2 hr.

The Ekman samples, from which the small subsamples were removed for the mud respiration experiment, were passed through a No. 40 mesh screen (0.417-mm aperture) to retain particulate matter and mud-dwelling organisms. After removal of the organisms for counting (see Section--Planktonic and Benthic Communities), the remaining samples were analyzed for organic matter content. Samples were oven dried (70 C) and weighed, then ignited at 550 C for 1.5 hours and reweighed. The weight loss by ignition was calculated per unit area (m^2) of mud surface and as percent of the total particulate matter retained by the screen (excluding the subsamples for respiration rates and the organisms).

Light and dark bottle method

Several attempts were made at the beginning of the study to estimate primary production by the use of diurnal changes in oxygen concentration of the water mass. These attempts were abandoned due to the erratic results from the error involved in the horizonal displacement of water masses of differing metabolic history.

The oxygen light and dark bottle method (Vollenweider 1969) was then used and stations for measurement were selected in the western, middle, and eastern areas of the lake (Figure 4). Water samples were collected with a three-liter Van Dorn bottle from the surface, and 1, 3, 6, and 11 m. After distributing each sample among an initial, light, and dark bottle (covered with black electrical tape and aluminum foil), the two latter bottles were returned to the depth from which they were collected for incubation. The initial bottles were fixed and placed in an insulated box to exclude sunlight and prevent excessive heating. The trials were usually duplicated at each station and the incubation time, in most cases, was for three hours, from about 0900 to 1200.

When possible, relatively cloudless mornings were chosen for the measurements and the three stations were measured on consecutive days. Total incoming radiation was measured in El Estor with a pyrheliometer (Solar Radiation Recorder 9-401, R.E. White Instruments, Inc.). Secchi disk values were recorded using a standard 20-cm diameter disk.

Results and Discussion

The bulk of the data for organic matter, measured as chemical oxygen demand (COD), is available from March through October 1972. Before March the procedure had not been modified sufficiently to yield reliable measurements of COD in moderate to less dilute concentrations; only measurements of net particulate organic matter are reported for December 1971, January and February 1972 in the Appendix (Table F-6).

The results will be reported as mg COD/liter or g COD/m^2 of lake surface, or as rates, i.e., g COD/m^2 day or g COD x 10^6/month. The results will not be converted into organic matter equivalents until the section , Balance of the Organic Matter Budget, because (1) the technique measured COD directly and organic matter only indirectly, (2) comparisons among stations, collection dates, and with data in the literature (often reported as mg COD/liter) can be made directly without conversion, and (3) the conversion requires some rounding off of data.

In a few cases the reported concentration of dissolved COD is higher than the total COD concentration. This is apparently due to variation in sampling or to error in the analysis of the samples. When further calculations were made, the higher of the two values was used as the total COD concentration.

The concentrations of COD will be examined first, followed by the rates of input, that is, the concentrations multiplied by the discharge rates of the rivers.

Concentrations of Chemical Oxygen Demand

The concentrations of COD in all samples (as mg/liter) are reported in the Appendix, Tables F-1 to F-6. For simplification and clarity, the data are partitioned into water types recognized earlier in the discussion of water characteristics (p. 66).

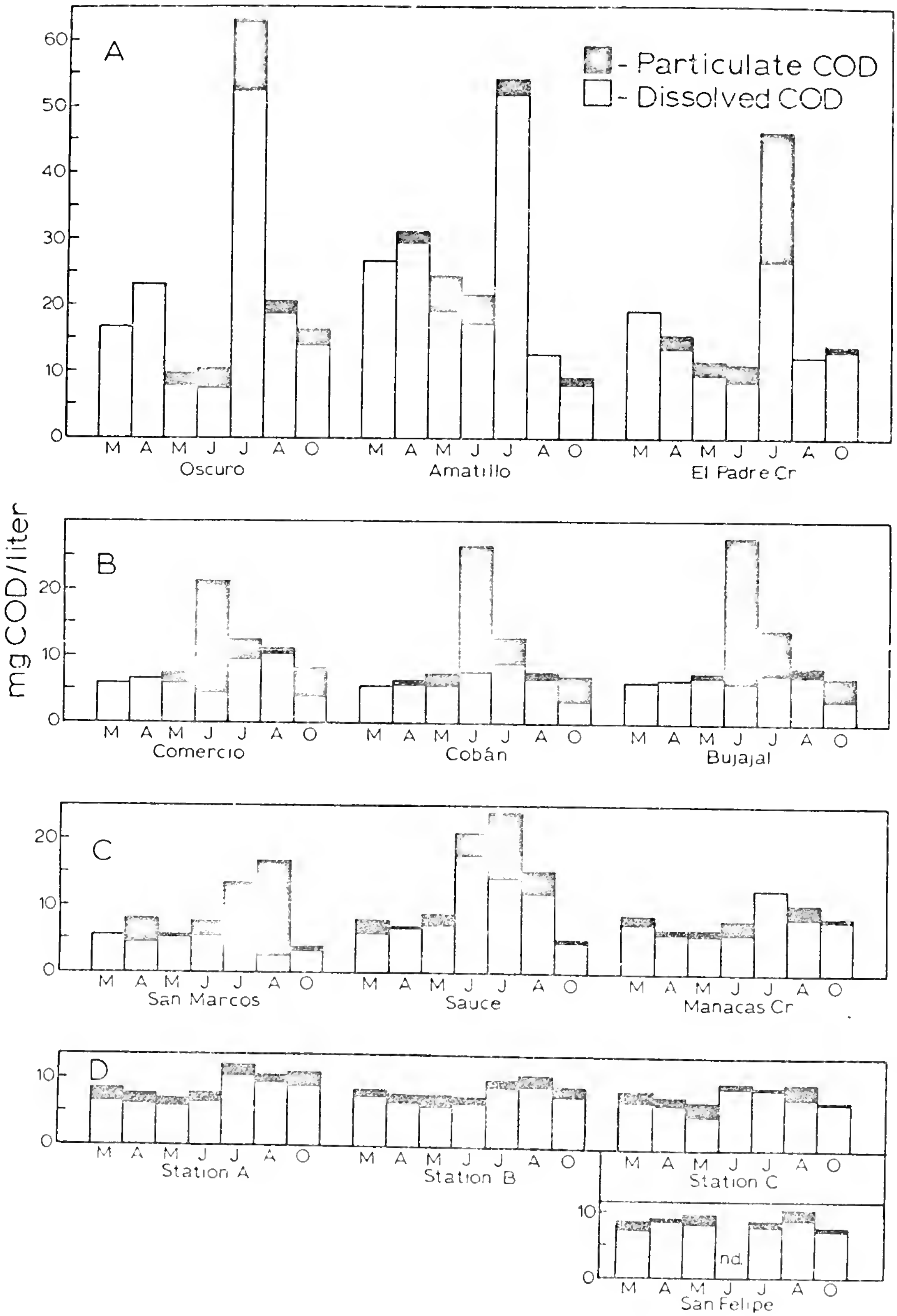
Swamp waters

The waters of the Rio Oscuro, Amatillo, and El Padre Creek are coffee-colored, visibly suggesting the presence of dissolved organic matter. The highest concentrations of total and dissolved COD were measured from this water type (Figure 34a). July represented the month of greatest total COD concentrations, with Rio Oscuro highest (63.13 mg/liter), Amatillo next (54.05 mg/liter) and El Padre Creek third (46.30 mg/liter). These maxima coincide with the first rains and appear to be a result of initial flushing of the swamp forest.

During the dry season (March-June), Rio Oscuro showed marked differences in COD concentration between the surface and 5 m (Appendix, Table F-1). This was due to the independent origin and stratification of the two water masses (as explained in the section-- Hydrology and Water Characteristics) with the more concentrated and warmer surface waters originating from the swamp.

The water column was thermally stratified at the Amatillo station also, but the two water masses were of the same origin and had similar

Figure 34.- Concentrations of particulate and dissolved COD (mg/liter) during the sampling period for (a) swamp waters, (b) Rio Polochic distributaries, (c) small rivers, and (d) lake stations (A, B, C, and San Felipe). March, April, and May are dry-season months; n.d. indicates that no data were collected.


mg COD/liter
A
Particulate COD
Dissolved COD
0
10
20
30
40
50
60
M A M J J A O
Oscuro
M A M J J A O
Amatillo
M A M J J A O
El Padre Cr
B
0
10
20
M A M J J A O
Comercio
M A M J J A O
Cobán
M A M J J A O
Bujajal
C
0
10
20
M A M J J A O
San Marcos
M A M J J A O
Sauce
M A M J J A O
Manacas Cr
D
0
10
M A M J J A O
Station A
M A M J J A O
Station B
M A M J J A O
Station C
nd
M A M J J A O
San Felipe

COD values. The slightly higher COD concentrations at 3 m (Appendix, Table F-1) in March and April may represent real differences (relative to surface) since the 3-m water was anaerobic. Inorganic reducing substances could have contributed to the COD at 3-m depth since the test does not distinguish between organic and inorganic reducing compounds.

The generally higher dry-season measurements of COD at Amatillo as compared with Rio Oscuro and El Padre Creek were likely the result of intense localized phytoplankton production. In these stagnant waters current was absent, whereas Rio Oscuro always had a slight dry-season flow. The high net particulate COD's from April through June support the visual observations that phytoplankton biomass was high.

Rio Polochic distributaries

The COD concentrations of all three distributaries show an almost continuous monthly increase until June, and a subsequent decline through October (Figure 34b). The differences between the distributaries for any one month were probably variations due to sampling. The COD concentrations of the July samples were predominately due to particulate matter, unlike the swamp waters of Figure 34a. The Rio Polochic samples were also quite high in the proportion of particulate COD in October.

Small rivers

Three small rivers were sampled for COD from March through October (Figure 34c). The range in total concentration of COD (3.69-24.06 mg/liter) was similar to the Rio Polochic distributaries (4.97-27.76 mg/liter). The Manacas Creek samples showed the least variation; particulate COD never increased above one-fifth of the total COD (August 21). Since the only noticeable discharge at Manacas Creek was during July and August (the months of the two highest COD concentrations), samples from other months contained dissolved and suspended COD probably unrelated to runoff.

The Rio Sauce had no detectable flow until June, accounting for the sharp increase in both particulate and dissolved COD at the beginning of the wet season. The July sample had an extremely high net particulate concentration (Appendix, Table F-3) which exceeded the sensitivity of the test used.

The Rio San Marcos was in constant flow throughout the year and differed from the Rio Sauce in that the watershed was mostly deforested, possibly contributing to the visibly higher silt load. Total COD concentrations never reached the high values of the Rio Sauce.

Lake stations and outlet

Stations A, B, and C, and the San Felipe outlet demonstrated fewer differences in seasonal COD concentrations than all river stations (Figure 34d). As a result, seasonal trends are harder to discern. However, by comparing dry-season with wet-season COD concentrations some differences can be noted. At Station A, March through June samples were below 9.00 mg total COD/liter, while from July through October total COD values were above 10 mg/liter. At Station B the differences between the two seasons were not as great. Station C had no samples above 10 mg total COD/liter. Only in June, July, and August did they exceed 9 mg/liter. At San Felipe there was no evidence of seasonal trends in COD concentration and values fluctuated around a mean of 8.96 mg/liter.

Monthly Flows of COD

The discharge rates of the rivers and watershed areas that are listed in Table 2 were used to calculate the rate of organic matter flow into Lake Izabal from March through October, the months for which COD measurements were available. The concentration of COD (mg/liter or g/m^3) multiplied by the monthly discharge (m^3 x 10^6) yields the monthly flow of total COD (g x 10^6). These calculations were performed on all COD fractions for the three Rio Polochic distributaries (Comercio, Cobán, and Bujajal), Rio Oscuro, Rio Amatillo, Rio San Marcos, Rio Sauce and the remaining watershed areas to the north and south of the lake (Appendix, Table G). The COD export at the San Felipe outlet was calculated from the outflow rates estimated by balancing the water budget (Table 5) and the COD concentrations measured from that station.

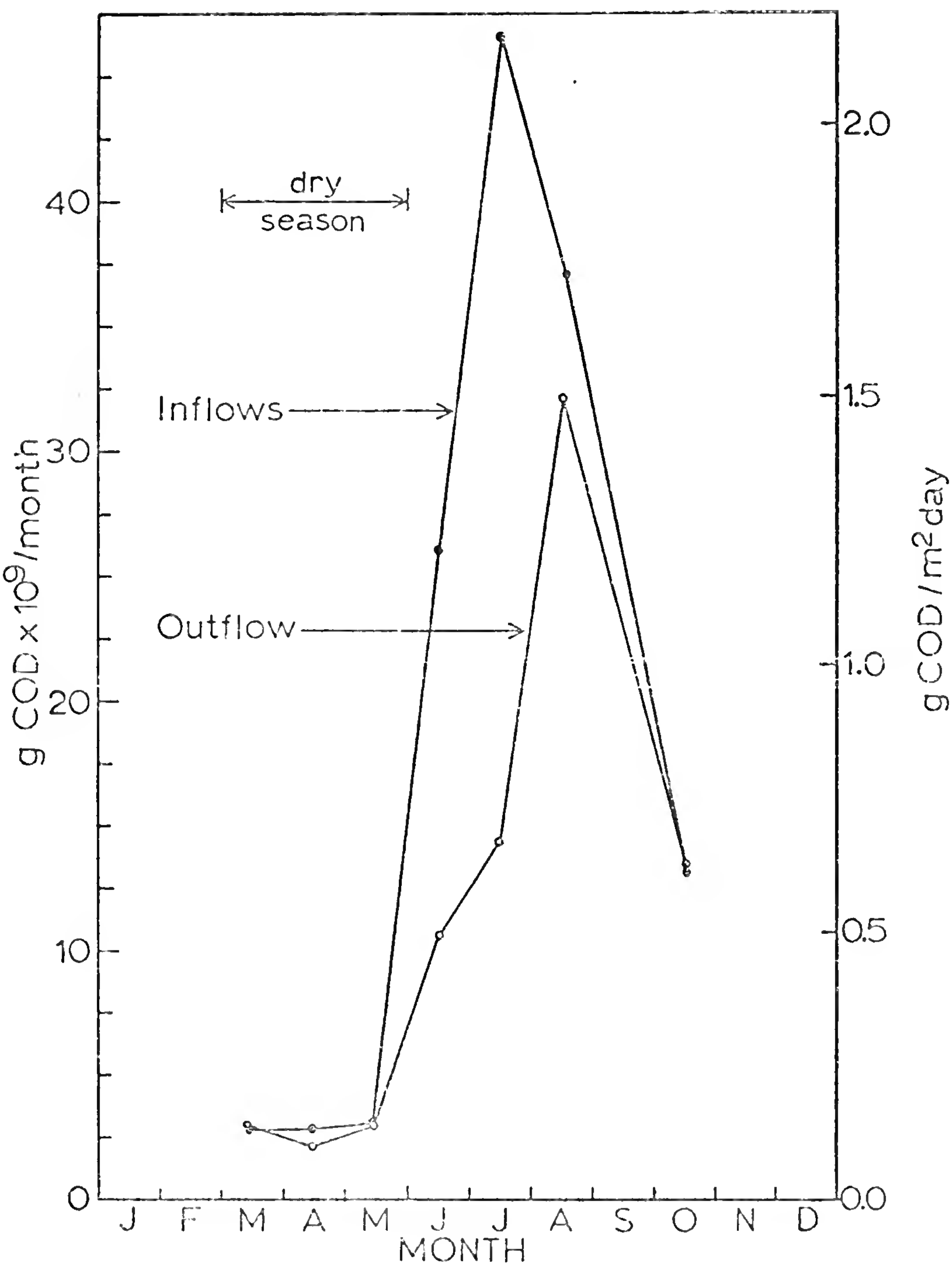
These data are summarized in Table 11 on the basis of calculations in the Appendix, Table G. Dry- and wet-season total inflows increased by approximately one order of magnitude between May and June, the transition to the wet season. Total COD inflow nearly doubled between June and July, and declined thereafter (Figure 35). The output at San Felipe was relatively constant and close to the total inflows for March, April, and May (dry season). June, July, and August outflows from San Felipe lagged behind the total inflows, but by October, the flow values were approximately the same. The average monthly inflows for the wet season (June, July, August, and October) were approximately 11 times the monthly inflows for the three dry-season months. For the purpose of later calculations, the September flows, for which no data were obtained, will be defined as the average of the August and October values. Accordingly, total September

Table 11.- Monthly COD inflows (g CODx 10^6) for individual rivers and watersheds, total monthly inflows to Lake Izabal, and monthly and total outflow at San Felipe. Wet-season rains beginning in June resulted in a sharp increase of COD inflow

Station	March	April	May	June	July	August	October
Oscuro	688.1	771.0	-	-	20,459.0	12,245.9	4,405.4
Amatillo	-	-	-	-	8,296.7	7,244.1	1,000.4
Comercio	372.6	239.3	411.2	3,635.1	2,416.7	3,210.3	1,650.0
Cobán	940.2	785.6	1,364.3	12,664.7	6,575.8	6,145.1	3,279.5
Bujajal	634.8	512.3	873.6	9,177.5	3,899.9	4,578.4	2,224.3
Sauce	-	-	-	266.7	2,172.6	455.0	131.8
San Marcos	27.9	86.1	17.7	50.1	268.0	470.1	62.7
North & South Watersheds	76.0	233.4	163.1	273.7	2,552.2	2,986.7	315.5
Total[a]	2,739.6	2,627.7	2,829.9	26,067.8	46,640.9	37,335.6	13,069.6
San Felipe	2,781.4	2,131.2	2,996.6	10,549.6	14,289.9	32,086.9	13,372.6

[a] Total organic runoff into the lake during the sampling period (March-October) assuming a September value of 25,202.6 g COD x 10^6, was 156,513.7 g COD x 10^6 for the eight months.

Figure 35.- Rates of organic matter inflows and outflows of Lake Izabal for the lake as a whole (g COD x 10^9/month) and for an average m^2 of surface area (g COD/m^2 day).


dry
season
Inflows
Outflow
g COD x 10^9/month
g COD / m^2 day
0
10
20
30
40
0.0
0.5
1.0
1.5
2.0
J F M A M J J A S O N D
MONTH

inflows would be 25,202.6 x 10^6 g COD, and the San Felipe outflow would be 22,729.8 x 10^6 g COD.

To evaluate the relative contribution of watershed areas to the total organic matter inflow, the Izabal Watershed can be divided into two runoff components. The Polochic Valley component is defined as those rivers which empty into the lake through the Polochic delta and include the three Rio Polochic distributaries, Rio Oscuro, and Rio Amatillo. These two latter "swamp rivers" are included because the Rio Polochic, during wet season flooding, spread over the delta and mixed with the waters of the Oscuro and Amatillo. The minor runoff component of the basin includes the Rio Sauce, Rio San Marcos, and the watersheds to the north and south of the lake. Table 12 compares the monthly percentage contribution of organic matter runoff from the Polochic Valley and the minor watershed components. The Polochic Valley watershed contributed between 87.8 and 96.2 percent of the total organic matter for the months sampled.

In summary, the flow of organic matter into Lake Izabal was strikingly seasonal, and not due only to increased wet-season runoff rates, but also to increased organic matter concentration of the runoff. The monthly percentage of total organic runoff during the sampling period averaged 1.7% for each of the three dry-season months (March-May) and 19.0% for each of the five wet-season months (June-October). At the beginning of the wet season, organic matter outflow at San Felipe lagged behind upstream inflows for approximately three months; thereafter outflows and inflows did not differ widely. The Polochic Valley alone accounts for 80 percent of the watershed area but more than 90% of the organic matter runoff into Lake Izabal.

Table 12.- Relative contribution (percent) of organic matter runoff into Lake Izabal from the Rio Polochic Valley and from the minor watersheds

	Mar	Apr	May	Jun	Jul	Aug	Oct
Polochic Valley Watershed	96.2	87.8	92.0	95.0	89.3	89.5	96.1
Minor watersheds	3.8	12.2	8.0	5.0	10.7	10.5	3.9

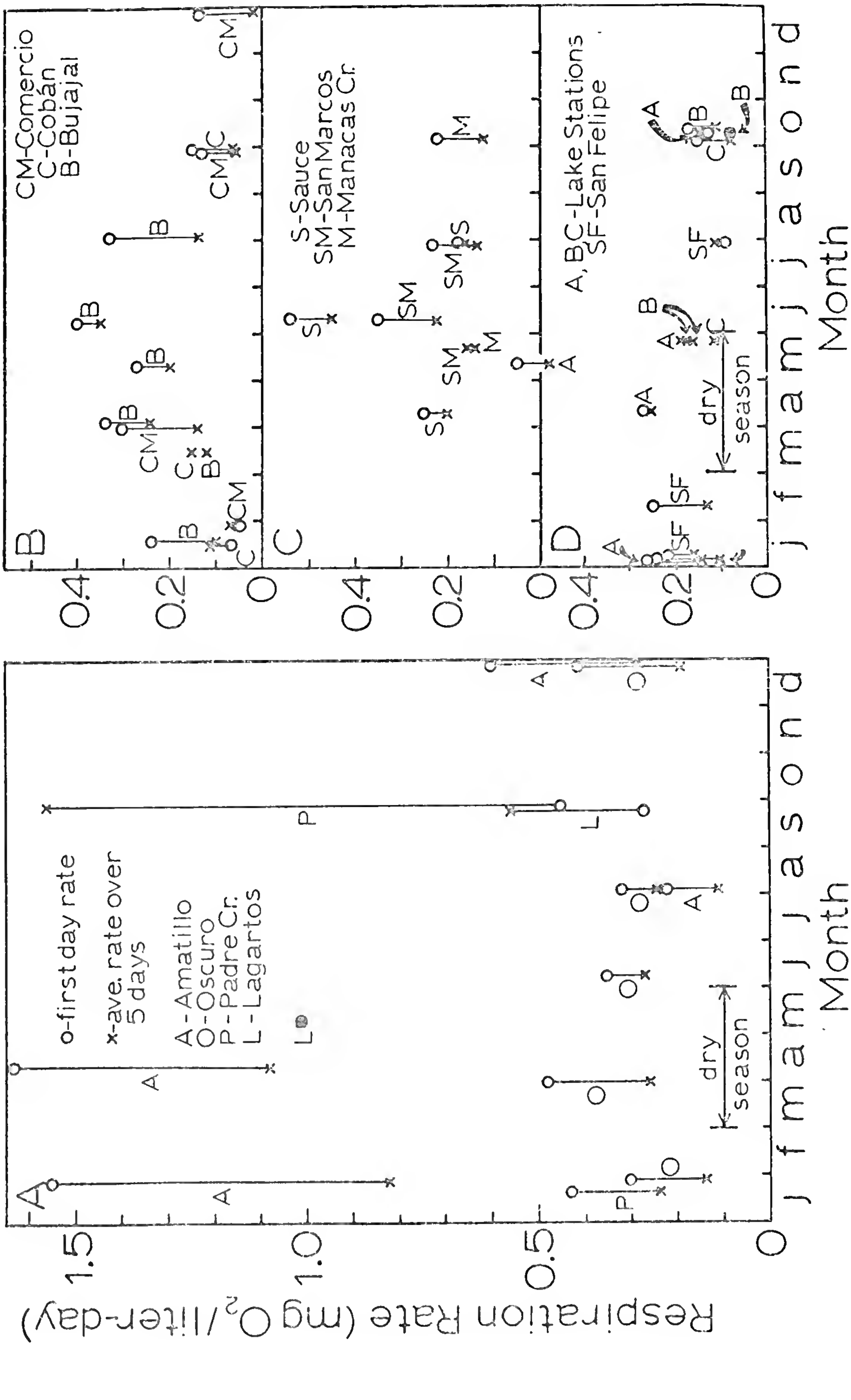
Respiration Rates (BOD)

The results of 48 experiments of respiration rates, 40 of which were 7-day incubation periods and 8 of which were 5-day incubations, are reported in Table H of the Appendix. These have been grouped according to water type and are summarized in Figure 36. The respiration rates of the swamp waters, represented by Rio Oscuro, Amatillo, El Padre Creek, and Lagartos stations were the most variable throughout the year and also had some of the highest rates of all stations. The three highest values (1.55, 1.63, and 1.56 mg O_2/liter day) from Amatillo and El Padre Creek, were apparently due to the accumulation of organic matter resulting from stagnation and anaerobic conditions.

The Rio Polochic samples resulted in generally lower and less variable rates than the swamp waters and ranged from a low rate of 0.02 mg O_2/liter day in December over a 5-day period to a high of 0.40 mg O_2/liter day in June during the first day of incubation. This latter value coincided with the beginning of high discharge rates initiated by upstream rainfall (see section--"Hydrology and Water Characteristics"). Likewise, samples from the small rivers were higher in June than other months. Of the lake station samples, the highest observed rate was 0.54 mg O_2/liter day (May 10) while most values ranged between 0.10 and 0.30 mg O_2/liter day.

The daily rates of respiration for any single sample were greater during the first day of incubation (day 0-day 1) than between day 3 and day 7. Thus the respiration rates of 1-day incubations (circles in Figure 36) were higher than the 5-day incubations (x's) when compared on a daily basis. There were some exceptions, most notably where rates of respiration

Figure 36.- Respiration rates (1-day and 5-day BOD) for (a) swamp waters, (b) Rio Polochic distributaries, (c) small rivers, and (d) lake stations.



Respiration Rate (mg O_2/liter-day)
Month
j f m a m j j a s o n d
dry season
A
o-first day rate
x-ave. rate over 5 days
A - Amatillo
O - Oscuro
P - Padre Cr.
L - Lagartos
B
CM-Comercio
C-Cobán
B-Bujajal
C
S-Sauce
SM-San Marcos
M-Manacas Cr.
D
A, BC-Lake Stations
SF-San Felipe

of the first day were low (Comercio, January 25; Coban, June 17; San Felipe, July 29). This may have been due to sampling error, but it is conceivable that the inside surface of the bottle, which provides an artificial surface for bacterial colonization, may have resulted in increased densities of bacteria, thereby resulting in higher respiration rates after the first day of incubation (Pratt and Berkson 1959).

The nature of the progressive decrease in respiration rate over a 7-day period can be examined by plotting the oxygen concentrations on semi-logarithmic paper. If the curve is linear, then the process is exponential. Figure 37 illustrates the curves generated by the data in Table H of the Appendix. By inspection, it can be seen that the curves are approximately linear, thus representing exponentially decreasing rates of oxygen consumption throughout the incubation period.

COD values were plotted against BOD rates to determine if there was any relationship (correlation) between organic matter concentration and respiration rate. No correlation was apparent between 1- and 5-day respiration rates and total or dissolved COD. This lack of correlation may have been partially attributable to variation introduced by not always collecting COD and BOD samples on the same day. However, more important was the restricted range of COD concentrations throughout the sampling period. This was especially well illustrated by the lake station samples (Figure 38), which demonstrated a broad range of respiration rates within a narrow range of COD concentrations. These concentrations could have been manipulated aritficially through dilution, but no experiment was designed for this purpose.

Figure 38 also shows the degree to which the water types overlap based on the two parameters. Only the lake stations and swamp waters

Figure 37.- Dissolved oxygen concentrations of water samples during 7-day incubation periods. Linear curves plotted on semi-log paper represent exponentially decreasing rates of oxygen consumption throughout the incubation period.

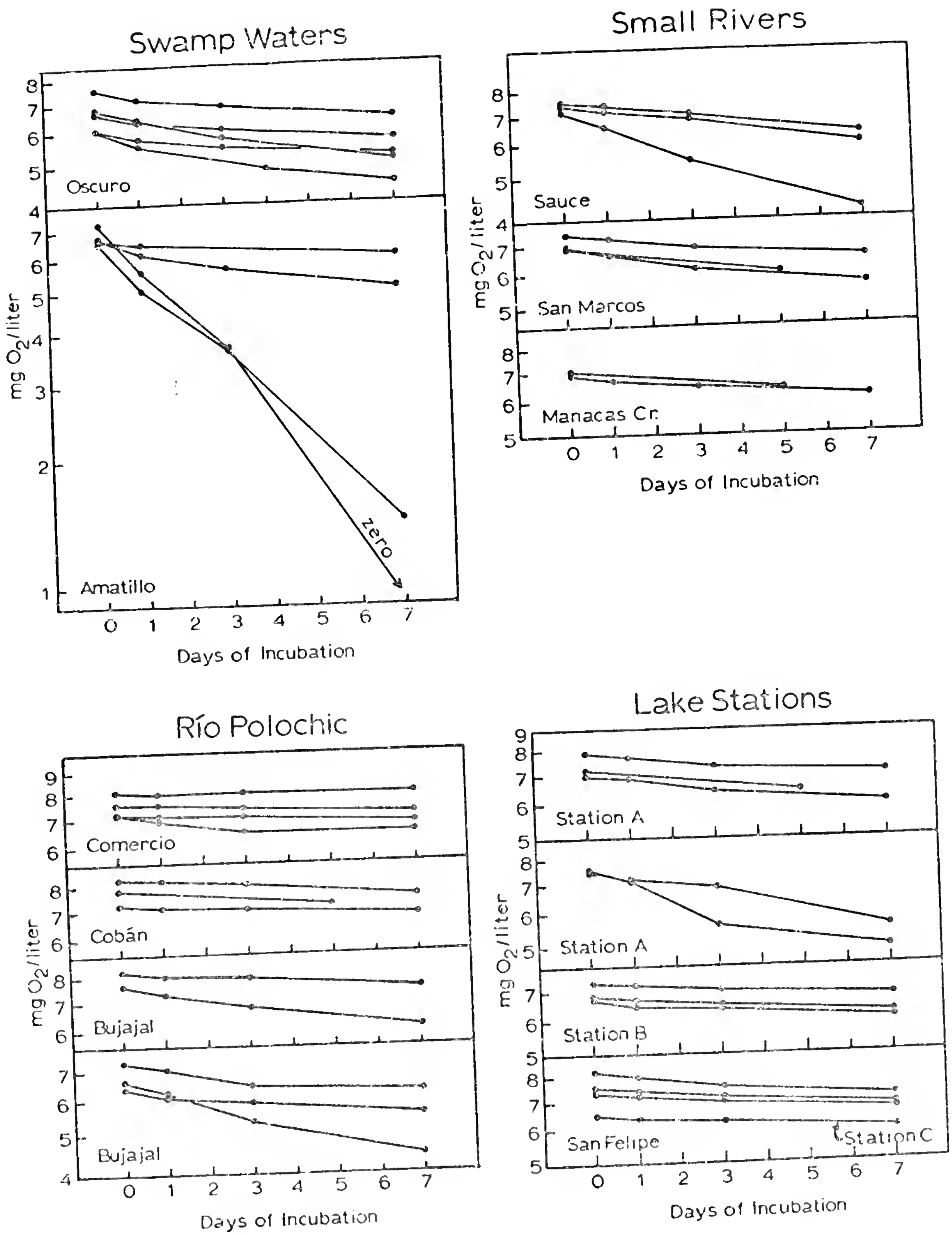
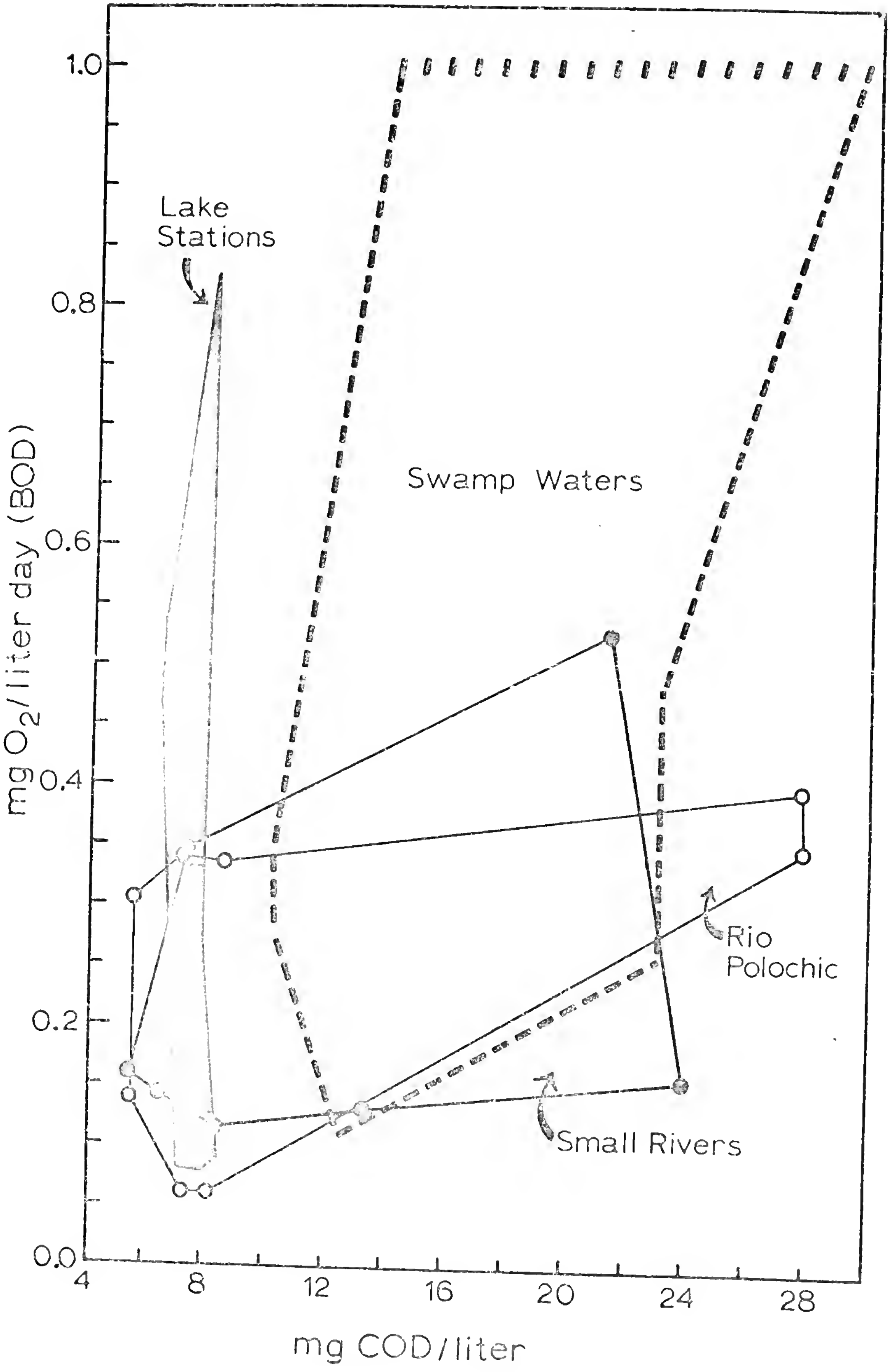

Swamp Waters
Oscuro
Amatillo
zero
mg O_2/liter
Days of Incubation
Small Rivers
Sauce
San Marcos
Manacas Cr.
mg O_2/liter
Days of Incubation
Río Polochic
Comercio
Cobán
Bujajal
Bujajal
mg O_2/liter
Days of Incubation
Lake Stations
Station A
Station A
Station B
San Felipe
Station C
mg O_2/liter
Days of Incubation

Figure 38.- Relationship between oxygen consumption rates (BOD) and total COD concentrations for the four water types characterized.


1.0
0.8
0.6
0.4
0.2
0.0
mg O_2/liter day (BOD)
4
8
12
16
20
24
28
mg COD/liter
Lake Stations
Swamp Waters
Rio Polochic
Small Rivers

are mutually exclusive while there is considerable overlap in the areas occupied by small rivers and the Rio Polochic. It is likely that the rate of respiration was more dependent on the quality of the organic matter, rather than the precise quantity.

Respiration and Organic Content of the Bottom Muds

Figure 39 illustrates the locations from which bottom mud samples were collected for respiration rate and organic content determinations. The results from the mud respiration experiments are presented graphically in Figure 40. In almost all cases the hourly respiration rate during the initial 2-hour incubation period was higher than during the second 2-hour period or the following 4-hour period. This can be attributed to the disturbance of filling the bottles which initially suspended the mud. The controls containing only lake water showed little or no respiration, so no correction was made for the overlying water.

The rates calculated after 4 and 8 hours were usually lower and more similar to each other than during the initial 2 hours. It was felt that the lower and more stable rates were more indicative of the respiration of undisturbed muds in the lake. Thus, the hourly rates, between 2 and 4 hours, and between 4 and 8 hours, were averaged to estimate the rate of in situ mud respiration. The daily values ranged between 0.258-0.452 g O_2/m^2 day with an overall average of 0.36 g O_2/m^2 day (Table 13).

These values compare favorably with results from the study by Hayes and MacAulay (1959) who used sophisticated coring devices to minimize disturbance of the mud structure. Most of their values for small Canadian lakes fall within the range of 0.10 to 0.40 g O_2/m^2 day (11 C incubation

Figure 39.- Organic composition of Ekman samples from Lake Izabal bottom muds.

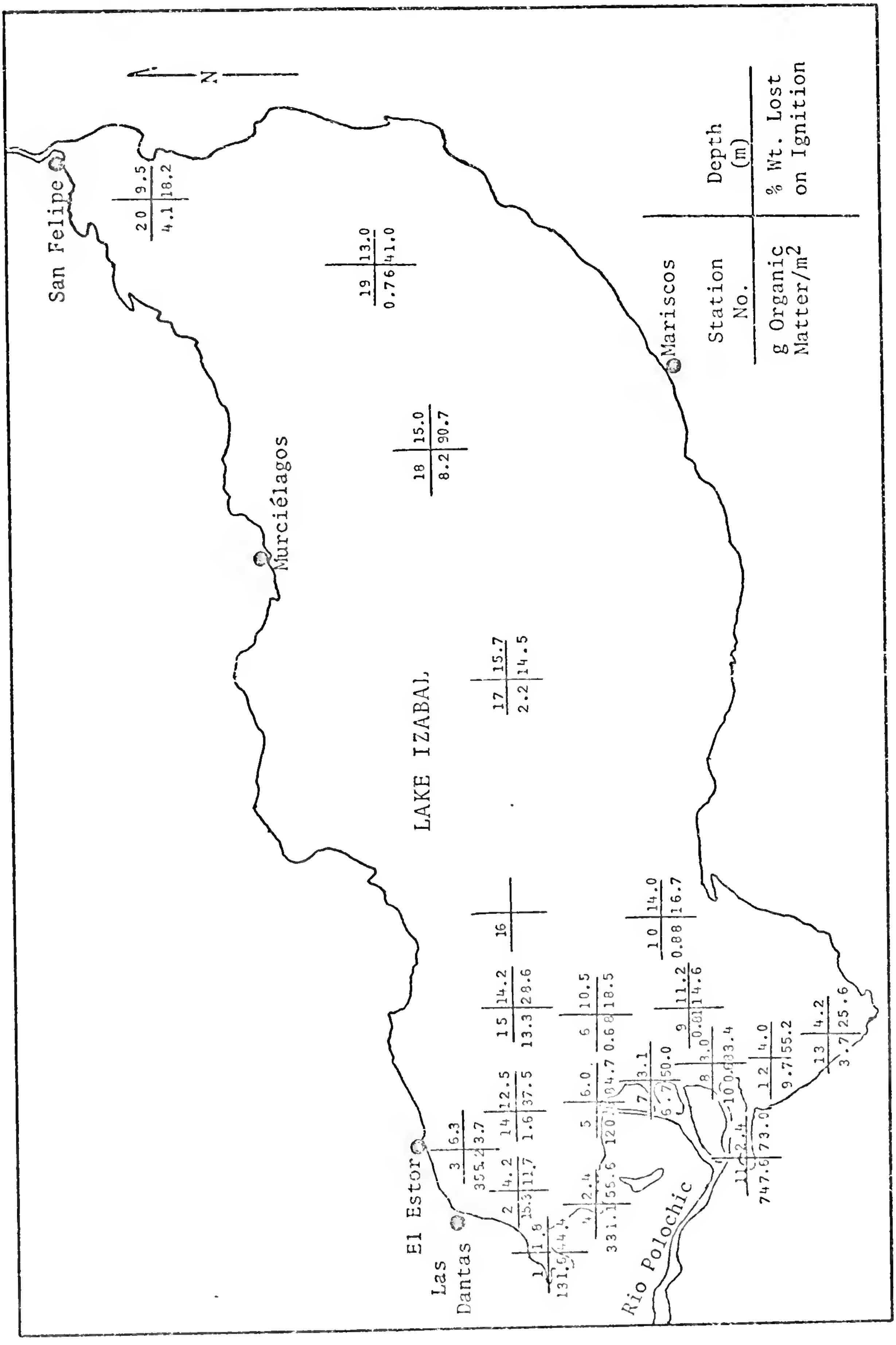

N
San Felipe
Murciélagos
Mariscos
LAKE IZABAL
El Estor
Las Dantas
Rio Polochic
Station No.
Depth (m)
g Organic Matter/m2
% Wt. Lost on Ignition
20 9.5 4.1 18.2
19 13.0 0.76 41.0
18 15.0 8.2 90.7
17 15.7 2.2 14.5
16
10 14.0 0.88 16.7
15 14.2 13.3 28.6
6 10.5 0.68 18.5
9 11.2 0.81 14.6
12 4.0 9.7 55.2
13 4.2 3.7 25.6

Figure 40.- Respiration rates of mud samples from Lake Izabal. Arrows on the horizontal axes indicate midpoints between samples and the lengths of vertical bars represent differences between duplicate rate determinations.

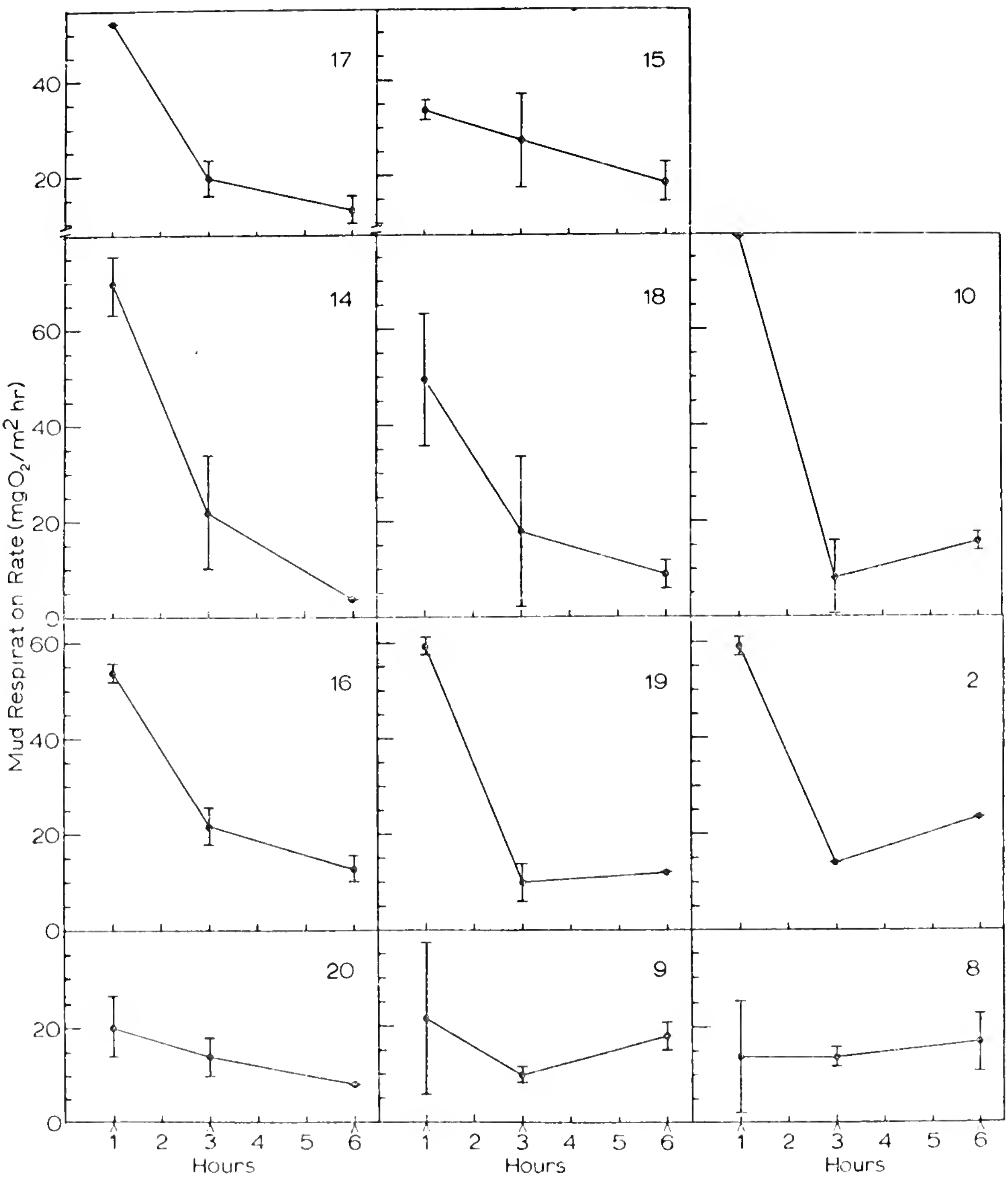

Mud Respirat on Rate (mgO$_2$/m^2 hr)
17
15
14
18
10
16
19
2
20
9
8
0
20
40
60
1
2
3
4
5
6
Hours
Hours
Hours

Table 13.- Hourly and daily respiration rates of Lake Izabal bottom muds

Station No.[a]	mg O_2/m^2 hr[b] 12 Oct	15 Oct	16 Oct	g O_2/m^2 day[c,d] 12 Oct	15 Oct	16 Oct
2		18.82			.452	
8		15.32			.368	
9		13.90			.334	
10		11.91			.286	
14	12.96			.311		
15			23.15			.556
16	17.39			.417		
17	16.21			.389		
18			13.24			.318
19			10.83			.260
20			10.76			.258

[a] Station numbers are those of Figure 39.

[b] Average of replicate rate determinations between 2 and 4 hours and between 4 and 8 hours of incubation.

[c] Hourly rates multiplied by 24.

[d] Average daily respiration rate for all stations listed in table was 0.359 g O_2/m^2 day.

temperature). Results are about an order of magnitude higher than this for river muds where stirring is used in the incubation chambers. McDonnell and Hall (1969) reported hourly rates of ca. 0.22 g O_2/m^2 for a "mildly polluted eutrophic stream," and similar values (0.10-0.20 g O_2/m^2 hr) were reported for river muds in England by Edwards and Rolley (1965).

The central, nearly flat basin of Lake Izabal is a very uniform clay-gyttja of moderately high organic content, while inshore regions contain considerable sand and gravel of alluvial origin (Tsukada and Deevey 1967). The moderately high organic content of the clay-gyttja (8.7-12.9% loss on ignition) is mostly carbonized plant fragments. Tsukada's cores, for which these analyses were reported, are well below the surface of the mud (to 3.2-m depth) and have long been unavailable to potential detritus feeders and decomposers.

To estimate the quantity and organic composition of the mud surface, especially the particulate detritus, Ekman samples were collected and treated as reported in the "Methods." Figure 39 illustrates the results obtained from samples collected throughout the lake basin. Samples from inshore stations near river outfalls and in bays and coves generally contained larger quantities and percentages of combustible particulate organic matter than did offshore samples. Offshore stations below 10.5-m depth (Nos. 6, 9, 10, 14, 17, 19), excluding stations where large pieces of plant material were collected (Nos. 15 and 18), yielded between 14.6 and 41.0 percent loss on ignition ($\bar{x}$ = 23.8%) for particulate organic matter. These values, all being proportionately higher in organic matter than the deeper muds, possibly reflect a bias toward higher organic content of the particulate fraction, but also imply that the mud surface contained substantial amounts of organic matter potentially available for detritus consumers.

Measurements of Primary Productivity

One of the chief difficulties of the light and dark bottle method for primary productivity measurements is expressing the results obtained during a 3-hour measurement on a daily basis. To do this the following calculations were made as follows:

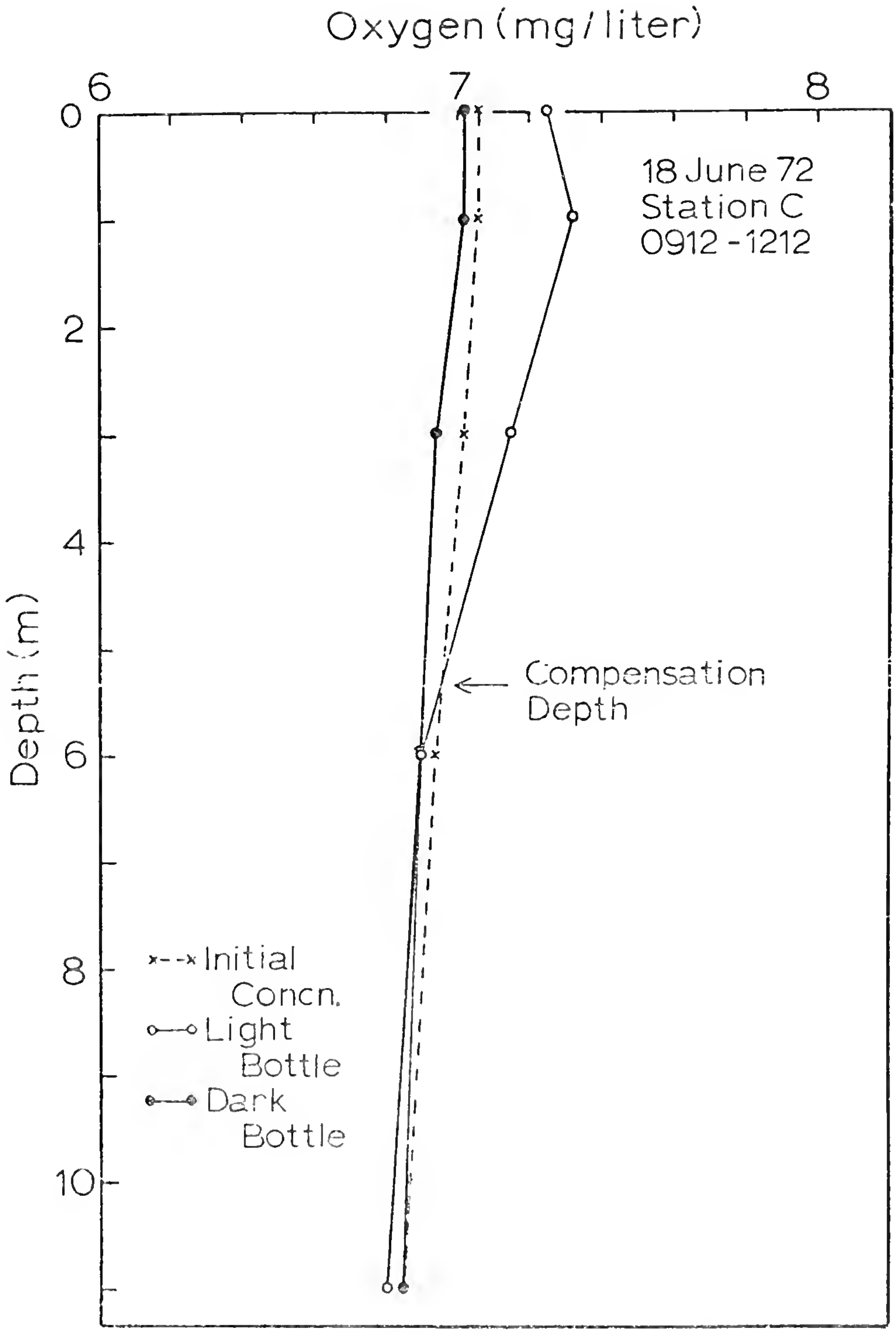
(1) The dissolved oxygen concentrations at the beginning of the experiment and those after incubation in the light and dark bottles were plotted on graph paper with oxygen (mg/liter) as the abscissa and depth (m) of incubation as the ordinate. The area between the light and dark bottle curves was integrated by planimetry, the averages were calculated for the duplicate experiments, and the value was defined as gross primary production (Pg) for the incubation period. The area between the dark bottle and initial readings was the respiration (R) (Figure 41).

(2) The Pg and R during the incubation period were divided by the number of hours of incubation to yield hourly gross primary productivity (Pg/hr) and hourly nighttime respiration (R/hr).

(3) The difference between the Pg/hr and R/hr was the net primary productivity (Pn/hr). All these values are listed in the first three columns of Table 14.

(4) Next, the hourly radiation received during incubation, calculated from the solar radiation recorder readings, was divided into the monthly average of daily radiation received. The result is the number of hours of effective radiation per day. The assumption is that daytime

Figure 41.- Example of curves generated from light and dark bottle experiments from which metabolism is determined planimetrically. The area between light and dark bottle curves is gross primary productivity (Pg), and the area between initial and dark bottle curves is respiration (R) for the incubation period. Net primary productivity is the arithmetic difference between Pg and R.


Oxygen (mg / liter)
6
7
8
0
2
4
6
8
10
Depth (m)
18 June 72
Station C
0912 - 1212
Compensation
Depth
Initial
Concn.
Light
Bottle
Dark
Bottle

primary production maintains the same proportional relationship to total daily light as hourly primary production during incubation does to hourly light received during incubation. It was believed to be more realistic to use a monthly average of daily radiation rather than radiation determined on a single day for extrapolating daily metabolism over longer periods. A hypothetical example of this calculation is given in Figure 42.

(5) Both Pn/hr and Pg/hr are multiplied by the effective hours of light per day to yield Pn/day and Pg/day respectively.

(6) The ratio of gross community metabolism (Pg) to 24-hour respiration (R_{24}) was calculated from the following formula:

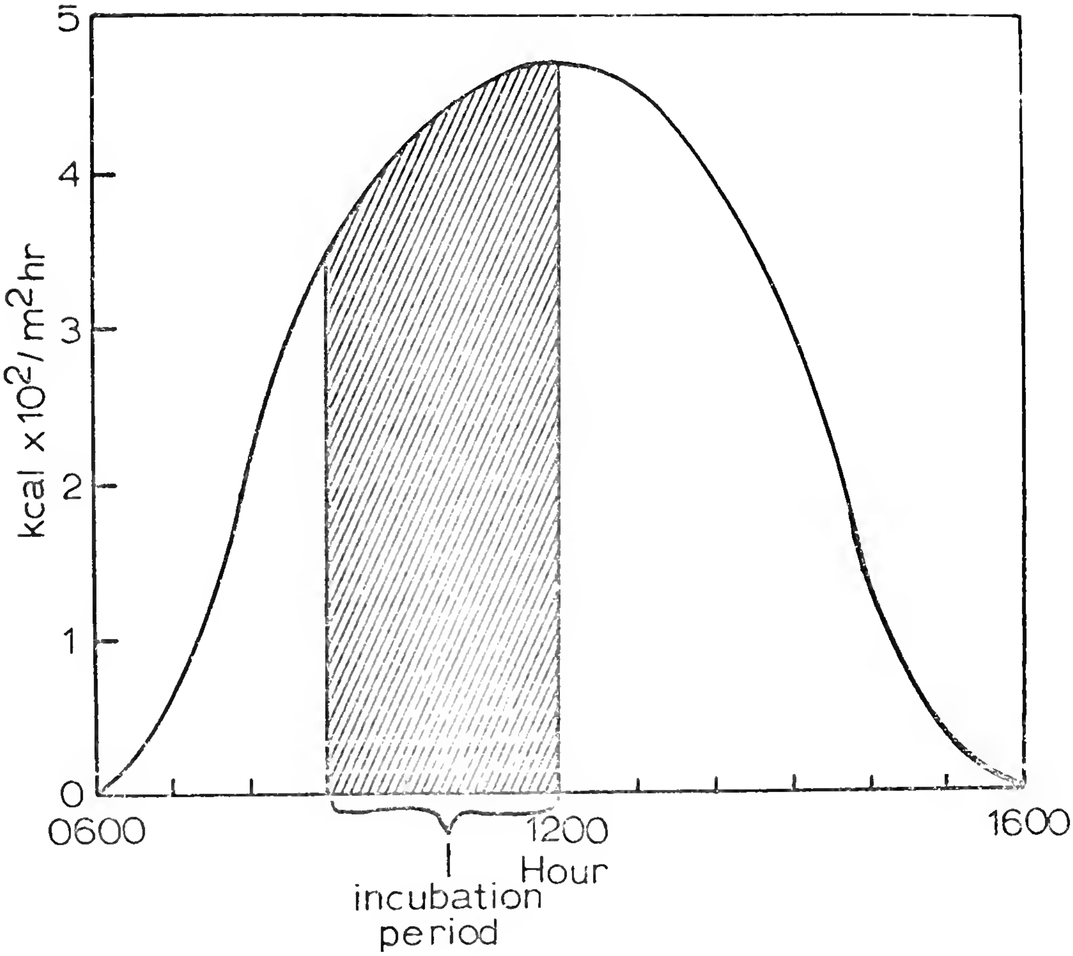
$$\frac{Pg/day}{R_{24}} = \frac{(Pg/hr)\ (hrs\ of\ effective\ light)}{(R/hr)\ (24\ hrs)}$$

This is the P/R ratio used by Odum (1956) and Margalef (1965) as an indicator of biomass accumulation ($P/R>1$) or consumption ($P/R<1$).

Seasonal rates of gross primary productivity and respiration

Although gross primary productivity (Pg) and respiration rates (R_{24}) were highly variable, some seasonal and spatial trends emerged (Table 14). Station A, for which data were taken from January through October, had highest Pg rates during the dry months of March and April, 6.09 and 7.30 g O_2/m^2 day, respectively. The lowest rates were in February (1.15 g O_2/m^2 day) before the dry season and September (1.72 g O_2/m^2) after the peak of the wet season. Respiration ranged from a low of 0.50 g O_2/m^2 day in March to a high of 7.42 g O_2/m^2 day in June. Ratios of Pg/R_{24} that deviated greatly from unity were 0.37 in February, 12.18 in March, 2.11 in April, and 0.58 in June.

Figure 42.- Method for calculating the number of hours of effective light per day.



50 kcal { 1 hr × $1cm^2$ } = 50 $kcal/m^2$

Total Radiation = 64.07 cm^2/day x 50 $kcal/m^2cm^2$ = 3,202.5 $kcal/m^2day$

Radiation during Incubation = 25.66 cm^2/3hr x 50 $kcal/m^2cm^2$ = 427.7 $kcal/m^2hr$

$$\frac{\text{Total Radiation}}{\text{Incubation Radiation}} = \frac{3{,}203.5 \text{ kcal/m}^2\text{day}}{427.7 \text{ kcal/m}^2\text{hr}} = 7.49 \text{ hours of effective light/day}$$

Table 14.- Metabolism calculations of light and dark bottle experiments for Stations A, B, and C during 1972. Rates of gross primary productivity (Pg), net primary productivity (Pn), and respiration (R) are in g O_2/m^2

Date	Pg/hr	R/hr	Pn/hr	Effective hrs of light/day	Pg/day[b]	R_{24}/day[c]	Pg/R_{24}
				Station A			
11 Jan	.629	.159	.470	6.53	4.11	3.82	1.08
29 Jan	.598	.133	.465	5.79	3.51	3.19	1.10
2 Feb	.214	.128	.086	5.38	1.15	3.07	0.37
4 Mar	.450	.021	.429	13.54	6.09	0.50	12.18
24 Apr	.981	.144	.837	7.45	7.31	3.46	2.11
6 May	.580	.251	.329	8.35	4.84	6.02	0.80
28 May	.781	.289	.492	7.49	5.85	6.94	0.84
20 Jun	.587	.309	.278	7.33	4.30	7.42	0.58
9 Aug	.684	.168	.516	6.58	4.50	4.03	1.12
27 Sep	.254	.111	.143	6.79	1.72	2.66	0.65
27 Oct	.470	.153	.317	5.68	2.67	3.67	0.73
				Station B			
3 May[a]	.493	.112	.381	6.69	3.30	2.68	1.23
5 Jun	.537	.077	.460	11.94	6.41	1.85	3.46
19 Jun	.715	.146	.569	6.72	4.80	3.50	1.37
8 Aug	.467	.349	.118	12.63	5.90	8.38	0.69
26 Sep	.333	.181	.152	7.28	2.42	4.34	0.56
				Station C			
5 May	.383	.105	.278	7.96	3.05	2.52	1.21
29 May[a]	.278	.134	.144	7.87	2.19	3.22	0.68
18 Jun	.443	.163	.280	6.20	2.75	3.91	0.70
7 Aug	.534	.132	.402	6.44	3.44	3.17	1.09
25 Sep	.200	.160	.040	6.12	1.22	3.84	0.32

[a] Respiration was not measured due to improper treatment of initial samples. The values used are hourly rates from 5-day BOD measurements of lake water.

[b] Product of effective hours of light per day and the Pg/hr.

[c] Product of R/hr and the number of hours per day (24).

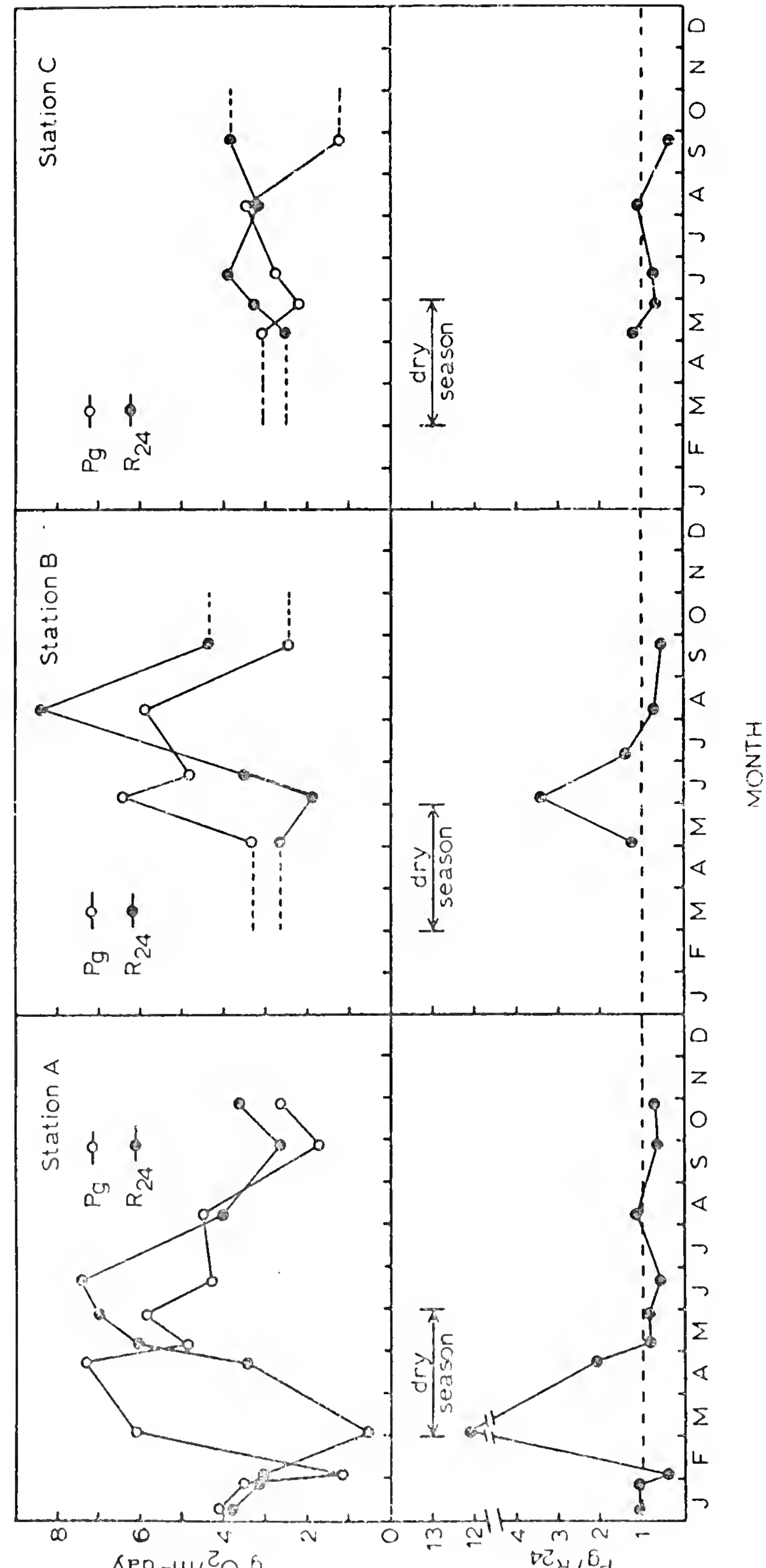
Data for Stations B and C are available for only May through September. At Station B the highest Pg (6.41 g O_2/m^2 day) occurred on June 5 decreasing to a low of 2.42 g O_2/m^2 day in September. Respiration was lowest on June 5 (1.85 g O_2/m^2 day) and highest in August (8.38 g O_2/m^2 day). The highest Pg/R24 ratio was on June 5, the day of highest Pg; the lowest ratio (0.56) was measured in September, the day of lowest Pg.

At Station C, Pg was highest August 7 (3.44 g O_2/m^2 day) and lowest September 25 (1.22 g O_2/m^2 day). Overall, respiration rates were less variable than those of other stations; a low of 2.52 g O_2/m^2 day was measured May 5 and a high of 3.91 g O_2/m^2 day on June 18. Ratios of Pg/R_{24} ranged between the May 5 high (1.21) to the September low of 0.32.

The Pg, R_{24}, and the Pg/R_{24} ratios are summarized graphically in Figure 43. Because eight months of data are available for Station A, the seasonal trend of metabolism is especially well developed. The increase in Pg during the dry season (February-May) was followed by an increase in R_{24}. This resulted in a change in P/R ratio from greater than one in April to less than one in May. Respiration continued to exceed gross primary production throughout the wet season except for the August reading. At Station B excess Pg over R_{24} continued until July, and thereafter the ratio was less than unity. At Station C metabolism rates were generally lower and less variable than at Station A and B. The highest rates of Pg at Station C were approximately one-half the values of the highest rates at Stations A and B.

To summarize, Stations A and B appeared to have trends of metabolism which roughly corresponded to the change from the wet to the dry season and had periods during which the P/R ratio was well above unity. At Station C

Figure 43.- Gross primary productivity (Pg), 24-hour respiration (R_{24}) and Pg/R_{24} ratios at Station A, B, and C. The extension of the curves with broken lines for Stations B and C are used to estimate the total organic matter budget for periods of missing data.


Station A
Station B
Station C
Pg
R24
dry season
g O2/m2 day
Pg/R24
MONTH
J F M A M J J A S O N D

similar seasonal trends were lacking; the P/R ratio was more commonly less than unity, and during no period did the P/R deviate far above one. Thus, the western and central parts of the lake (Stations A and B) seem to be areas where production seasonally exceeded respiration, whereas the eastern part of the lake (Station C) demonstrated less of a seasonal pulse in metabolism.

Efficiency of gross primary productivity

The efficiency of primary productivity will be defined as the fraction or percentage of incoming radiant energy (available to photosynthesis) that is converted into chemical energy by gross primary productivity. The energy of the spectral region available for photosynthesis (400-770 mμ) was assumed to be 50% of the energy recorded by the pyrheliometer.

Total solar radiation, recorded almost continually from October 1971 through November 1972, is reported in Table 15. Daily readings were averaged on a weekly and monthly basis. The monthly averages were used to calculate efficiencies of Pg/day, and the hourly radiation, determined during the incubation period, was used to calculate efficiency of Pg/hr (Table 16).

Since solar radiation was expressed as kcal/time, the productivity had to be converted from grams oxygen to equivalent energy and time units. The choice of 4 kcal/g O_2 lies between the value for one of the products of photosynthesis (glucose) and the final products of biomass (plankton). If glucose were the only product of photosynthesis, approximately 118 kcal of solar radiation would be required per mole of oxygen, or 3.7 kcal/g O_2. If biomass were the product of photosynthesis, the 4.8-5.0 kcal /g biomass (or O_2 equivalent) represents the energy content of plankton (Maciolek

Table 15.- Total daily incoming radiation averaged on a weekly and monthly basis from October 1971 through October 1972

Dates of Measurement		No. Days Measured	$kcal/m^2$ day (weekly)	$kcal/m^2$ day (monthly)
Oct.	8-15, '71	7	4,142	4,112
	16-23	7	4,558	
	24-31	8	3,635	
Nov.	1-7, '71	7	3,325	3,294
	8-14	7	3,113	
	15-21	7	3,479	
	22-30	9	3,258	
Dec.	1-7, '71	7	3,906	3,499
	8-14	7	3,515	
	15-21	7	3,240	
	22-31	10	3,335	
Jan.	1-7, '72	7	3,617	3,474
	8-14	7	3,698	
	15-21	7	2,707	
	22-31	10	3,872	
Feb.	1-7, '72	7	2,959	3,522
	8-14	7	4,115	
	15-21	7	3,372	
	22-29	8	3,643	
Mar.	1-7, '72	7	4,522	4,550
	8-14	7	3,628	
	15-22	7	4,953	
	23-31	9	5,098	
Apr.	1-7, '72	7	4,111	4,566
	8-14	7	4,879	
	16-22	7	4,499	
	23-30	8	4,776	
May	1-7, '72	7	4,561	4,561
	8-14	7	4,477	
	15-21	7	4,487	
	22-31	9	4,718	
Jun.	1-7, '72	7	3,555	4,399
	8-14	7	4,372	
	15-21	7	4,906	
	22-27	6	4,762	

Table 15.- continued

Dates of Measurement	No. Days Measured	kcal/m^2 day (weekly)	kcal/m^2 day (monthly)
Jul. 2-7, '72	6	4,041	3,974
8-14	7	4,070	
19-25	7	4,327	
26-31	6	3,459	
Aug. 1-7, '72	7	4,441	4,485
8-14	7	4,137	
15-21	7	4,544	
22-31	10	4,816	
Sep. 1-7, '72	7	4,163	4,172
8-14	7	4,271	
17-23	7	4,097	
25-28	4	4,155	
Oct. 1-7, '72	7	4,016	3,718
9-15	7	3,498	
16-22	7	3,386	
23-28	6	3,972	
Daily average for October 1971-1972....			4,025

Table 16.- Daily efficiencies of energy conversion from visible solar energy to energy fixed by gross primary productivity (Pg). The energetic equivalent of one gram of oxygen was assumed to be 4 kcal and visible solar radiation was assumed to be 50% of total incoming radiant energy

Station - Date	Pg/day g O_2/m^2	Pg/day kcal/m^2	50% of Total Radiation[a] (kcal/m^2 day)	Percent Efficiency
Station A				
11 Jan	4.11	16.44	1,737	0.95
29 Jan	3.51	14.04	1,737	0.81
2 Feb	1.15	4.60	1,761	0.26
4 Mar	6.09	24.36	2,275	1.07
24 Apr	7.31	29.24	2,283	1.28
6 May	4.84	19.36	2,281	0.85
28 May	5.85	23.40	2,281	1.03
20 Jun	4.30	17.20	2,200	0.78
9 Aug	4.50	18.00	2,243	0.80
27 Sep	1.72	6.88	2,086	0.33
27 Oct	2.67	10.68	1,859	0.57
				0.79 Ave.
Station B				
3 May	3.30	13.20	2,281	0.58
5 Jun	6.41	25.64	2,200	1.17
19 Jun	4.80	19.20	2,200	0.87
8 Aug	5.90	23.60	2,243	1.05
26 Sep	2.42	9.68	2,086	0.46
				0.83 Ave.
Station C				
5 May	3.05	12.20	2,281	0.53
29 May	2.19	8.76	2,281	0.38
18 Jun	2.75	11.00	2,200	0.50
7 Aug	3.44	13.76	2,243	0.61
25 Sep	1.22	4.88	2,086	0.23
				0.45 Ave.

[a] Average daily radiation for the month in which station was sampled.

1962). Since neither glucose nor highly structured plankton biomass are the sole products represented by O_2 evolution in the experiments, the intermediate value of 4 kcal/g O_2 seems justified.

The daily efficiencies of gross primary productivity reported in Table 16 ranged between 0.23-1.28%. Solar radiation was more constant that primary productivity which resulted in efficiencies being more proportional to productivity than to radiation. Efficiencies greater than 1% were exceeded only three times at Station A and twice at Station B when the primary productivity was greater than 20 kcal/m^2 day.

Light penetration and compensation depth

At least twice monthly, Secchi disk transparency measurements (except July) were recorded at Stations A, B, and C (Figure 44). There was a general trend of decreased transparency as the dry season progressed; the least transparent readings were during July (1.5-1.7 m). Thereafter, a trend toward greater transparency increased values to 3.1-4.2 m in October.

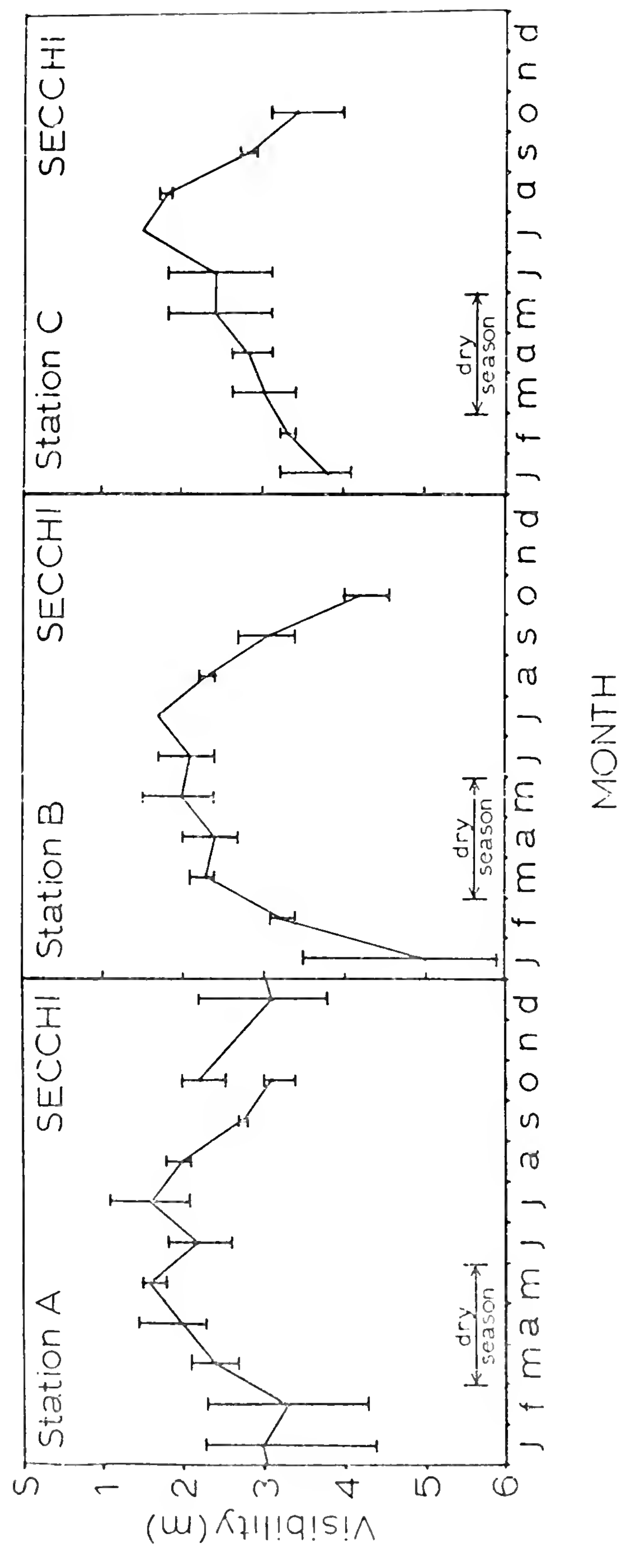
A submarine photometer was not available at Lake Izabal to measure the percent extinction at the depth of Secchi disk transparency. The extinction coefficients were calculated from Secchi disk transparencies from the relationship

$$\eta = \frac{1.4}{z_m}$$

where η is the extinction coefficient and z is the depth in meters of the Secchi disk transparency. The choice of the constant 1.4 is explained in the following paragraphs.

The light intensity at the limit of Secchi disk transparency is about 15% of the subsurface intensity according to several authors (Poole and

Figure 44.- Secchi disk transparency measurements recorded at Stations A, B, and C. Vertical represent the range of readings and the curve connects monthly mean values.


Station A
SECCHI
Station B
SECCHI
Station C
SECCHI
dry season
Visibility (m)
0
1
2
3
4
5
6
j f m a m j j a s o n d
MONTH

Atkins 1929; Clarke 1941; Ichimura 1956; Beeton 1957). According to Beer's Law[1] of light extinction

$$Iz = I_o e^{-\eta z_m}$$

where I_z represents the light intensity at depth z, I_o the incident light impinging upon the water surface, and η the extinction coefficient.

If I_z is 15% of I_o, then,

$$15 = 100 e^{-\eta z_m}$$

$$\ln 100 - \ln 15 = \eta z_m$$

$$4.605 - 2.708 = \eta z_m$$

$$\frac{1.897}{z_m} = \eta$$

Assuming that the factor 1.9 remains constant, then the extinction coefficient can be calculated from the following formula:

$$\eta = \frac{1.9}{z_m}$$

Using the factor 1.9 would result in an extinction coefficient of greater than one for low Secchi disk values such as the one recorded on April 24 at Station A (1.45 m). An extinction coefficient greater than one would be unlikely, especially since the Secchi disk was visible down to the 1.45-m depth. Vollenweider (1969) reported that this value varies from 1.4-3 and more depending on local conditions and the observer. Thus a factor of 1.4 was chosen for calculating extinction coefficients since it is less than the shallowest Secchi transparency (1.45 m) which avoids a $\eta > 1$, and it is within the range of values reported by Vollenweider (1969). Back calculation, using the formula from Beer's Law, resulted

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[1] The equation strictly applies only to monochromatic light, but is adequate and useful in the present context for white light.

in 24.7% of the surface intensity reaching the depth of Secchi disk visibility.

Table 17 presents the data for Secchi disk transparencies and calculations which relate to primary productivity experiments. Compensation depths were determined from the graphs used for planimetric determination of primary productivity and represent that depth where the light bottle O_2 concentration at the end of the incubation period crosses the initial O_2 concentration (Figure 41). Extinction coefficients ranged between 0.412 and 0.966. The percent of surface intensity reaching the compensation depth ranged between 1.68 and 3.29, which is slightly greater than the 1% level generally considered to be the compensation intensity (Ruttner 1963). The disagreement is probably due to two factors: (1) an error in the assumed light intensity of Secchi disk readings and (2) the lack of good resolution in determining the compensation depth due to bottles not being used at 1-m intervals in depth. In spite of these factors, the observed compensation depths (3.75-8.93 m) overlapped to a large degree with the calculated depths of 1% light penetration (4.94-11.18 m).

Balance of the Organic Matter Budget

The results presented in the preceding sections represent most of the principal flows and storages of organic matter in the lake. In order to evaluate these data, a simplified model was used as a tool for comparing the relative importance and magnitude of the organic matter flows in relationship to the seasonal regime (Figure 45). The energy language of Odum (1971) was used to illustrate these flows and storages. The central pool or storage represents total organic matter (living and dead) which either gains or loses organic matter depending on the relative magnitudes

Table 17.- Calculation of light intensity at compensation depths as percent of surface intensity. Compensation depth and Secchi disk transparency are empirical values, while the extinction coefficient (η) and percent of surface intensity (x) were calculated according to assumptions stated in footnotes and text

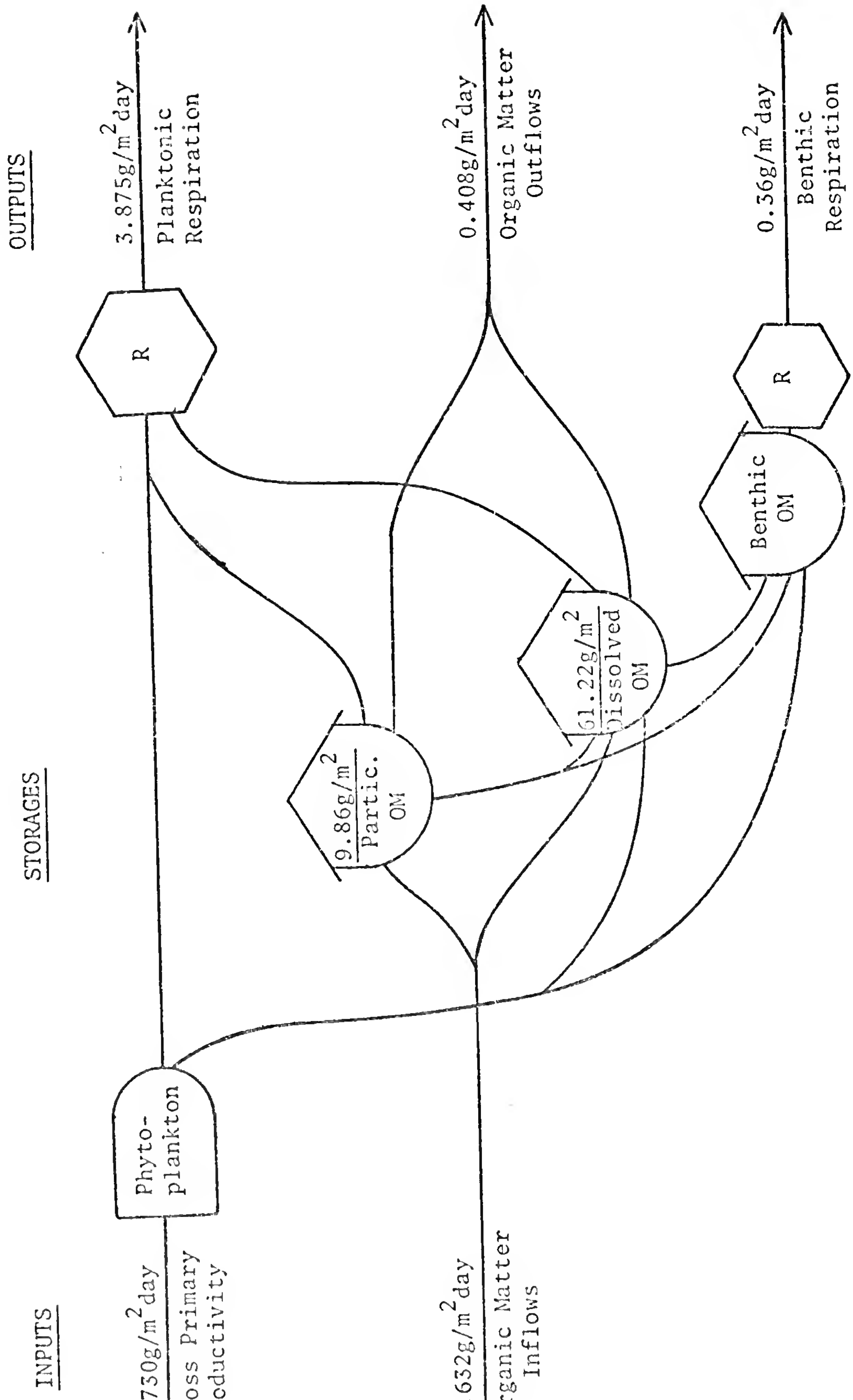
Station - Date	Compensation Depth (m) First Reading	Second Reading	Average	Secchi Disk Transparency (z_m)	η[b]	Percent[c] of Surface Intensity at Compensation depth (x)
Station A						
11 Jan[a]			7.60	2.3	.608	2.73
29 Jan[a]			6.40	2.3	.608	2.33
4 Mar[a]			7.25	2.7	.519	2.26
24 Apr	5.50	5.75	5.67	1.45	.966	3.28
6 May	5.25	5.35	5.30	1.5	.933	2.93
28 May	6.00	5.75	5.88	1.5	.933	3.29
20 Jun	8.35	9.50	8.93	2.6	.538	2.84
9 Aug	5.70	5.05	5.38	2.1	.667	2.18
27 Sep	6.00	6.00	6.00	2.8	.500	1.92
Station B						
3 May	6.50	6.00	6.25	1.6	.875	3.28
5 Jun	5.50	6.70	6.10	1.75	.800	2.89
19 Jun	6.30	6.50	6.40	2.4	.583	2.25
8 Aug	4.50	3.00	3.75	2.2	.636	1.68
26 Sep	6.00	6.00	6.00	3.4	.412	1.71
Station C						
5 May	8.25	6.90	7.58	3.0	.467	2.16
29 May	6.00	6.75	6.38	2.4	.583	2.24
18 Jun	6.75	5.25	6.00	1.8	.778	2.76
7 Aug	5.70	7.00	6.35	1.76	.795	2.99
25 Sep	7.25	6.00	6.63	2.82	.496	2.04

[a] No replications were made.

[b] Extinction coefficient: $\eta = \frac{1.4}{z_m}$

[c] $\ln x = \frac{\eta z_m}{\ln 100}$

Figure 45.- Simplified model of the principal organic matter flows and storages in Lake Izabal as averaged over the period of study. The average residence time of the organic matter storage was 16.3 days [(Total OM/m^2) ÷ (OM Inputs/m^2 day)].


INPUTS
3.730g/m^{2}day
Gross Primary
Productivity
0.632g/m^{2}day
Organic Matter
Inflows
STORAGES
Phyto-
plankton
9.86g/m^2
Partic.
OM
61.22g/m^2
Dissolved
OM
Benthic
OM
R
R
OUTPUTS
3.875g/m^{2}day
Planktonic
Respiration
0.408g/m^{2}day
Organic Matter
Outflows
0.36g/m^{2}day
Benthic
Respiration

of the inflows and outflows from the pool. Inflows are represented by importation of organic matter from the watershed and by the contribution of gross primary production. Losses from the pool include exports of organic matter, loss by planktonic respiration, and by benthic respiration.

The components of the model parallel measurements that were made in the field over an eight-month period, except for benthic respiration (one month of data). It must be remembered, however, that these were not measurements for every day of the month, but rather one to several measurements during a single month at a limited number of sampling sites. The eight-month sampling period included three months of dry season (March-May) and four months of wet season (June-October). Since the Izabal Basin was characterized by a longer wet than dry season, the balance of the sampling period was toward the wet season, thus closely representing the hydrological regime over a full year. Also the sampling period included what could be considered the maxima of the two seasons, i.e., the dryest part of the dry season, and the wettest part of the rainy season.

Table 18 summarizes the organic matter flow data according to the flows defined in the model. The values are daily rates and are assumed to be the average for each day in the month. The calculations on which Table 18 is based are given in the Appendix, Tables I and J. Oxygen production and consumption values were assumed to be equivalent to organic matter (OM) values.

Some interesting ecosystem characteristics become apparent upon examination of Table 18. For example, Pg remained relatively constant from March-August (above 4 g OM/m^2 day) and then declined to below 2 g OM/m^2 day be October. However, when Pn was examined, there was a net

Table 18.- Summation of organic matter (OM) flows for Lake Izabal from March to October 1972. All values are expressed in g OM/m^2 day

Month	Pg	R_{24}	Pn	OM Imports	OM Exports	Net Gain or loss	Benthic Respiration	Balance of Gains or Losses[b]	Gross Organic Matter Production[c]
Mar	4.240	2.120	+2.120	0.088	0.090	-0.002	-0.36	+1.758	4.328
Apr	4.433	2.743	+1.690	0.085	0.069	+0.016	-0.36	+1.346	4.518
May	4.173	3.837	+0.337	0.091	0.097	-0.006	-0.36	-0.029	4.264
Jun	4.270	4.590	-0.320	0.842	0.341	+0.501	-0.36	-0.179	5.112
Jul	4.290	5.033	-0.743	1.506	0.461	+1.045	-0.36	-0.058	5.796
Aug	4.087	4.897	-0.810	1.205	1.036	+0.169	-0.36	-1.001	5.292
Sep	2.380	3.970	-1.590	0.814[a]	0.734[a]	+0.080[a]	-0.36	-1.870	3.194
Oct	1.970	3.813	-1.843	0.422	0.432	-0.010	-0.36	-2.213	2.392
Ave.	3.730	3.875	-0.145	0.632	0.408	+0.224	-0.36	-0.281	4.362

[a] Missing data were calculated as the average of the August and October values.

[b] Sum of Pn, net OM gain or loss, and benthic respiration.

[c] Sum of all organic matter flowing through or metabolized under a unit area of ecosystem, which includes Pg and OM imports.

positive gain only during the dry months (March-May) and values became increasingly negative throughout the wet months (June-October). The excess production by photosynthesis during the dry-season maximum was ca. 2 g OM/m^2 day, a value close to the maximum consumption over production in October.

The organic detritus imports and exports can be evaluated best by examining their net gains and losses. In June and July there were net gains of 0.501 and 1.045 g OM/m^2 day respectively, which compensated for the net loss from respiration exceeding gross primary production during those months. For all other months, the net gains or losses of organic detritus were small when compared to other flows.

Consumption of organic matter by benthic respiration was assumed constant at 0.36 g OM/m^2 day for all months. It was clearly a flow of importance to the overall balance of organic matter, for it represented a relatively large percentage of the total energy drain from the ecosystem when compared with other flows.

The balance of ecosystem gains or losses reflected the same general trend as did Pn with some modifications. For example, the May value was slightly negative, owing mostly to benthic respiration cancelling the gain due to Pn. June and July losses were somewhat ameliorated by the large positive gains of organic detritus during those months.

The average values for each of the organic matter flows were calculated in order to arrive at an overall evaluation of potential and realized ecosystem metabolism. Likens (1972) used the term "ecosystem source carbon" to include all reduced carbon compounds that can provide energy for consumers (and presumably decomposers). In Lake Izabal where horizontal displacement was of considerable magnitude due to the short residence time of the water mass (6.6 months), Likens' term would be equivalent to all the organic matter that flowed through or was metabolized under a unit area of ecosystem. This would be represented by the Pg and OM imports. As calculated in Table 18 (last column) this value averaged 4.362 g OM/m^2 day or an annual total of 1,592 g OM/m^2. This value can be compared with the production of other tropical and temperate lakes listed in Table 19. Lake Izabal ranks below that of several other tropical lakes, but above the range in annual rates for eutrophic temperate lakes.

The overall balance during the sampling period was a negative average of -0.281 g OM/m^2 day and would imply that there was a rather large deficit in the annual energy budget for the lake. The negative balance may be attributed to a series of factors, such as the failure to account for measurements during the remaining four months of the year. Another possibility is failure to measure the energy flows with exact precision. Measurements that may have slightly underestimated organic sources and overestimated organic losses would have the combined effect of producing a deficit in the final estimate of the budget.

However, the purpose of the organic matter budget was not so much to prove that the ecosystem was or was not at steady state, but rather to compare the relative magnitude of organic flows and to demonstrate the seasonal activity of metabolism and organic balance. This it clearly does, and the positive dry-season gain of "surplus" organic matter corresponded closely with an increase in the activity of consumers in the lake, especially fishes.

Table 19.- Daily and annual rates of gross primary productivity (Pg) for some tropical lakes and comparative ranges for temperate lakes

Location or Lake Type	Altitude (m)	Surface Area (km^2)	Mean Depth (m)	Daily Pg (g C/m^2 day)	Annual Pg (g OM/m^2 yr)	Source
			Tropical Polymictic			
L. George, Africa	914	270	2	4-6	3,650	Dunn et al. 1969
L. Gatún, Panama	423	-	-	2.3	1,679	Gliwiz pers. comm; Cole 1966
			Tropical Menomictic			
L. Victoria, Africa	1,134	68,600	40	3.5	2,555	Talling 1965
L. Amatitlán, Guatemala	1,189	15.3	18.9	2[a]	1,460	Deevey 1957
L. Atitlán Guatemala	1,555	137	183	1-52	?	Dorris 1972
L. Güija, El Salvador	426	45	16.5	0.6-3.7	1,570	Deevey 1957
L. Lanao, Phillipines	702	357	60	-	1,300	Lewis 1973
			Temperate-Zone Lakes			
oligotrophic				.03-.10	14-50	Rodhe 1969
natural eutrophic				.3-1.0	150-500	Rodhe 1969
pelluted eutrophic				1.5-3.0	700-1,400	Rodhe 1969

[a] Measurement taken in 1950.

Summary Statement

In the Izabal Watershed, the transfer or flow of organic matter from the terrestrial to the aquatic ecosystem was tightly linked to the hydrologic regime. However, the flow did not perfectly parallel the movement of water because of the higher organic matter concentration that occurred at the beginning of the wet season. This initial "flushing out" of organic matter from the watershed occurred during June for the Rio Polochic, but a month later for the colored swamp waters of the delta. During these months, the waters contained far higher proportions of particulate organic matter than during the remainder of the sampling period. During this initial flushing pulse, the inflow of organic matter exceeded the outflow at the San Felipe outlet. By August, the rates of inflow and outflow began to converge and both continued to decline at the end of the sampling period. Organic matter that discharged into the western end of the lake from the Polochic Delta accounted for approximately 90% of the organic detritus contributed by runoff. No correlation was observed between organic matter (COD) concentration and respiration rates (BOD) of any of the inflowing or lake waters.

Gross primary productivity (Pg) by phytoplankton represented the major source of organic matter for the lake, and the efficiency of Pg to total solar radiant energy ranged between 0.23 and 1.28%. Whereas Pg remained relatively constant throughout most of the sampling period, respiration in the water column was relatively low during the dry-season months compared to respiration rates that followed the onset of the wet season. The resulting balance of Pg and respiration (e.g. net primary production) was positive during the dry season, and became increasingly negative during the wet season.

Respiration by the bottom muds was approximately one-tenth the rate of planktonic respiration per unit area of lake. Thus it represented an important sink for organic matter, as might be expected in a shallow lake. The particulate component of benthic organic matter may have been an important source of energy for activity in the muds. Over half of the organic matter contributed by the Rio Polochic in June was of the particulate fraction, yet it did not appear to measureably increase the particulate fraction in the lake samples during June or the months that followed Figure 34d). The disappearance of particulate matter would have been, by inference, from the water column to the bottom muds through sedimentation. The profile-bound density current of the Rio Polochic outfall may have served to isolate the particulate matter from the overlying waters and thus facilitated its sedimentation.

The primary productivity of Lake Izabal was within the range of polluted eutrophic temperate lakes, but below the productivity of many tropical lakes. The replacement of a large portion of the lake water by high-turbidity runoff water possibly reduced transparency sufficiently such that the primary productivity did not approach the maximum theoretically possible for planktonic systems.

Data are lacking to help determine the direct causal effects which resulted in a net positive balance of energy during the dry season and its apparent consumption during the following wet season. However, these seasonal pulses of production and consumption suggest a mechanism by which the Lake Izabal ecosystem, and perhaps other similarly structured ecosystems, can achieve a steady-state balance of organic matter storage.

CONCLUSIONS

In the preceding chapters it has become clearly apparent that Lake Izabal is not an isolated ecosystem, but a unit of a larger ecosystem by virtue of flows that couple it with the upstream watershed and the downstream marine environment. The overriding force that controls this coupling is the hydrologic regime, whose seasonality is responsible for the pulses and oscillations characteristic of the ecosystem.

By determining the relationship between different components (subsystems) of the Izabal Watershed, one can assign distinguishing features, or attributes, that make this ecosystem distinct from others. It follows that any implications of the study for ecosystem management may be applicable to other ecosystems with similar attributes and vice versa. The following are attributes that seem to be of importance for characterizing the Izabal Watershed:

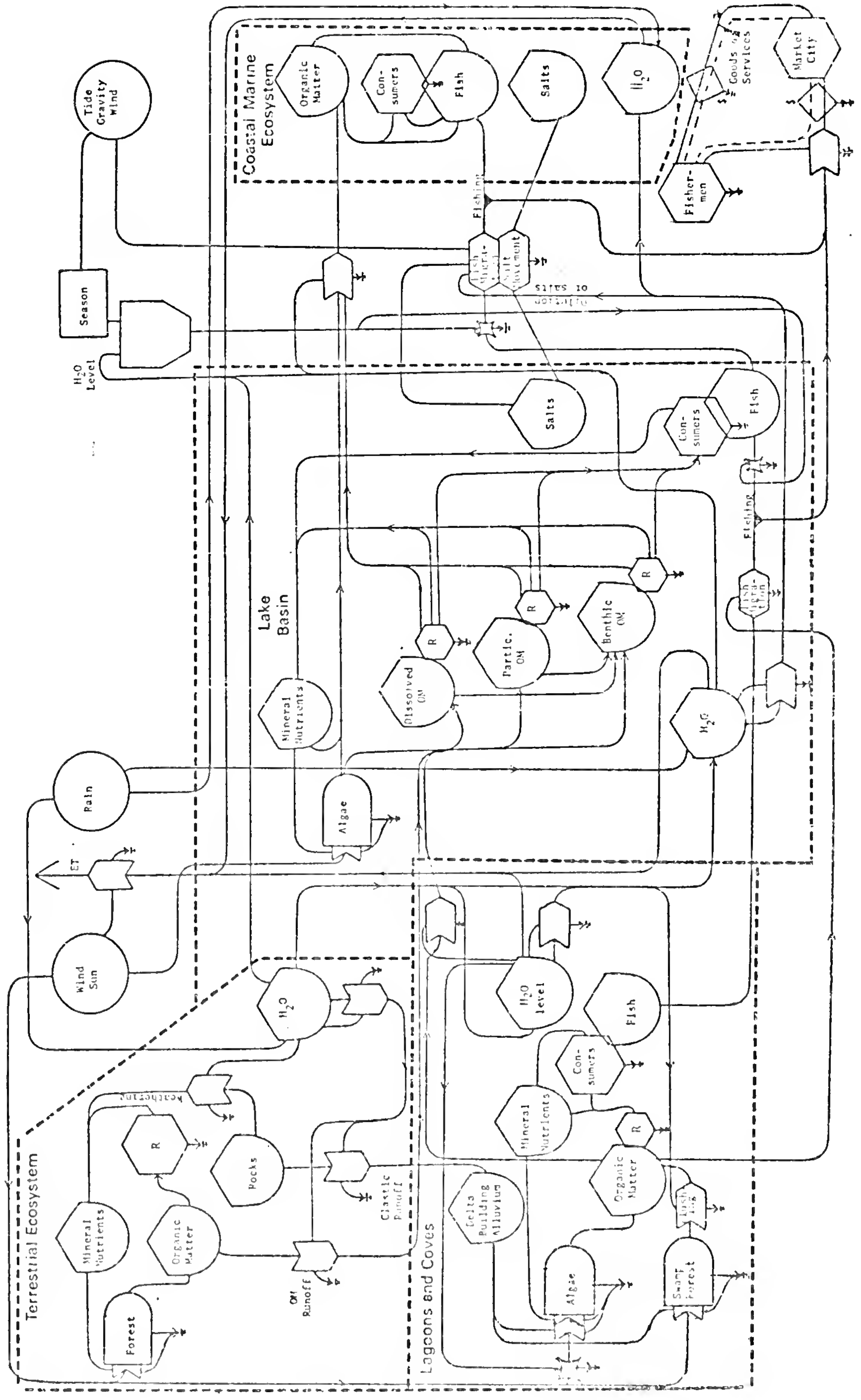
(1) The ecosystem possesses a seasonal pulse of organic detritus movement.

(2) The lacustrine component of the watershed experiences oscillations in food concentration and consumer activity.

(3) The connection of the lake to a marine environment provides easy access for euryhaline marine fishes that can adapt to fresh-water conditions.

These attributes are illustrated in Figure 46 as storages and flows of energy and matter between the subsystems of the Izabal Watershed. The

Figure 46.- Summary diagram of energy and matter flows and storages that characterize the Izabal Watershed.



Tide Gravity Wind
Coastal Marine Ecosystem
Organic Matter
Con-sumers
Fish
Salts
H_2O
Goods & Services
Market City
Fisher-men
Fishing
Salt Movement
Season
H_2O Level
Lake Basin
Salts
Con-sumers
Fish
Fishing
R
Benthic OM
Partic. OM
Dissolved OM
Mineral Nutrients
H_2O
Rain
Algae
ET
Wind Sun
H_2O
Terrestrial Ecosystem
R
Rocks
Mineral Nutrients
Organic Matter
Forest
OM Runoff
Clastic Runoff
Lagoons and Coves
H_2O level
Fish
Con-sumers
Mineral Nutrients
R
Organic Matter
Delta Building Alluvium
Algae
Swamp Forest

energy diagram is representative of the regional situation before the additional influences of modern agricultural and industrial man. The four main subsystems are (1) the terrestrial ecosystem (watershed), (2) the lagoons and coves in the Polochic Delta, (3) the main basin of Lake Izabal, and (4) the coastal marine ecosystem. The forcing functions that provide the energy for ecosystem power, maintenance, and inter-subsystem coupling are (1) sun and wind which drive primary productivity and evapotranspiration, (2) rainfall, which in connection with seasonality, controls the hydrologic regime and water movement, and (3) tide, gravity, and wind whose seasonal regimes act with water level to control fish migration and salt water movement from the coastal marine ecosystem.

Terrestrial ecosystem material exports to the lagoons and coves and the lake basin are carried by the energy provided by the downhill flow of water. Exports from the lagoons and coves to the lake basin include organic matter originating in the swamp forest of the delta region as well as organic matter from algal production. These exports occur in proportion to the water level of the lagoons and coves.

The lake basin not only receives inputs from upstream ecosystems, but also receives salts and fish from the coastal marine ecosystems. Many of the internal flows and storages of the lake have already been discussed. Fishermen take advantage of the seasonal migration of fish which is possibly stimulated by factors such as salt-water movement, water levels, and other seasonal phenomena, especially the food concentration resulting from dry-season net productivity of phytoplankton in the coves and lagoons. These interactions and ecosystem attributes will be discussed in relationship to their ecological implications for the aquatic ecosystem.

Seasonal Pulse of Organic Detritus Movement

It was shown that nearly half of the total organic detritus movement from the watershed to the lake occurred during 3 months, or just one-fourth of the year. The timing of this event coincided with the transition from a positive balance of gross primary production and respiration, to a negative balance. Although there was no direct evidence to demonstrate that this transition was a result of increased organic matter input to the lake, the change from an autotrophic ($P/R > 1$) to a heterotrophic ($P/R < 1$) balance suggests that it was at least a seasonal phenomenon associated with the hydrologic regime.

Rates of gross primary productivity remained nearly constant during the dry season and continued at nearly a constant rate during the initial months of the wet season. Thus the change from a P/R ratio of greater than unity to a P/R ratio of less than one was due to an increase in respiration rate. The wet-season inflow of allochthonous organic matter represents an auxiliary energy source for the maintenance of high respiration rates of the lacustrine ecosystem. Similarly, increased respiration rates have been documented for estuarine ecosystems during periods of increased fresh-water inflows which contain organic detritus (Cooper and Copeland 1973; Odum 1967). Lake Izabal thus has metabolic characteristics similar to shallow estuaries, although physical features such as depth and salinity may be different.

Movement of Organic Matter to Site of Consumption

The swamp forest in the Polochic Delta is the source of some of the organic detritus that is discharged into the lake. This represents a displacement from anaerobic conditions (the swamp forest) where organic matter consumption occurs slowly, to an aerobic environment (the lake) where the consumption of organic matter is more rapid and complete. Thus the physical flushing of the swamp forest is a mechanism that prevents large accumulations and storages of energy.

The movement of organic matter from other regions of the watershed occurs in two phases. First, there is the initial flushing at the beginning of the wet season, when a high percentage of the organic detritus arrives at the lake in particulate form. Following this, the composition of influent detritus is predominately in dissolved form, and represents a more steady leakage from the terrestrial ecosystem. It is not clear whether this movement is from an environment of relatively slow organic matter consumption to a more rapid one, or to what extent metabolism that occurs in the rivers is responsible for altering the quality and quantity of detritus before it reaches the lake. In the case of the particulate detritus, the bottom muds of the lake and its associated fauna may provide conditions for the effective consumption of particulate organic matter.

By dividing the total annual OM runoff from the Izabal Watershed (163,031.25 x 10^6 g OM) by the area of the watershed (6,860 km^2) a value of 23.8 g OM/m^2 is obtained. This is well above the annual runoff of 5.3 g OM/m^2 for the Hubbard Brook Experimental Forest (Likens 1972). The higher value for the Izabal Watershed might be due to increased OM runoff from a partially deforested ecosystem. However, it is likely that terrestrial ecosystems in the humid tropics may experience more OM leakage than their temperate counterparts. Until more data on OM runoff from a broader spectrum of latitudes and rainfall regimes are available, this supposition is tentative. However, based on what is known about ecosystem strategy toward the conservation of mineral nutrients, it is unlikely that OM would be regarded a "scarce" material because of its abundance in relatively productive terrestrial ecosystems.

There is evidence in this study and others (Nelson and Scott 1962; Bormann et al. 1969) that in a given watershed OM runoff increases in greater proportion than hydrologic runoff. Thus, in an assemblage of watersheds with a gradient from low to high hydrologic runoff on an annual basis, OM runoff could be expected to increase in greater proportion than hydrologic runoff. Assuming that the OM produced in one part of a watershed is utilized or consumed in another region leads to the possibility that regional coupling mechanisms are more predominant in areas of higher hydrologic runoff, i.e. higher rainfall. The conceptual image that emerges is a region composed of a mosaic of subsystems where upstream subsystems export potential energy in the form of organic matter to the more predominately heterotrophic sybsystems downstream. The export of this energy is subsidized upstream by the weathering of rocks which yields nutrients for primary production.

Mechanisms for Steady-State Balance

According to the measurements during the sampling period, the organic matter budget shows a deficit, but his should not be interpreted to mean that the lake is a strictly "heterotrophic" ecosystem. Interpretation of the budget needs some qualification with respect to the year of study and adequacy of sampling. The hydrologic regime during 1972 was unusual due to greater than average rainfall in the region of the lake. Not only was rainfall intensity greater during the wet season, but the dry season

(<100 mm per month), which typically begins in December, did not start until March 1972. Thus, the 1972 dry season was only three months duration, while five months constitutes the average dry season (Snedaker 1970).

The balance of organic production to consumption is positive during the dry season and negative during the wet season as the data clearly demonstrate (Table 18). A year of atypical wetness, such as that experienced during the year of study, may be responsible for the "heterotrophic" character of the lake. Measurements would be required on more typical years in order to establish if the lake is characteristically heterotrophic.

Regardless of the nature of the annual balance, positive gains of organic matter during the dry season are followed by net losses during the wet season. This may be a mechanism by which the lake achieves steady state with respect to organic matter loading. Flows or sinks which prevent organic matter overloading are respiration (planktonic and benthic) and export at the lake's outlet. Lesser flows which were not measured would include the fossil sink for organic matter in the sediment of the lake and emigration of fish to the marine environment.

Positive gains in net production were probably underestimated because the intense dry-season primary productivity of the deltaic lagoons (which are some of the highest daily rates for the region) (Brinson 1973), were not calculated as part of the budget. Although these lagoons represent only a small percentage of the total surface area of the lake, their regional importance is magnified by attributes found in no other part of the Izabal Watershed.

Oscillations in Food Concentration for Consumers

As mentioned in the description of the study area, the shallow coves and lagoons of the Polochic Delta are popular areas for the activities of fishermen and fish-eating birds during the dry season. The high rates of net primary productivity and high densities of planktonic standing crop provide conditions attractive to fishes. The shallow depth relative to that of the lake basin offers the distinct advantage of reducing energy expended in feeding by concentrating the food in a compressed column of water. Dry-season activities of the consumers coincide with cloudless days which provide optimal conditions for photosynthesis and low or negligible rates of flushing during the hydrological minimum. Cichlasoma gutulatum that spawn in these shallow waters have an adaptive life cycle that entails breeding during the dry season when high planktonic densities provide a concentrated food source for their offspring. The seasonal availability of a concentrated food source in fresh-water systems could also be of selective advantage to those marine euyhaline species that can reach this energy source before runoff and flushing of the lagoons and coves dilute the accumulated organic matter by the time it reaches the sea. A similar account of seasonal food exploitation is the tismiche described by Gilbert and Kelso (1971) in the estuary at Tortuguero, Costa Rica.

Following these dry-season activities, wet-season rains flush the lagoons of their plankton with anaerobic black waters from the surrounding swamp forest, and the majority of the fish leave to become dispersed throughout the lake. The pulse is somewhat analogous to management practices used in fish pond culture, whereby ponds are periodically drained before a new crop of fish is cultivated.

Consequences of the Connection to a Marine Ecosystem

The dominance of the lake's fishery by marine fishes provides clear evidence that the Rio Dulce-El Golfete waterway has profound effects on the faunal composition of the lake. The extent to which a brackish water gradient to the lake regulates migration or facilitates the adaptation of euryhaline marine species to fresh water is probably dependent on the inherent physiological mechanisms for osmoregulation possessed by each species. However, the dry-season penetration of brackish water into the lake may serve to stimulate migration. The periodicity and intensity of migrations is an obvious research need before the fishery can be rationally managed.

There is substantial evidence for control of the Na:Cl ratio in the lake by seasonal inflow of brackish water from the sea. Regardless, the lake water did not approach oligohaline concentrations during the study period, but there is evidence that suggests salinities are higher during some years. Because of the short residence time of the water in the lake (<1 year), it would be difficult for higher salinities to escape being diluted and flushed out during the ensuing wet season. Therefore, those euryhaline species that do populate the lake must either be extremely well adapted to fresh water, or have behavioral patterns that facilitate extensive and frequent migrations to conditions of higher salinity.

Ecosystem Management

In the "Introduction," I suggested that watersheds, because of their well-defined boundaries, make conceptually attractive ecological units for demonstrating regional relationships and coupling. The Izabal Watershed has been described as one that fits this criterion and many of the mechanisms by which this ecosystem sustains or manages itself have been discussed.

Wherever man lives, he manages or manipulates ecosystems to some degree and the Izabal Watershed is no exception. There has been a long history of moderate human activity there, but the recent rate of increased development could conceivably put a strain on the free services the ecosystem provides to man without man-made reciprocal investments of energy or materials (feedback rewards).[1] The apparent decline of the fishery exemplifies this notion.

Fishery Management

In the section--"Regional Setting"--the status of the lake's fisheries was briefly described and the need for management was emphasized. In addition to the extensive management of the natural fish populations through fishing controls and regulations, intensive management methods, by means of aquaculture, deserve consideration. Where aquacultural techniques are employed successfully in other humid tropical regions (Hickling 1961), they are usually closely associated with cultural diet patterns and often accompany wetland rice cultivation. Raising fish in cages has been suggested for Lake Izabal (T.C. Dorris, personal communication), and rearing of *Cichlasoma gutulatum* fingerlings to marketable size has been tried in an enclosure near the lake's edge by one individual.

The question is not whether aquacultural techniques will work in Lake Izabal, but whether the energetic subsidies required for fish production

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[1] See H.T. Odum (1971) for a full discussion of man's partnership with nature.

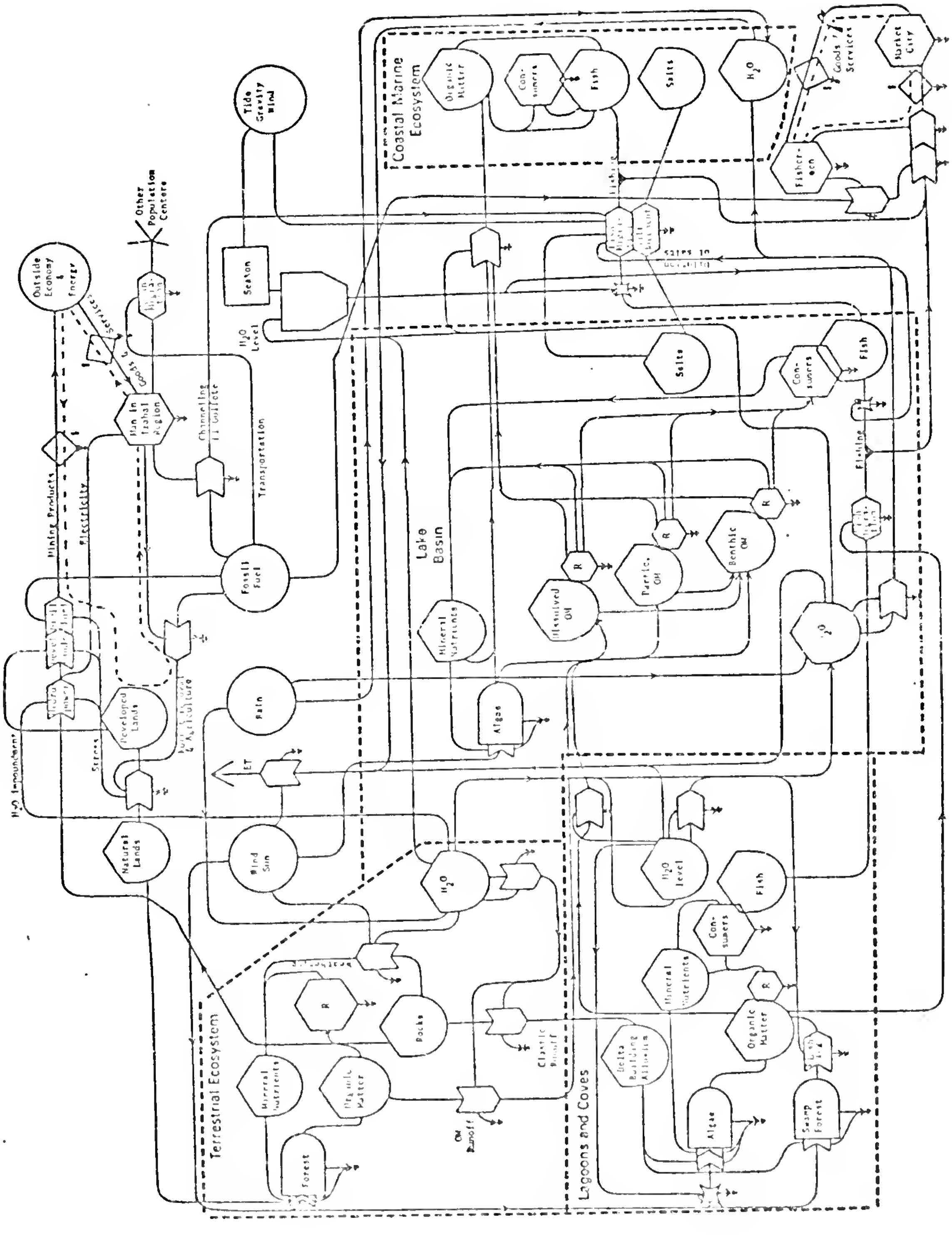
can be provided. The present fish production in Lake Izabal is provided as a free service by nature. Raising fish in cages necessitates additional energetic subsidies in equipment, feed, and human labor, not to mention possible disease control measures. Projects in which aquaculture is attempted should account for these extra costs, and balance them with the marketable value of the fish produced. At the same time these costs should be compared with the cost of extensive management techniques that would be necessary for maintaining a maximum sustained yield for the free-living fish populations.

Modern Agricultural and Industrial Man

The energy diagram in Figure 47 illustrates the possible influences and modifications that industrial and agricultural development could have in the Izabal Watershed. Additional forcing functions not included in the previous diagram (Figure 46) include fossil fuel and outside energy and economy. Supplies from outside the ecosystem, such as nylon gill nets, outboard motors, and gasoline have already increased the rate of fish removal from the aquatic ecosystem. Preliminary mining activities have stimulated immigration of people into the region and have increased the exchange of money, goods, and services. The eventual export of mining products would presumably provide capital inputs for more land development. Since the hydrologic pattern of the watershed is the overriding feature that regulates the attributes associated with special characteristics of this ecosystem, schemes that involve alteration of this pattern should receive careful study and consideration.

Two schemes for development that could potentially alter hydrologic patterns are (1) impoundment of water in the Polochic Valley for hydropower

Figure 47.- Summary diagram of energy and matter flows and storages of the Izabal Watershed which includes some of the possible influences of development by modern agricultural and industrial man.


Outside Economy & Energy
Other Population Centers
Tide Gravity Wind
Coastal Marine Ecosystem
Organic Matter
Con-sumers
Fish
Salts
Fisher-men
Goods & Services
Market City
Season
Transportation
Fossil Fuel
Mining Products
Electricity
Developed Lands
Natural Lands
Rain
Wind Sun
ET
Lake Basin
Mineral Nutrients
Algae
Dissolved OM
Benthic OM
Fishing
Terrestrial Ecosystem
Rocks
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Mineral Nutrients
Organic Matter
Forest
OM Runoff
Clastic Runoff
Lagoons and Coves
Delta Building Alluvium
Swamp Forest

and (2) channeling the shallow El Golfete to facilitate access to the lake by ships with deep draft. The first alteration might have downstream effects on the Polochic Delta. Some regions of the delta are currently growing toward the lake as determined by comparing old maps with present conditions. Entrapment of the sediment load of rivers by upstream impoundments would reduce the alluvium available for delta growth. The small embayments protected by the levees of the Polochic distributaries are the areas where high rates of primary production during the dry season provide a concentrated food source for consumers. The continued maintenance of these coves depends upon the degree to which the protective levees are dependent on sediment loads received during the wet-season flood stage of the Polochic distributaries. Also the upstream impoundments would tend to dampen oscillations between wet and dry season discharge rates. These pulses currently function as the seasonal controls on consumer activity in the lagoons and coves.

Channeling the relatively shallow El Golfete (4.5-m depth) that provides a formidable barrier to brackish water penetration may aid in dry-season movement of saline water to the lake. Water impoundment in the Polochic Valley may deter the upstream penetration of brackish water by discharging wet-season storages during the dry season. However, the effectiveness of a fresh-water current from the lake in displacing brackish water must be weighed against the opposing forces of tides, winds, and gravity that facilitate the upstream penetration of brackish water. In the event that channeling El Golfete facilitates the upstream movement of coastal waters, one can only speculate on the consequences of massive inputs of saline water into the lake. Some changes surely could be expected, and Lake Maracaibo, Venezuela may be a good model upon which to judge these effects.

Some of the basic data obtained in this study may be of use in determining the consequences of large scale hydrologic changes. Questions raised by this investigation, especially with respect to fisheries management, will require specific data for answers. However, the unknown periodicity of shallow tropical lakes referred to by Talling (1969) has been established for at least one of these lakes by demonstrating that the watershed is closely coupled with activities in the lake.

APPENDICES

Table A.- Monthly and annual rainfall for Mariscos (south shore of lake) and Las Dantas (north shore of lake) during the study period (November 1971 - October 1972). Superscripts represent the number of days of rainfall

Station	Nov 1971	Dec 1971	Jan 1972	Feb 1972	Mar 1972	Apr 1972	May 1972	Jun 1972	Jul 1972	Aug 1972	Sep 1972	Oct 1972	12-Month Total
Mariscos	^{14}395	^{11}126	^{10}179	^{12}170	^{6}134	^{4}78	^{4}21	^{18}284	^{27}544	^{20}630	^{24}298	^{20}377	^{170}3,236
Las Dantas	^{16}293	^{11}81	^{12}118	^{14}37	^{8}55	^{8}59	^{3}37	^{25}309	^{28}309	^{23}426	^{24}253	^{22}233	^{194}2,210
Average	^{15}344.0	^{11}103.5	^{11}148.5	^{13}103.5	^{7}94.5	^{6}68.5	$^{3.5}$29.0	$^{21.5}$296.5	$^{27.5}$426.5	$^{21.5}$528.0	^{24}275.5	^{21}305.0	^{182}2,723

Table B.- Average annual rainfall, the annual maximum, and rainfall during the study period (November 1971 - October 1972) for the Polochic Valley and surrounding areas[a]

Station	Average Annual Rainfall (mm)	Years Recorded	Maximum Rainfall (mm)	Year of Maximum Rainfall	Rainfall (mm) During Study Period
El Porvenir	2,963	1966-69	3,240	1968	3,473.0
Cobán	2,057	1971-72	2,184	1972	2,186.2
Chilascó	1,724	1960-69	2,026	1967	1,450.3
Cahabón	2,462	1960,62,65,66	3,381	1966	-
Argentina	3,234	1960-69	3,657	1962	3,131.0
Mocca	4,001	1960-69	4,488	1966	3,986.5
Seamay	3,990	1960-69	4,462	1966	4,175.5
San Juan	3,836	1967-69	6,128	1969	4,890.3
Constancia	2,625	1960-69	3,099	1960	3,171.1
Cabañas	2,618	1960-69	3,054	1962	2,523.0

[a] Data were provided by the Observatorio Nacional, Guatemala.

Table C.- Cross-sectional areas, velocities, and monthly discharges for the major influent rivers sampled

Sampling Date	Cross-Sectional Area (m^2)	Maximum Velocity (m/sec)	Maximum Discharge (m^3/sec)	Average[a] Discharge (m^3/sec)	Monthly[b] Discharge ($m^3 \times 10^6$)
		Comercio (Polochic)			
4 Nov 71	119	0.538	64.02	51.22	132.76
30 Nov 71	124	0.699	86.68	69.34	179.73
27 Dec 71	119	0.447	53.19	42.55	110.30
31 Jan 72	120	0.458	54.96	43.97	113.97
10 Mar 72	114	0.263	29.98	23.99	62.17
11 Apr 72	118	0.169	19.94	15.95	41.35
16 May 72	116	0.222	25.75	20.60	53.40
7 Jun 72	120	0.685	82.20	65.76	170.45
11 Jul 72	127	0.736	93.47	74.78	193.82
4 Aug 72	147	0.237	34.84	27.87	72.24
29 Sep 72	131	0.658	86.20	68.96	178.74
23 Oct 72	127	0.729	92.58	74.07	199.98
		Cobán (Polochic)			
2 Nov 71	234	0.870	203.58	162.86	422.14
1 Dec 71	238	1.007	239.67	191.73	496.97
29 Dec 71	232	0.676	156.83	125.47	325.21
29 Jan 72	235	0.793	186.36	149.08	386.43
10 Mar 72	226	0.357	80.68	64.55	167.30
11 Apr 72	231	0.260	60.06	48.05	124.54
16 May 72	230	0.393	90.39	72.31	187.43
7 Jun 72	239	0.956	228.48	182.79	473.78
11 Jul 72	245	0.998	244.51	195.61	507.02
29 Sep 72	251	0.892	223.89	179.11	464.26
21 Oct 72	246	1.106	272.08	217.66	564.18
		Bujajal (Polochic)			
2 Nov 71	137	0.797	109.19	87.35	226.41
1 Dec 71	140	0.981	137.34	109.87	284.79
29 Dec 71	136	0.635	86.36	69.09	179.08
29 Jan 72	137	0.770	105.49	84.39	218.74
10 Mar 72	131	0.375	49.13	39.30	101.87
11 Apr 72	136	0.279	37.94	30.36	78.68
16 May 72	134	0.413	55.34	44.27	114.76
7 Jun 72	139	1.147	159.43	127.55	330.60
11 Jul 72	147	0.906	133.18	106.55	276.17
4 Aug 72	165	0.458	75.57	60.46	156.70
29 Sep 72	149	0.469	69.88	55.90	144.91
22 Oct 72	146	1.068	155.93	124.74	323.33

Table C.- continued

Sampling Date	Cross-Sectional Area (m^2)	Maximum Velocity (m/sec)	Maximum Discharge (m^3/sec)	Average Discharge[a] (m^3/sec)	Monthly Discharge[b] ($m^3 \times 10^6$)
		Rio Oscuro			
3 Nov 71	258	0.168	43.34	34.68	89.88
30 Nov 71	266	0.521	138.59	110.87	287.37
27 Dec 71	257	0.076	19.63	15.63	40.50
31 Jan 72	257	0.111	28.53	22.82	59.15
10 Mar 72	252	0.079	19.91	15.93	41.28
11 Apr 72	257	0.064	16.45	13.16	34.11
16 May 72	-	0.0	0.0	0.0	0.0
7 Jun 72	-	0.0	0.0	0.0	0.0
6 Jul 72	270	0.508	137.16	109.73	284.4
11 Jul 72	272	0.648	176.26	141.00	365.48
4 Aug 72	302	0.952	287.50	230.00	596.17
29 Sep 72	276.6	0.606	167.62	134.10	347.58
21 Oct 72	268.6	0.342	91.86	73.49	190.48
23 Oct 72	268.9	0.346	93.04	74.43	192.93
		Rio Sauce			
5 Nov 71	39.2	0.010	0.39	0.314	0.81
1 Dec 71	39.2	0.349	13.68	10.94	28.37
28 Mar 72	-	0.0	0.0	0.0	0.0
21 Apr 72	-	0.0	0.0	0.0	0.0
19 May 72	-	0.0	0.0	0.0	0.0
9 Jun 72	42.9	0.143	6.13	4.91	12.72
29 Jul 72	45.1	0.965	43.52	34.82	90.25
21 Aug 72	52.3	0.622	32.53	26.02	67.46
1 Oct 72	39.2	0.368	14.43	11.54	29.91
26 Oct 72	38.2	0.331	12.64	10.12	26.22
		Rio San Marcos			
28 Mar 72	13.9	0.199	2.766	2.213	5.74
21 Apr 72	13.8	0.381	5.258	4.206	10.90
19 May 72	13.9	0.110	1.529	1.223	3.17
9 Jun 72	15.8	0.211	3.334	2.667	6.91
29 Jul 72	17.7	0.546	9.664	7.731	20.04
21 Aug 72	19.3	0.071	1.370	1.096	2.84
5 Oct 72	15.9	0.498	7.918	6.335	16.42
26 Oct 72	15.0	0.545	8.175	6.540	16.95

[a] Maximum discharge was multiplied by a factor of 0.8 to give average discharge to correct for friction (Welch, 1948).

[b] Monthly discharge was calculated from average discharge by multiplying by a factor of 2.592×10^6 (number of seconds per month).

Table D.- Weekly and monthly averages of lake level at Las Dantas, relative to the lowest weekly average during March 1972. All numbers are centimeters and weekly averages represent 4-7 days of measurement

	Nov 1971	Dec 1971	Jan 1972	Feb 1972	Mar 1972	Apr 1972	May 1972	Jun 1972	Jul 1972	Aug 1972	Sep 1972	Oct 1972
First Week	16.8	17.9	11.4	8.9	6.2	18.6	4.6	8.2	39.2	105.7	68.0	34.2
Seccnd Week	21.0	17.9	8.2	8.2	0.0	12.0	7.2	18.2	42.6	93.2	54.9	27.6
Third Week	15.4	12.3	12.8	10.4	5.8	7.2	6.2	18.0	38.6	100.3	53.2	34.7
Fourth Week	37.3	13.4	15.0	2.6	5.9	8.0	2.6	12.0	55.2	90.6	55.8	-
Monthly Average	22.6	15.4	11.9	7.5	4.5	11.5	5.2	14.1	43.9	97.5	58.0	32.2

Table E.- Concentrations of dissolved minerals[a] of water samples collected from the Lake Izabal - Rio Dulce ecosystem. The April samples were collected during the dry season and the October samples during the wet season

Station	Ca	Mg	Na	Si	K	Mn	Cl	Fe	NO_3	P	Zn	Ni
14 April 1972												
Rio Zarquito	22.0	11.1	1.6	14.0	0.3	-	2.6	0.05	2.2	.10	-	-
Oscuro Bay	21.1	8.3	4.8	8.0	0.6	-	11.5	-	4.2	.165	.01	.05
Amatillo	23.0	7.85	3.4	4.5	0.7	.066	8.2	0.05	6.6	.05	.01	-
Comercio	30.5	10.2	3.1	13.0	0.5	-	4.9	-	1.45	.075	.01	-
El Padre Creek	23.5	8.45	4.1	9.0	0.6	.033	12.0	0.05	2.9	.110	.01	-
Ensenada El Padre	25.0	8.3	4.1	7.0	0.5	-	9.2	0.05	1.55	.175	.01	-
Cobán	30.3	10.2	3.1	14.0	0.5	-	4.5	-	1.85	.065	.01	.05
Bujajal	30.5	10.0	3.1	11.0	0.5	-	1.9[b]	-	<0.62	.055	-	.05
Ancha	27.3	8.8	4.5	9.0	0.6	-	6.4	-	<0.62	.040	.01	-
Lagartos	26.0	9.0	4.1	8.0	0.5	-	6.0	-	<0.62	.065	-	-
Station A, S	24.0	8.0	4.5	10.0	0.5	-	7.8	-	<0.62	.055	-	-
Station A, 11.5m	24.0	7.95	4.3	11.0	0.6	-	8.2	-	<0.62	.040	.01	.05
Station B, S	23.9	7.85	4.3	11.0	0.5	-	8.8	-	<0.62	.050	.01	-
Station B, 15m	23.9	7.95	4.3	10.0	0.5	-	8.8	0.05	1.1	.065	.01	.05
Station C, S	23.5	7.95	4.3	11.0	0.6	-	8.2	0.05	<0.62	.055	.01	.05
Station C, 12.5m	23.5	8.1	8.2	12.0	1.7	-	10.5	0.05	<0.62	.075	.01	.05
San Marcos	17.2	3.65	3.1	10.0	0.4	.033	4.1	0.15	<0.62	.075	.01	-
San Felipe, S & 13m	23.5	8.3	7.7	10.0	0.7	-	15.55	0.05	<0.62	.055	.01	-
Manacas Creek	9.0	25.75	2.2	34.0	0.3	-	6.8	0.05	0.86	.065	.01	-
Agua Caliente	71.0	30.75	6.4	36.0	0.7	-	7.5	-	1.6	.040	-	-
Rio Sauce	14.5	20.0	3.5	33.0	0.4	-	4.9	-	<0.62	.075	.01	-
23 October 1972												
Rio Oscuro	18.7	7.0	1.9	8.0	0.5	.033	1.85	0.4	<0.62	.085	.01	-
Rio Zarquito	23.9	12.0	1.4	12.0	0.2	.033	<1.0	0.10	0.86	.065	.01	.05
Oscuro Bay	18.0	6.9	2.5	11.0	0.5	-	17.0[b]	0.10	0.86	.055	.01	-
Amatillo	29.0	7.0	2.2	14.0	0.4	.033	<1.0	0.25	<0.62	.055	-	-

Table E.- continued

Station	Ca	Mg	Na	Si	K	Mn	Cl	Fe	NO_3	P	Zn	Ni
Comercio	29.5	6.6	1.9	13.0	0.4	-	<1.0	0.05	<0.62	.125	-	-
Padre Creek	25.5	7.2	2.8	12.0	0.4	.033	4.2	0.20	<0.62	.055	.02	-
Ensenada El Padre	15.0	7.15	3.0	11.0	0.5	-	1.4	0.05	0.86	.055	.01	.05
Cobán	29.5	6.6	2.2	13.0	0.4	-	<1.0	0.05	<0.62	.05	.01	-
Bujajal	29.0	6.7	2.0	12.0	0.4	.033	1.7	0.05	1.10	.05	.01	-
Ancha	30.5	7.6	2.2	14.0	0.6	-	1.2	0.10	<0.62	.05	.01	.05
Lagartos	27.0	10.6	2.5	18.5	0.6	.066	4.4	0.20	<0.62	.085	.02	-
Station A, S	22.0	7.7	3.3	14.0	0.5	-	4.1	0.05	<0.62	.025	.01	-
Station A, 12m	27.2	8.2	3.2	14.0	0.7	-	2.4	0.05	<0.62	.055	.01	.05
Station B, S	22.0	7.3	3.5	14.0	0.5	-	6.0	0.05	<0.62	.055	-	-
Station B, 15.5m	26.5	7.6	2.7	13.0	0.5	.033	1.6	0.05	0.94	.110	-	.05
Station C, S	21.5	7.3	3.6	13.0	0.6	-	5.5	0.05	<0.62	.055	.01	-
Station C, 12m	21.1	7.4	3.6	14.0	0.6	-	6.4	0.05	0.76	.05	-	-
San Marcos	15.0	3.15	3.3	11.0	0.3	-	2.7	0.20	<0.62	.04	.01	-
San Felipe	21.5	7.2	3.7	14.0	0.4	-	4.6	0.0	<0.62	.05	.01	-
Manacas Creek	18.5	15.5	3.3	20.5	0.5	-	3.4	0.10	0.86	.055	.01	-
Agua Caliente	44.5	23.25	3.7	38.0	0.3	-	6.4	0.05	2.75	.025	-	-
Rio Sauce	9.5	25.25	2.6	48.0	0.3	-	4.1	0.05	1.25	.040	.01	.05
Amatique Bay[c]	36.8	53.0	380.0	11.0	15.7	-	600.0	0.0	8.5[b]	.05	.01	-
Rio Dulce - Salt Spring[c]	47.0	10.6	57.0	6.5	2.6	-	110.0	0.10	2.7[b]	.10	.01	.05

[a] Water samples filtered through a 0.45 μ-pore membrane filter.

[b] Anomalous concentrations that are suspected to be in error.

[c] Collection date - October 19, 1972.

Table F-1.- Monthly concentrations of organic matter (mg COD/liter) for dark-water rivers originating in the deltaic swamp created by the Rio Polochic[a]

Month	Rio Oscuro Depth (m)	Rio Oscuro Total (mg COD/liter)	Rio Oscuro Dissol. (mg COD/liter)	Rio Oscuro Part. (mg COD/liter)	Rio Oscuro Net (mg COD/liter)	Amatillo Depth (m)	Amatillo Total (mg COD/liter)	Amatillo Dissol. (mg COD/liter)	Amatillo Part. (mg COD/liter)	Amatillo Net (mg COD/liter)	El Padre Creek Depth (m)	El Padre Creek Total (mg COD/liter)	El Padre Creek Dissol. (mg COD/liter)	El Padre Creek Part. (mg COD/liter)	El Padre Creek Net (mg COD/liter)
Mar	S	16.66	-	-	.008	S	26.57	-	-	.338	S	20.48	-	-	.055
	5	9.44	-	-		3	29.57	-	-		2	18.29	-	-	
Apr	S	22.12	23.09	-	.011	S	30.98	29.49	1.49	.582	S	15.04	14.45	0.59	.092
	5	10.77	13.00	-		3	32.50	33.95	-		2	15.91	13.00	2.91	
May	S	9.78	7.95	1.83	.141	S	24.42	19.34	5.08	1.638	S	11.69	9.61	2.08	.967
	5	5.78	4.45	1.33											
Jun	S	10.41	7.55	2.86	.051	S	21.64	17.18	4.46	.675	S	11.21	8.66	2.55	.153
	5	7.23	5.08	2.15											
Jul	S	62.80	52.90	9.90	.076	S	54.05	51.74	2.31	.076	S	46.30	26.66	19.64	.127
	5	63.13	51.91	11.22											
Aug	S	20.54	18.78	1.76	.045	S	10.75	12.68	-	.087	S	12.20	12.36	-	.003
Oct 1	S	16.38	14.09	2.29	.019	S	9.22	8.05	1.17	.013	S	13.81	13.44	0.37	.004
Oct 23	S	16.26	15.86	0.40											

[a] The four fractions represent Total COD, Dissolved COD (<0.80μ), Particulate COD (>0.80μ), and Net Particulate COD (>76μ).

Table F-2.- Monthly concentrations of organic matter (mg COD/liter) for the large distributaries of the Rio Polochic[a]

	Comercio					Cobán					Bujajal				
		mg COD/liter					mg COD/liter					mg COD/liter			
Month	Depth (m)	Total	Dissol.	Part.	Net	Depth (m)	Total	Dissol.	Part.	Net	Depth (m)	Total	Dissol.	Part.	Net
Mar	S	5.78	-	-	.005	S	6.27	-	-	.004	S	5.13	-	-	.006
	5	6.19	-	-		5	4.97	-	-		5	7.32	-	-	
Apr	S	4.66	5.53	-	.008	S	6.31	6.01	.30	.004	S	6.89	7.18	-	.014
	5	6.89	7.95	-		5	4.76	6.89	-		5	6.12	6.11	.01	
May	S	7.70	6.03	0.67	.117	S	7.28	5.70	1.58	.119	S	7.61	7.03	0.58	.130
Jun	S	21.32	4.68	16.64	.338	S	26.73	7.63	19.10	.660	S	27.76	6.27	21.49	.520
Jul	S	12.47	9.57	2.90	.136	S	12.97	9.08	3.89	.257	S	14.12	7.43	6.69	.308
Aug	S	11.07	10.59	0.48	.041	S	7.54	6.90	0.64	.711	S	8.51	7.38	1.13	.034
Oct 1	S	8.25	3.94	4.31	.626	S	7.20	3.46	3.74	.232	S	6.88	3.54	3.34	.343
Oct 23						S	5.70	3.13	2.57						

[a] The four fractions represent Total COD, Dissolved COD ($<0.80\mu$), Particulate COD ($>0.80\mu$), and Net Particulate COD ($>76\mu$).

Table F-3.- Monthly concentrations of organic matter (mg COD/liter) for small rivers of the lake basin

	San Marcos mg COD/liter				Rio Sauce mg COD/liter				Manacas Creek mg COD/liter				Rio Tunico mg COD/liter			
Month	Total	Dissol.	Part.	Net	Total	Dissol.	Part.	Net	Total	Dissol.	Part.	Net	Total	Dissol.	Part.	Net
Mar	4.89	5.51	-	.005	7.80	5.93	1.87	.006	8.63	7.49	1.14	.024				
Apr	7.90	4.50	3.40	.041	6.90	6.80	0.10	.008	6.60	6.00	0.60	.007				
May	5.52	5.43	0.09	.004	8.76	7.14	0.62	.040	6.57	6.09	0.48	.009				
Jun	7.26	5.46	1.81	.008	21.00	17.86	3.14	.065	7.97	7.18	0.79	.003				
Jul	13.40	4.04	9.36	.521	24.06	14.21	9.85	>3.182	10.17	12.76	-	.158				
Aug 4	-	-	-	-	6.74	7.06	-	.010	-	-	-	-				
Aug 21	16.85	2.65	14.20	.153	15.29	11.86	3.43	.291	10.45	8.42	2.03	.030	8.27	7.33	0.94	.064
Oct 1	3.69	3.41	0.28	.097	5.03	4.83	0.20	.023	8.51	8.19	0.32	.010	6.91	6.34	0.57	-

[a] The four fractions represent Total COD, Dissolved COD (<0.80μ), Particulate COD (>0.80μ), and Net Particulate COD (>76μ).

Table F-4.- Monthly concentrations of organic matter (mg COD/liter) for lake Stations A, B, and C[a]

	Station A					Station B					Station C				
		mg COD/liter					mg COD/liter					mg COD/liter			
Month	Depth (m)	Total	Dissol.	Part.	Net	Depth (m)	Total	Dissol.	Part.	Net	Depth (m)	Total	Dissol.	Part.	Net
Mar	S	8.63	6.86	1.77	.079	S	8.42	7.59	0.83	.043	S	8.63	7.18	1.45	.094
	11					14	13.42	7.49	5.93		11				
Apr	S	7.90	6.40	1.50	.112	S	7.80	6.90	0.90	.071	S	7.80	6.80	1.00	.053
	11					14					11				
May	S	7.33	6.00	1.33	.116	S	7.90	6.38	1.52	.200	S	7.14	5.33	1.81	.051
	11					14	8.28	6.38	1.90		11				
Jun	S	7.97	6.55	1.42	.126	S	7.58	6.55	1.03	.085	S	9.93	9.38	0.55	.099
	11					14	8.36	7.58	0.78		11				
Jul	S	12.07	10.77	1.30	.139	S	10.04	9.23	0.81	.095	S	9.48	9.23	0.25	.077
	11					14					11				
Aug	S	10.53	9.59	0.95	.092	S	10.92	9.36	1.56	.111	S	9.98	7.64	2.34	.066
	11					14	10.37	8.50	1.87		11				
Oct 1	S	-	7.19	-	.059	S	9.15	7.67	1.48	.069	S	7.39	7.19	0.20	.045
	11					14	6.75	6.06	0.69		11				
Oct 23	S	11.18	9.14	2.04											
	11														

[a] Where two depths are indicated but only one set of determinations reported, analysis was made on a mixture of samples from two depths. The four fractions represent Total COD, Dissolved COD (<0.80μ), Particulate COD (>0.80μ), and Net Particulate COD (>76μ).

Table F-5.- Monthly concentrations of organic matter (mg COD/liter) for the San Felipe outflow[a]

		mg COD/liter			
Month	Depth (m)	Total	Dissol.	Part.	Net
Mar	S 10	8.63	7.38	1.25	.023
Apr	S 10	9.00	8.60	0.40	.030
May	S 10	9.62	8.09	1.53	.021
Jun		-	-	-	.047
Jul	S 10	8.67	7.78	0.89	.081
Aug	S 10	10.37	8.81	1.56	.058
Oct	S 10	7.55	7.27	0.28	.057

[a] Where two depths are indicated but only one set of determinations reported, analysis was made on a mixture of samples from two depths. The four fractions represent Total COD, Dissolved COD (<0.80μ), Particulate COD (>0.80μ), and Net Particulate COD (>76μ).

Table F-6.- Net particulate organic matter concentrations (mg COD/liter) for December 1971, January 1972, and February 1972, when other values were not obtained

Station	Net Particulate (mg COD/liter)		
	Dec	Jan	Feb
Oscuro	.013 .018 .017		.033
Amatillo	.046		.037
Padre Creek	.004		
Comercio	.024		.121
Cobán	.103		.119
Bujajal	>.170		.186
Station A	.024	.048	.106
Station B		.038	.029
Station C		.050	.049
San Felipe	.009	.033	.070

Table G.- Concentrations of chemical oxygen demand (COD) fractions and the monthly flow of COD fractions as calculated from the discharge rates of the major rivers, north and south watershed areas, and the San Felipe outflow. The average COD concentrations for Stations A, B, and C were converted to the amounts below one m^2 of lake surface[a]

	mg COD/liter				Discharge	g COD x 10^6/month			
Date	Total	Dissol.	Part	Net Part.	($m^3 \times 10^6$/month)	Total	Dissol.	Part.	Net Part.
					Comercio (Polochic)				
10 Mar	5.99	-	-	0.0050	62.2	372.6	-	-	0.311
11 Apr	5.78	-	-	0.0082	41.4	239.3	-	-	0.339
16 May	7.70	6.03	0.67	0.1171	53.4	411.2	322.0	35.8	6.253
7 Jun	21.32	4.68	16.64	0.3384	170.5	3,635.1	797.9	2,837.1	57.70
11 Jul	12.47	9.57	2.90	0.1363	193.8	2,416.7	1,854.7	562.0	26.41
4 Aug	11.07	10.59	0.48	0.0409	290.0	3,210.3	3,071.1	139.2	11.86
1 Oct	8.25	3.94	4.31	0.6255	200.0	1,650.0	788.0	862.0	125.10
					Cobán (Polochic)				
10 Mar	5.62	-	-	0.0041	167.3	940.2	-	-	0.686
11 Apr	6.31	6.01	0.30	0.0039	124.5	785.6	748.2	37.35	0.486
16 May	7.28	5.70	1.58	0.1186	187.4	1,364.3	1,068.2	296.1	22.23
7 Jun	26.73	7.63	19.10	0.6604	473.8	12,664.7	3,615.1	9,049.6	312.9
11 Jul	12.97	9.08	3.89	0.2567	507.0	6,575.8	4,603.6	1,972.2	130.1
4 Aug	7.54	6.90	0.64	0.7112	815.0	6,145.1	5,623.5	(521.6)	579.6
1 Oct	7.20	3.46	3.74	0.2321	464.3	3,343.0	1,606.5	1,736.5	107.8
23 Oct	5.70	3.13	2.57	0.2226	564.2	3,215.9	1,765.9	1,450.0	125.59

Table G.- continued

Date	mg COD/liter Total	Dissol.	Part.	Net Part.	Discharge ($m^3 x 10^6$/month)	g COD x 10^6/month Total	Dissol.	Part.	Net Part.
					Bujajal (Polochic)				
10 Mar	6.23	-	-	0.0058	101.9	634.8	-	-	0.591
11 Apr	6.51	-	-	0.0136	73.7	512.3	-	-	1.070
16 May	7.61	7.03	0.58	0.1295	114.8	873.6	807.0	66.58	14.87
7 Jun	27.76	6.27	21.49	0.5204	330.6	9,177.5	2,072.9	7,104.6	172.0
11 Jul	14.12	7.43	6.69	0.3075	276.2	3,899.9	2,052.2	1,847.8	84.93
4 Aug	8.51	7.38	1.13	0.0344	538.0	4,578.4	3,970.4	607.9	18.51
1 Oct	6.88	3.54	3.34	0.3426	323.3	2,224.3	1,144.5	1,079.8	110.8
					Rio Oscuro				
10 Mar	16.66	-	-	0.0084	41.3	688.1	-	-	0.347
11 Apr	22.61	-	-	0.0110	34.1	771.0	-	-	0.375
16 May	9.78	7.95	1.83	0.1406	0.0	-	-	-	-
7 Jun	10.41	7.55	2.86	0.0511	0.0	-	-	-	-
11 Jul	62.97	52.41	10.56	0.0757	324.9	20,459.0	17,028.0	3,430.9	24.59
4 Aug	20.54	18.78	1.76	0.0448	596.2	12,245.9	11,196.6	1,049.3	26.71
1 Oct	16.38	14.09	2.29	0.0189	347.6	5,693.7	4,897.7	796.0	6.57
23 Oct	16.26	15.86	0.40	0.0821	191.7	3,117.0	3,040.4	76.68	15.74

Table G.- continued

Date	mg COD/liter Total	Dissol.	Part.	Net Part.	Discharge (m^3x10^6/month)	g COD x 10^6/month Total	Dissol	Part.	Net Part.
					Rio Amatillo				
10 Mar	28.07	-	-	0.3380					
11 Apr	31.74	-	-	0.5824					
16 May	24.42	19.34	5.08	1.638					
7 Jun	21.64	17.18	4.46	0.6753					
11 Jul	54.05	51.74	2.31	0.0761	153.5	8,296.7	7,942.1	354.6	11.68
4 Aug	12.68	-	-	0.0868	571.3	7,244.1	-	-	49.59
1 Oct	9.22	8.05	1.17	0.0129	108.5	1,000.4	873.4	126.9	1.400
					Rio Sauce				
28 Mar	7.80	5.93	1.87	0.0060	0.0	-	-	-	-
21 Apr	6.90	6.80	6.10	0.0077	0.0	-	-	-	-
19 May	8.76	7.14	0.62	0.0403	0.0	-	-	-	-
9 Jun	21.00	17.86	3.14	0.0649	12.7	266.7	226.8	39.9	0.824
29 Jul	24.06	14.21	9.85	3.1824	90.3	2,172.6	1,283.2	889.5	287.4
4 Aug	6.74	-	-	0.0100	67.5	455.0	-	-	0.675
21 Aug	15.29	11.86	3.43	0.2905	29.9	457.2	354.6	102.6	8.691
1 Oct	5.03	4.83	0.20	0.0229	26.2	131.8	126.5	5.24	0.600

Table G.- continued

Date	mg COD/liter				Discharge ($m^3 x 10^6$/month)	g COD x 10^6/month			
	Total	Dissol.	Part.	Net Part.		Total	Dissol.	Part.	Net Part.
					Rio San Marcos				
28 Mar	4.89	-	-	0.0054	5.7	27.87	-	-	0.031
21 Apr	7.90	4.50	3.40	0.0405	10.9	86.11	49.05	37.06	0.441
19 May	5.52	5.43	0.09	0.0039	3.2	17.66	17.38	0.29	0.012
9 Jun	7.26	5.46	1.81	0.0076	6.9	50.09	37.67	12.49	0.052
29 Jul	13.40	4.04	9.36	0.5208	20.0	268.0	80.8	187.2	10.42
21 Aug	16.85	2.65	14.20	0.1534	27.9	470.1	73.9	396.2	4.28
5 Oct	3.69	3.41	0.28	0.0568	17.0	62.73	57.97	4.76	0.966
					Combined North & South Watersheds[b]				
28 Mar	4.89	-	-	0.0054	15.55	76.04	-	-	0.084
21 Apr	7.90	4.50	3.40	0.0405	29.54	233.37	132.93	100.44	1.20
19 May	5.53	5.43	0.09	0.0039	8.55	163.06	160.40	2.66	0.12
9 Jun	7.26	5.46	1.81	0.0076	37.70	273.70	205.84	68.24	0.29
29 Jul	13.40	4.04	9.36	0.5208	190.46	2,552.16	769.46	1,782.71	99.19
21 Aug	16.85	2.65	14.20	0.1534	177.25	2,986.66	469.71	2,516.95	27.19
5 Oct	3.69	3.41	0.28	0.0568	85.51	315.53	291.59	23.94	4.86

Table G.- continued

Date	mg COD/liter				Discharge ($m^3 x 10^6$/month)	g COD x 10^6/month			
	Total	Dissol.	Part.	Net Part.		Total	Dissol.	Part.	Net Part.
					San Felipe Export				
Mar	8.63	7.38	1.25	0.0226	322.3	2,781.4	2,378.6	402.9	7.284
Apr	9.00	8.60	0.40	0.0296	236.8	2,131.2	2,036.5	94.7	7.009
May	9.62	8.09	1.53	0.0209	311.5	2,996.6	2,520.0	476.6	6.510
Jun	9.93[c]	9.38[c]	0.55[c]	0.0470	1,062.4	10,549.6	9,965.3	584.3	49.933
Jul	8.67	7.78	0.89	0.0808	1,648.2	14,289.9	12,823.0	1,466.9	133.175
Aug	10.37	8.81	1.56	0.0582	3,094.2	32.086.9	27,259.9	4,827.0	180.082
Oct	7.55	7.27	0.28	0.0568	1,771.2	13,372.6	12,876.6	495.9	100.604
					Average for Stations A, B, and C				
	mg COD/liter					g COD/m^2[d]			
Mar	8.56	7.21	1.35	.072	11.19	95.79	80.68	15.11	.81
Apr	7.83	6.70	1.13	.079	11.14	87.23	74.64	12.59	.88
May	7.46	5.90	1.56	.122	11.18	83.40	65.96	17.44	1.36
Jun	8.49	7.49	1.00	.103	11.27	95.68	84.41	11.27	1.16
Jul	10.53	9.74	.79	.104	11.57	121.83	112.69	9.14	1.20
Aug	10.48	8.86	1.62	.090	12.10	126.81	107.21	19.60	1.09
Oct	9.24	8.00	1.24	.058	11.45	105.80	91.60	14.20	.66

[a] Fractions of COD (total, dissolved, particulate, and net particulate) are defined in the text.

[b] Values of COD concentration are those of the Rio San Marcos.

[c] Station C values were used for COD concentrations.

[d] Calculated by multiplying the concentration in g COD/m^3 (i.e. mg COD/liter) by the depth in meters.

Table H.- Results of respiration experiments (BOD) in which duplicate samples were sacrificed after one, three, and seven days of incubation. Values represent oxygen concentrations (mg O_2/liter) and values in parentheses are the rates (mg O_2/liter day) between sampling dates[a]

Collection Date	Initial		Day 1		Day 3		Day 7	5-Day BOD
			Comercio (Polochic)					
27 Dec 71	8.10	(0.14)	7.96	(-)	8.08	(0.04)	7.94	(0.02)
25 Jan 72	7.59	(0.05)	7.54	(0.08)	7.38	(0.06)	7.16	(0.07)
1 Apr 72	7.20	(0.30)	6.91	(0.20)	6.51	(0.07)	6.49	(0.14)
29 Sep 72	7.22	(0.13)	7.09	(0.04)	7.06	(0.06)	6.81	(0.06)
			Cobán (Polochic)					
17 Jan 72	8.32	(0.07)	8.25	(0.10)	8.05	(0.13)	7.54	(0.11)
14 Mar 72	8.06							(0.16)
29 Sep 72	7.26	(0.15)	7.11	(0.03)	7.05	(0.05)	6.83	(0.06)
			Bujajal (Polochic)					
17 Jan 72	8.30	(0.24)	8.07	(0.03)	8.00	(0.10)	7.61	(0.10)
14 Mar 72	7.85							(0.12)
1 Apr 72	7.68	(0.34)	7.34	(0.25)	6.85	(0.17)	6.16	(0.24)
10 May 72	7.35	(0.27)	7.08	(0.31)	6.46	(0.05)	6.25	(0.20)
7 Jun 72	6.64	(0.40)	6.25	(0.46)	5.34	(0.22)	4.44	(0.35)
2 Aug 72	6.42	(0.33)	6.09	(0.10)	5.89	(0.09)	5.52	(0.14)
			Amatillo (Swamp Waters)					
27 Dec 71	6.76	(0.60)	6.16	(0.27)	5.63	(0.14)	5.08	(0.28)
25 Jan 72	6.59	(1.55)	5.04	(0.69)	3.65	(0.58)	1.33	(0.82)
10 Apr 72	7.23	(1.63)	5.60	(0.95)	3.70	(0.92)	0.00	(1.08)
2 Aug 72	6.70	(0.22)	6.48	(0.08)	6.32	(0.09)	5.98	(0.11)
			Padre Creek (Swamp Waters)					
18 Jan 72	6.75	(0.43)	6.32	(0.29)	5.74	(0.10)	5.35	(0.24)
29 Sep 72	4.38	(1.56)	2.82	(0.18)	2.46	(0.16)	1.82	(0.45)
			Lagartos (Swamp Waters)					
10 May 72	7.23	(1.07)	6.16	(1.52)	3.13	(0.55)	0.94	(1.04)
29 Sep 72	6.81	(0.56)	6.26	(0.19)	5.87	(0.14)	5.32	(0.27)

Table H.- continued

Collection Date	Initial		Day 1		Day 3		Day 7	5-Day BOD
			Oscuro (Swamp Waters)					
27 Dec 71	7.57	(0.41)	7.16	(0.15)	6.86	(0.12)	6.37	(0.19)
25 Jan 72	6.04	(0.30)	5.74	(0.14)	5.47	(0.07)	5.18	(0.14)
1 Apr 72	6.00	(0.48)	5.53	(0.23)	4.83	(0.12)	4.48	(0.26)
7 Jun 72	6.74	(0.35)	6.39	(0.31)	5.77	(0.19)	5.02	(0.27)
2 Aug 72	6.62	(0.32)	6.30	(0.13)	6.05	(0.10)	5.63	(0.24)
			Sauce (Small Rivers)					
10 Apr 72	7.41	(0.25)	7.16	(0.15)	6.86	(0.22)	5.99	(0.20)
9 Jun 72	7.14	(0.54)	6.60	(0.55)	5.50	(0.32)	4.24	(0.45)
29 Jul 72	7.56	(0.18)	7.38	(0.17)	7.04	(0.17)	6.37	(0.17)
			San Marcos (Small Rivers)					
19 May 72	6.92							(0.16)
9 Jun 72	6.99	(0.35)	6.64	(0.25)	6.14	(0.13)	5.64	(0.22)
29 Jul 72	7.45	(0.23)	7.22	(0.16)	6.90	(0.08)	6.57	(0.14)
			Manacas Creek (Small Rivers)					
19 May 72	7.10							(0.14)
5 Oct 72	6.94	(0.22)	6.73	(0.11)	6.51	(0.09)	6.15	(0.12)
			Station A (Lake)					
3 Jan 72	7.96	(0.26)	7.70	(0.18)	7.34	(0.05)	7.14	(0.15)
10 Apr 72	7.56	(0.27)	7.29	(0.20)	6.90	(0.32)	5.60	(0.26)
10 May 72	7.71	(0.54)	7.17	(0.77)	5.64	(0.16)	5.00	(0.48)
19 May 72	7.54							(0.18)
8 Oct 72 (11m)	6.99	(0.13)	6.86	(0.20)	6.47	(0.10)	6.08	(0.14)
			Station B (Lake)					
3 Jan 72	6.73	(0.24)	6.49	(0.05)	6.40	(0.08)	6.06	(0.10)
19 May 72 (surf)	7.30							(0.17)
19 May 72 (15.5m)	7.10							(0.17)

Table H.- continued

Collection Date	Initial		Day 1		Day 3		Day 7	5-Day BOD
			Station B (Lake) - continued					
8 Oct 72 (surf)	7.36	(0.08)	7.28	(0.11)	7.06	(0.05)	6.86	(0.08)
8 Oct 72 (15 m)	6.88	(0.17)	6.71	(0.10)	6.51	(0.07)	6.25	(0.10)
			Station C (Lake)					
19 May 72 (surf)	7.36							(0.12)
5 Oct 72	6.53	(0.15)	6.39	(0.07)	6.26	(0.06)	6.00	(0.08)
			San Felipe (Lake)					
3 Jan 72	8.21	(0.22)	7.99	(0.23)	7.53	(0.10)	7.13	(0.16)
8 Feb 72	7.62	(0.25)	7.37	(0.14)	7.11	(0.08)	6.80	(0.13)
29 Jul 72	7.36	(0.09)	7.28	(0.16)	6.97	(0.07)	6.70	(0.11)

[a] The 5-Day BOD rates (mg O_2/liter day) were calculated by dividing the difference between the initial concentration and the Day 5 concentration (average of Day 3 and Day 7 concentrations) by 5.

Table I.- Organic matter (OM) and COD inflows and outflows on a daily and monthly basis. The last column represents the arithmetic difference (gain or loss) between the daily inflow and outflow as grams of organic matter per m^2 of lake surface

Date	COD Inflow ($g \times 10^6$)	OM Inflow ($g \times 10^6$)[a]	OM Inflow (g/m^2 day)[b]	COD Outflow ($g \times 10^6$)	OM Outflow ($g \times 10^6$)[a]	OM Outflow (g/m^2 day)[b]	OM Net Gain or Loss (g/m^2 day)
Mar	2,739.6	1,902.5	0.088	2,781.4	1,931.5	0.090	-0.002
Apr	2,627.7	1,824.8	0.085	2,131.2	1,480.0	0.069	+0.016
May	2,829.9	1,965.2	0.091	2,996.6	2,081.0	0.097	-0.006
Jun	26,067.8	18,102.6	0.842	10,549.6	7,326.1	0.341	+0.501
Jul	46,640.9	32,389.5	1.506	14,289.9	9,923.5	0.461	+1.045
Aug	37,335.6	25,927.5	1.205	32,086.9	22,282.6	1.036	+0.169
Oct	13,069.6	9,076.1	0.422	13,372.6	9,286.5	0.432	-0.010

[a] Organic matter calculated by dividing the COD value by 1.44.

[b] Daily inflows and outflows per m^2 calculated by dividing the monthly totals by 30 (days per month) and by 717×10^6 m^2 (surface area of lake).

Table J.- Calculation of the average rates of gross primary productivity (Pg), respiration (R_{24}), and net primary productivity (Pn) for the three lake stations (A, B, and C). All values are g O_2/m^2 day (oxygen being equivalent to organic matter)

	Station A			Station B			Station C			Average		
Month	Pg	R_{24}	Pn	Pg	R_{24}	Pn	Pg	R_{24}	Pn	Pg	R_{24}	Pn
March	6.37	1.21	+5.16	3.30	2.65	+0.65	3.05	2.50	+0.55	4.240	2.120	+2.120
April	6.95	3.08	+3.87	3.30	2.65	+0.65	3.05	2.50	+0.55	4.433	2.743	+1.690
May	5.41	6.35	-0.94	4.47	2.35	+2.12	2.64	2.81	-0.17	4.173	3.837	+0.337
June	4.73	7.16	-2.43	5.45	2.95	+2.50	2.63	3.66	-1.03	4.270	4.590	-0.320
July	4.38	5.66	-1.28	5.35	5.94	-0.59	3.14	3.50	-0.36	4.290	5.033	-0.743
August	4.02	3.85	+0.17	5.21	7.56	-2.35	3.03	3.28	-0.25	4.087	4.897	-0.810
September	2.36	3.01	-0.65	3.12	5.21	-2.09	1.66	3.69	-2.03	2.380	3.970	-1.590
October	2.26	3.24	-0.98	2.45	4.35	-1.90	1.20	3.85	-2.65	1.970	3.813	-1.843

LITERATURE CITED

American Public Health Association. 1965. Standard Methods for the Examination of Water and Wastewater, 12th ed. APHA. 769 p.

Anderson, G.C. 1958. Seasonal characteristics of two saline lakes in Washington. Limnol. Oceanogr. 3:51-68.

Barlow, J.P., C.J. Lorenzen, and R.T. Myren. 1963. Eutrophication of a tidal estuary. Limnol. Oceanogr. 3:251-262.

Beeton, A.M. 1957. Relationship between Secchi disk readings and light penetration in Lake Huron. Trans. Amer. Fish. Soc. 87:73-79.

Bormann, F.H., G.E. Likens, and J.S. Eaton. 1969. Biotic regulation of particulate and solution losses from a forest ecosystem. Bio-Science 19:600-610.

Brezonik, P.L., W.H. Morgan, E.E. Shannon, and H.D. Putnam. 1969. Eutrophication factors in north central Florida lakes. Engineering and Industrial Experiment Station. Bull. Ser. No. 134. 101 p.

Brinson, L.G. 1973. A comparison of seasonal plankton abundance and primary productivity in five tropical fresh-water deltaic embayments. M.S. thesis, University of Florida, Gainesville, Fla.

Brooks, H.K. 1969. A preliminary report to the Organization for Tropical Studies, Inc. on Lake Izabal, Geology and Hydrology. 19 p.

Carr, A.F., III. 1971. The commercial snook (_Centropomus undecimalis_) fishery of Lake Izabal, Guatemala. M.S. thesis, University of Florida, Gainesville, Fla. 105 p.

Carter, W.E. 1969. New Lands and Old Traditions: Kekchi Cultivators in the Guatemalan Lowlands. Latin American Monographs: No. 6. University of Florida Press, Gainesville. 153 p.

Clarke, G.L. 1941. Observations on the transparency in the South-Western section of the North Atlantic Ocean. J. Mar. Res. 4:221-230.

Cole, G.A. 1966. The American Southwest and Middle America, p. 393-434. In: D.G. Frey (Ed.), Limnology in North America. Univ. Wisconsin Press, Madison.

Cooper, D.C. and B.J. Copeland. 1973. Responses of continuous-series estuarine microecosystems to point-source input variations. Ecol. Monogr. 43:213-236.

Darnell, R.M. 1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. Ecology 42:553-568.

__________. 1967. Organic detritus in relation to the estuarine ecosystem, p. 376-382. In: G. Lauff (Ed.), Estuaries. Am. Ass. Advmt. Sci. Publ. No. 83.

Debski, K. 1966. Continental hydrology. Vol. II. Physics of Water, Atmospheric Precipitation and Evaporation. Scientific Publ. Foreign Coop. Center. 606 p.

Deevey, E.S. 1941. Limnological studies in Connecticut. VI. The quantity and composition of the bottom fauna in thirty-six Connecticut and New York lakes. Ecol. Monogr. 11: 413-455.

__________. 1957. Limnological studies in Middle America, with a chapter on Aztec limnology. Trans. Conn. Acad. Arts Sci. 39:213-328.

Dengo, G., and O. Bohnenberger. 1969. Structural development of northern Central America. Bull. Amer. Assoc. Petrol. Geol., Mem. 11:203-220.

Dickinson, J.C., III. (in press) Fisheries of Lake Izabal, Guatemala.

Dorris, T.C. 1972. La ecologia y la pesca del Lago de Atitlán. Publicación Especial No. 1. El Centro de Investigaciones de Embalses de La Universidad Estatal de Oklahoma. 34 p.

Dunn, I.G., J.J. Burgis, G.G. Ganf, L.M. McGowan, and A.B. Viner. 1969. Lake George, Uganda: A limnological survey. Verh. Internat. Verein. Limnol. 17:284-288.

Edmondson, W.T. (Ed.). 1959. H.B. Ward and G.C. Whipple Fresh-water Biology, 2nd ed. John Wiley & Sons, New York and London. 1248 p.

Edwards, R.W., and H.L.J. Rolley. 1965. Oxygen consumption of river muds. J. Ecol. 53:1-19.

Forbes, S.A. 1887. The lake as a microcosm. Reprinted 1925. Bull. Ill. Nat. Surv. 15:537-550.

Frey, D.G. 1969. A limnological reconnaissance of Lake Lanao. Int. Ver. Theor. Angew. Limnol. Verh. 17:1090-1102.

Gibbs, R.J. 1967. The geochemistry of the Amazon river system: Part I. The factors that control the salinity and the composition and concentration of the suspended solids. Geol. Soc. Amer. Bull. 78:1203-1232.

Gilbert, C.R., and D.P. Kelso. 1971. Fishes of the Tortuguero Area, Caribbean Costa Rica. Bull. Florida State Mus., Biol. Sci. 16:1-54.

Golley, F.B., J.T. McGinnis, R.G. Clements, G.I. Child, and M.J. Duever. 1971. Mineral Cycling in a Tropical Moist Forest Ecosystem. Athens, Georgia. (1971).

Golterman, H.L. (Ed.). 1969. Methods for Chemical Analysis of Fresh Waters. IBP Handbook No. 8. Blackwell Scientific Publications, Oxford. 166 p.

Grove, A.T. 1972. The dissolved and solid load carried by some West African Rivers: Senegal, Niger, Benue, and Shari. J. Hydrol. 16:277-300.

Harbeck, G.E., G.E. Koberg, and G.H. Hughes. 1959. The effect of the addition of heat on the thermal structure and evaporation of Lake Colorado City, Texas. U.S. Geol. Survey Prof. Paper 272-B.

Hayes, F.R., and M.A. MacAulay. 1959. Lake water and sediment. V. Oxygen consumed in water over sediment cores. Limnol. Oceanogr. 4:291-298.

Heald, E.J. 1971. The production of organic detritus in a south Florida estuary. Sea Grant Tech. Bull. No. 6. Univ. of Miami. 110 p.

Hickling, C.F. 1961. Tropical Inland Fisheries. John Wiley & Sons, New York. 287 p.

Holdridge, L.R. 1967. Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica. 206 p.

Holloway, A.D. 1948. Recommendations for the Development of the Fishery Resources of Guatemala. U.S. Fish and Wildlife Service, Washington. 114 p.

Hutchinson, G.E. 1957. A Treatise on Limnology. Vol. 1. Geography, Physics, and Chemistry. John Wiley & Sons, Inc. New York. 1015 p.

_______________. 1967. A Treatise on Limnology. Vol. 2. Introduction to lake biology and the limnoplankton. John Wiley & Sons, Inc. New York. 1115 p.

Ichimura, S. 1956. On the ecological meaning of transparency for the production of matter in phytoplankton community of lake. Bot. Mag., Tokyo 69:219-226.

Instituto Geográfico Nacional. 1966. Atlas preliminar de Guatemala, Tercera edición. Litografia, Guatemala. 25 p.

Kaushik, N.K., and H.B.N. Hynes. 1968. Experimental study on the role of autumn-shed leaves in aquatic environments. J. Ecol. 56:229-243.

Lawacz, W. 1969. The characteristics of sinking materials and the formation of bottom deposits in a eutrophic lake, p. 319-331. In: D.G. Frey (Ed.), Symposium on paleolimnology. Int. Assoc. Limnol., Commun. no. 17. 448 p.

Lefèvre, M., H. Jacob, and M. Nisbet. 1952. Auto- et hetero-antagonisme chez les algues d'eau douce. Annls St. Cant. Hydrobiol. appl. 4:5-197.

Lewis, W. 1973. Factors controlling primary production in a tropical lake. Paper presented to: II International Symposium on Tropical Ecology, February 8, 1973, at Caracas, Venezuela.

Likens, G.E. 1972. Eutrophication and aquatic ecosystems, p. 3-13. In: G.E. Likens (Ed.), Nutrients and Eutrophication: The limiting-nutrient controversy. Amer. Soc. Limnol. Oceanogr. Special Symposia, Vol. I. 328 p.

_____________, F.H. Bormann, N.M. Johnson, D.W. Fisher, and R.S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook Watershed-Ecosystem. Ecol. Monogr. 40:23-47.

Lund, J.W.G. 1950. Studies on Asterionella formosa Hass. II. Nutrient depletion and the spring maximum. J. Ecol. 38:1-35.

Maciolek, J.A. 1962. Limnological organic analysis by quantitative dichromate oxidation. Res. Report No. 60 of Bur. Sport. Fish. and Wildlife, U.S. Fish and Wildlife Service. 61 p.

Margalef, R. 1963. On certain unifying principles in ecology. Amer. Nat. 97:357-374.

McConnell, W.J. 1963. Primary productivity and fish harvest in a small desert impoundment. Trans. Amer. Fish. Soc. 92:1-12.

McDonnell, A.J., and S.D. Hall. 1969. Effect of environmental factors on benthal oxygen uptake. Jour. WPCF. Res. Supp. 41:353-363.

Nelson, D.J., and D.C. Scott. 1962. Role of detritus in the productivity of a rock-outcrop community in a Piedmont stream. Limnol. Oceanogr. 7:396-413.

Nordlie, F.G. 1970. Lake Izabal -- Energetics. Final report to the Organization for Tropical Studies, Inc. 22 p.

Odum, E.P. 1971. Fundamentals of Ecology, 3rd ed. W.B. Saunders Company, Philadelphia. 574 p.

_________, and A.A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem, p. 383-388. In: G. Lauff (Ed.), Estuaries. Am. Ass. Advmt. Sci. Publ. No. 83.

Odum, H.T. 1956. Primary production in flowing waters. Limnol. Oceanogr. 1:102-117.

_________. 1967. Biological circuits and the marine systems of Texas, p. 99-158. In: T.A. Olson and F.J. Burgess (Eds.), Pollution and Marine Ecology. Interscience Publ., New York.

_________. 1971. Environment, Power, and Society. Wiley-Interscience, New York. 331 p.

Odum, W.E. 1971. Pathways of energy flow in a south Florida estuary. Sea Grant Tech. Bull. No. 7. Univ. of Miami. 162 p.

Pennak, R.W. 1953. Freshwater Invertebrates of the United States. Ronald Press Co., New York. 769 p.

Pescod, M.B. 1969. Photosynthetic oxygen production in a polluted tropical estuary. Jour. WPCF. Res. Supp. 41:309-320.

Poole, H.H., and W.R.G. Atkins. 1929. Photoelectric measurements of submarine illumination throughout the year. J. Mar. Biol. Ass. U.K. 16:297-324.

Popenoe, H.L. 1960. Effects of shifting cultivation on natural soil constituents in Central America. Ph.D. dissertation, University of Florida, Gainesville. 158 p.

Pratt, D.M., and H. Berkson. 1959. Two sources of error in the oxygen light and dark bottle method. Limnol. Oceanogr. 4:328-334.

Pride, R.W., F.W. Meyer, and R.M. Cherry. 1966. Hydrology of Green Swamp area in central Florida. Florida Geol. Survey Rept. Inv. 42. 106 p.

Ray, C.L. 1931. Evaporation in the Eastern Caribbean. Mon. Weather Rev. 59:192-193.

Reiser, C.O. 1969. Analysis of evaporation control system of the Sea of Galilee. Water Resour. Res. 5:380-394.

Remane, A., and C. Schlieper. 1971. Biology of Brackish Water. John Wiley & Sons, New York. 372 p.

Roberts, R.J., and E.M. Irving. 1957. Mineral deposits of Central America. U.S. Geol. Survey Bull. 1034. 205 p.

Rodhe, W. 1969. Crystallization of eutrophication concepts in northern Europe, p. 50-64. In: Eutrophication: Causes, consequences and correctives. Nat. Acad. Sci./Nat. Res. Council, Publ. 1700.

Ruttner, F. 1952. Planktonstudien der Deutschen Limnologischen. Sundan-Expedition. Arch. Hydrobiol. Suppl. 21:1-274.

__________. 1963. Fundamentals of Limnology. 3rd ed. Translated by D.G. Frey and F.E.J. Fry. Univ. Toronto Press. 295 p.

Seki, H., J. Skelding, and T.R. Parson. 1968. Observations on the decomposition of a marine sediment. Limnol. Oceanogr. 13.440-447.

Simmons, C.S., J.M. Tárano T., and J.H. Pinto Z. 1959. Clasificación de Reconocimiento de los Suelos de la Republica de Guatemala. Editorial del Ministerio de Educación Pública, Guatemala. 1,000 p.

Smith, G.M. 1950. The Fresh-water Algae of the United States, 2nd ed. McGraw-Hill Book Co., New York. 719 p.

Snedaker, S.C. 1970. Ecological studies on tropical moist forest succession in eastern lowland Guatemala. Ph.D. dissertation, University of Florida, Gainesville. 133 p.

Szeicz, G., and G. Endrödi. 1969. Aerodynamic and surface factors in evaporation. Water Resour. Res. 5:380-394.

Talling, J.F. 1965. Comparative problems of phytoplankton production and photosynthetic productivity in a tropical and temperate lake, p. 401-424. In: C.R. Goldman (Ed.), Primary Productivity in Aquatic Environments. Mem. Ist. Ital. Idrobiol., 18 Suppl., University of California Press, Berkeley.

__________. 1966. The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). Int. Revue ges. Hydrobiol. 51:545-621.

__________. 1969. The incidence of vertical mixing, and some biological and chemical consequences, in tropical African lakes. Verh. Internat. Verein. Limnol. 17:998-1012.

Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614-624.

Tergas, L.E. 1965. Correlation of nutrient availability in soil and uptake by native vegetation in the humid tropics. M.S. thesis. University of Florida, Gainesville. 64 p.

Thorson, T.B., C.M. Cowan, and D.E. Watson. 1966. Sharks and sawfish in the Lake Izabal--Rio Dulce System, Guatemala. Copeia 3: 620-622.

Tsukada, M., and E.S. Deevey. 1967. Pollen analysis from four lakes in southeastern Maya area of Guatemala and El Salvador, p. 303-331. In: E.J. Cushing and H.E. Wright (Eds.), Quaternary Paleoecology. Yale University Press, New Haven.

Turner, J.F., Jr. 1966. Evaporation study in a humid region, Lake Michie, North Carolina. U.S. Geol. Survey. Prof. Paper 272-G.

Vollenweider, R.A. (Ed.). 1969. Primary Production in Aquatic Environments. IBP Handbook No. 12. Blackwell Scientific Publications, Oxford. 213 p.

Voorhies, B. 1969. A prehistoric Maya hinterland: the Izabal zone of eastern Guatemala. Paper presented to: Amer. Anthropol. Ass., November 20, 1969, at New Orleans, La.

Walper, J.L. 1960. Geology of Cobán-Purulhá area, Alta Verapaz, Guatemala. Bull. Amer. Assoc. Petrol. Geol. 44:1273-1313.

Walter, H. and H. Leith. 1960-67. Klima diagram -- welt atlas. V.B. Gustav Fisher Verlag; Jena.

Welch, P.S. 1948. Limnological Methods. Blakiston Co., Philadelphia. 381 p.

BIOGRAPHICAL SKETCH

Mark McClellan Brinson was born October 6, 1943, in Shelby, Ohio. He lived there with his parents, Glen and Geneva, until graduation from Shelby High School in 1961. He graduated with the degree Bachelor of Science in biology at Heidelberg College in June, 1965, where he was awarded membership to Who's Who in American Colleges and Universities and Tower Men, an academic honorary.

In August, 1965, he entered graduate studies at The University of Michigan where he received the Newcombe Fellowship in botany. Upon receipt of a Master of Science in Botany in May, 1967, he went to Central America as a Peace Corps Volunteer. There he worked as a fisheries biologist for two years in Turrialba, Costa Rica.

He entered graduate school at the University of Florida in September, 1969, where he is presently a candidate for the degree Doctor of Philosophy. While there he was awarded a Research Fellowship from the Program for Latin America and the Caribbean sector of the Foreign Area Fellowship Program. He is a member of the American Society of Limnology and Oceanography, Phi Sigma Society, The Ecological Society of America, and the American Institute of Biological Sciences.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Ariel E. Lugo, Chairman
Assistant Professor of Botany

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Dean, Graduate School