A LIMNOLOGICAL RECONNAISSANCE OF LAKE LANAO

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Lake Lanao on northern Mindanao in the Philippines is of great interest limnologically if for no other reason than that it contains endemic species of various kinds of animals, including a species flock of cyprinids that have evolved in the lake (most recent review by Myers, 1960, but see also Brooks 1950, and Herre 1933). Contrary to the opinion of Bailey Willis (quoted in Myers 1960) that the lake is only about 10,000 years old, based on the short length of the canyon below Maria Cristina Falls, evidence is accumulating that the lake is much older than this, possibly even deriving from the late Tertiary.

Relatively little has been published concerning the lake and its limnology, aside from taxonomic studies of the fishes by Herre (see bibliography in Myers 1960). The fragmentary and still incompletely published observations of the Wallacea Expedition in 1932 include a maximum depth sounding of 107 m, more than 1 ppm dissolved oxygen at 90 m on 7 May (in contrast to nearly all other deep lakes of the Philippines in which the oxygen completely disappears relatively close to the surface), and the inclusion of the lake by Woltereck in his group of deep tropical lakes with a complete circulation in winter (Woltereck 1933, 1941). This last statement is entirely presumptive, as up to now there have been no seasonal observations on the lake. Besides this there are partial lists of organisms (to genera in most cases, species in some) that occur in the inshore and offshore plankton, and to a lesser extent in the shallow-water benthos (Woltereck 1941). These observations, being very fragmentary, do more to suggest limnological processes than define them.

The present paper is a brief summary of limnological studies conducted from August 1967 through June 1968, during which time almost

40 half-day trips were made on the lake. A Koden echo sounder was used to map the bathymetry of the lake. The area of the lake and of the various tributary watersheds was measured with a planimeter from 1:50,000 maps available from the Board of Technical Surveys and Maps in Manila. Data on the fluctuations in lake level and discharge of water from the lake were made available by the National Power Corporation. Also available are rainfall data for three stations and temperature data for one station located near the lake (obtained from the Weather Bureau in Manila) and short, although valuable, series of measurements of discharge of the major rivers tributary to Lake Lanao (Williams & Gochoco 1924).

Bathymetry

The lake basin is shallowest toward the north end and becomes progressively deeper toward the south (Fig. 1), with an extensive area east of the two southern islands greater than 110 m in depth and with a maximum depth of approximately 112 m, the same maximum depth quoted by Halbfass (1922: fide Hutchinson 1957). This datum undoubtedly derives from studies by the U.S. Army Engineers, when they were at Camp Keithley at Marawi City during the early decades of this century (Villaluz 1966). Based on a limited number of soundings, Woltereck (1941) concluded that the northern half of the lake (roughly north of a line between Uato and Tamparan in Fig. 3) was quite shallow, and that the bottom dropped off rapidly from here toward the south. Fig. 1 shows that there is a distinct increase in slope here, indicated by the closer spacing of the 10-m countours, but nothing approaching the gradient implied by Woltereck, nor is the northern half so shallow as inferred from the few soundings on his simple map. The maximum depth of 107 m recorded by Woltereck was to the east of the two islands in the south. The base datum for water depths on the bathymetric map is the mean lake level of 701.89 m as determined from records of the National Power Corporation.

During the period of the survey (January through May 1968) the monthly mean lake level varied from 701.12 to 701.40 m. These differences below base datum were overcompensated by a positive error in the echo sounder, which varied asystematically with depth. Since in

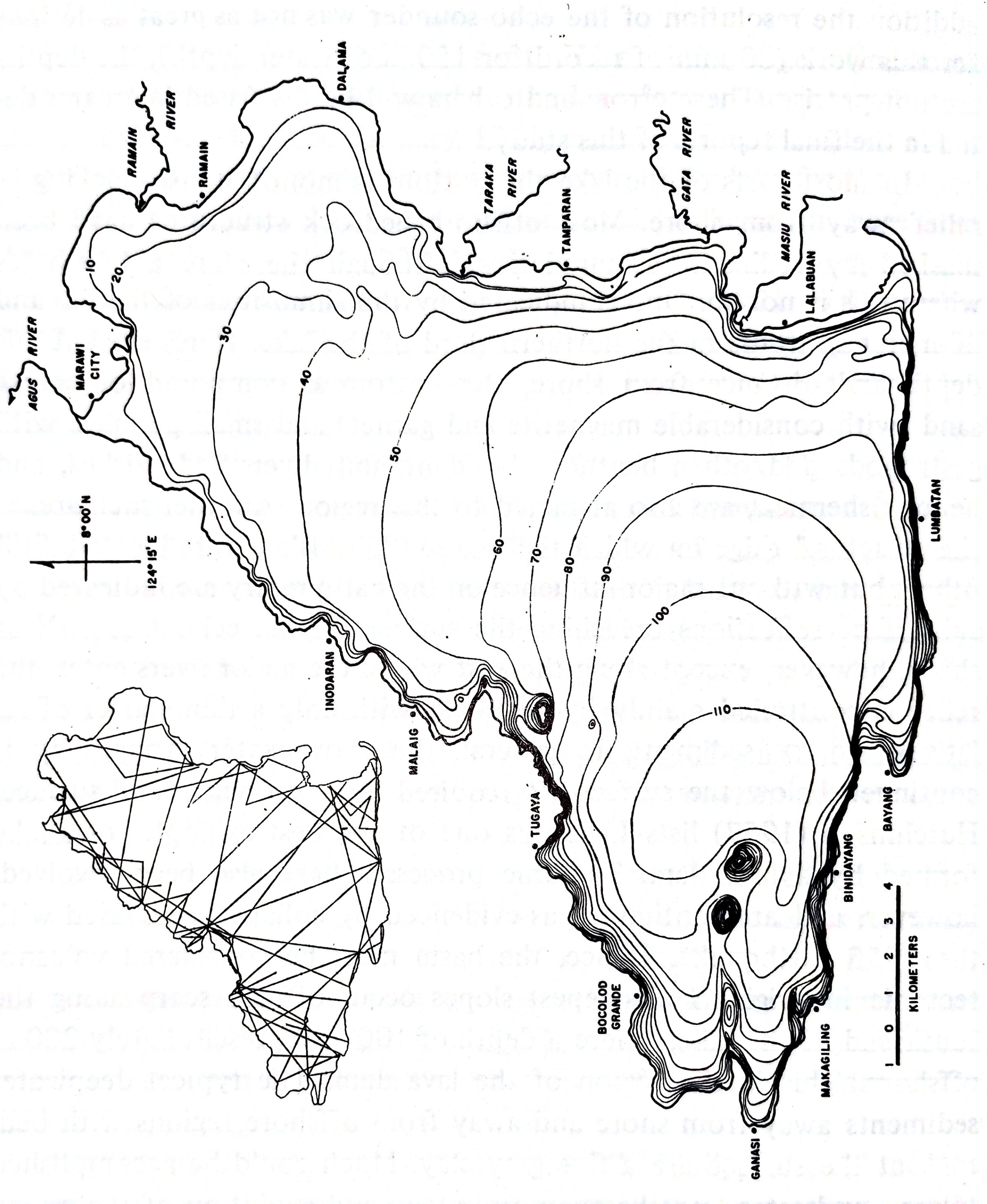

Fig. 1. Bathymetric map of Lake Lanao, prepared with the aid of a Koden echo sounder, model SR-390 D. The various sounding runs made with the boat are shown on the small insert map. Offshore contours are reasonably accurate because of the low relief here. Nearshore contours are only approximate on a map of this size. There are many topographic irregularities within several hundred meters of shore, reflecting bedrock control of a drowned land surface. Contour intervals are 10 meters below the mean lake level of 701.89 m.

addition the resolution of the echo sounder was not as great as desired for this work (80 mm of record for 150 m of water depth), the depths are not precise. These errors and others will be discussed in greater detail in the final reports of this study.

In most parts of the lake the bottom is monotonously lacking in relief away from shore. Most offshore bedrock structures have been masked by sediment accumulation, although there are a few areas where this is not so. One is indicated by the sinuosities of the 30- and 40-meter contours in the northern third of the lake. Here, even at this depth and distance from shore, the bottom is composed of coarse sand (with considerable magnetite and garnet) and small pebbles, with gastropods and other benthos abundant and diversified. Fishes, and hence fishermen, are also attracted to this region. Another such area is the structural ridge on which the two southern islands are located. Still others but without major influence on the bathymetry are indicated by subsurface reflections breeching the surface on the echo traces. Near shore, however, except along the east where the major rivers enter, the relief is controlled mainly by bedrock, with only a thin veneer of relatively coarse sediment. In general, the above-water topography is continued below the surface, as required by a drowned land surface. Hutchinson (1957) lists Lanao as one of the best examples of a lake formed by a lava dam. Tectonic processes have also been involved, however, and are continuing, as evidenced by collapse associated with the 1955 earthquake. Hence, the basin must be considered volcano-tectonic in origin. The steepest slopes occur off the scarp along the south end of the lake, where a depth of 100 m is present barely 200 m offshore. This is the region of the lava dam. The typical deepwater sediments away from shore and away from offshore regions with bedrock at the surface are a fine gray clay. Much could be accomplished toward understanding the geomorphology and evolution of the region with an echo sounder having greater depth resolution and sufficient energy for penetrating the sediments.

Several morphometric statistics of the lake are: area – 357 km^2; volume – 21.5 km^3; maximum depth – 112 m; mean depth (volume/area) – 60.3 m; replacement time (volume/mean annual discharge) – 6.5 years.

Meteorology

Rainfall records are available for the Marawi City region (including Camp Keithley) at the north end of the lake for various intervals over the period May 1918 to January 1954, encompassing a total of about 25 years; for Ganasi at the southwest corner of the lake for the period May 1919 to January 1933; and for Lumbatan on the south shore from April 1919 to December 1932. Maximum and minimum temperatures are available only for Marawi City from January 1921 to December 1932. No official weather station is being maintained in the province of Lanao del Sur at the present time, although one is to be established at Mindanao State University.

The mean annual rainfall at these stations is remarkably consistent: Marawi City – 2865 mm, Ganasi – 2890 m, and Lumbatan – 2864 m, for an overall average of 2873 mm. The number of rainy days per year, however (a rainy day is defined as one with at least 0.1 mm precipitation), is not consistent: Marawi City – 237 days, Ganasi – 180 days, Lumbatan – 194 days. The average precipitation per rainy day varies inversely with these numbers. Thus Ganasi has fewer rainy days per year than Marawi City (and hence probably more hours of sunshine, although there are no data to substantiate this), but the rains when they do come are more intense.

The lake exerts considerable control over the local climate, which affects the insolation amount and pattern. Typically the sky is relatively cloudless until mid morning. The small updraft clouds that form over the land tend to dissipate as they move out over the cooler water. As a result the lake is frequently surrounded by clouds, but the sky overhead is clear. This permits almost maximum insolation and undoubtedly affects the primary productivity.

As is typical of many monsoon areas of the Philippines, the months December through April are relatively dry, the other seven months relatively wet. This is the pattern evident in the climatograph for Marawi City (Fig. 2), which also shows the markedly colder mean daily temperatures from December through March. This is the period during which the lake turns over, based on the records for this one year. Stratification is reestablished in late March and early April during the period of rapid warming. Peak precipitation occurs in June, with a lesser

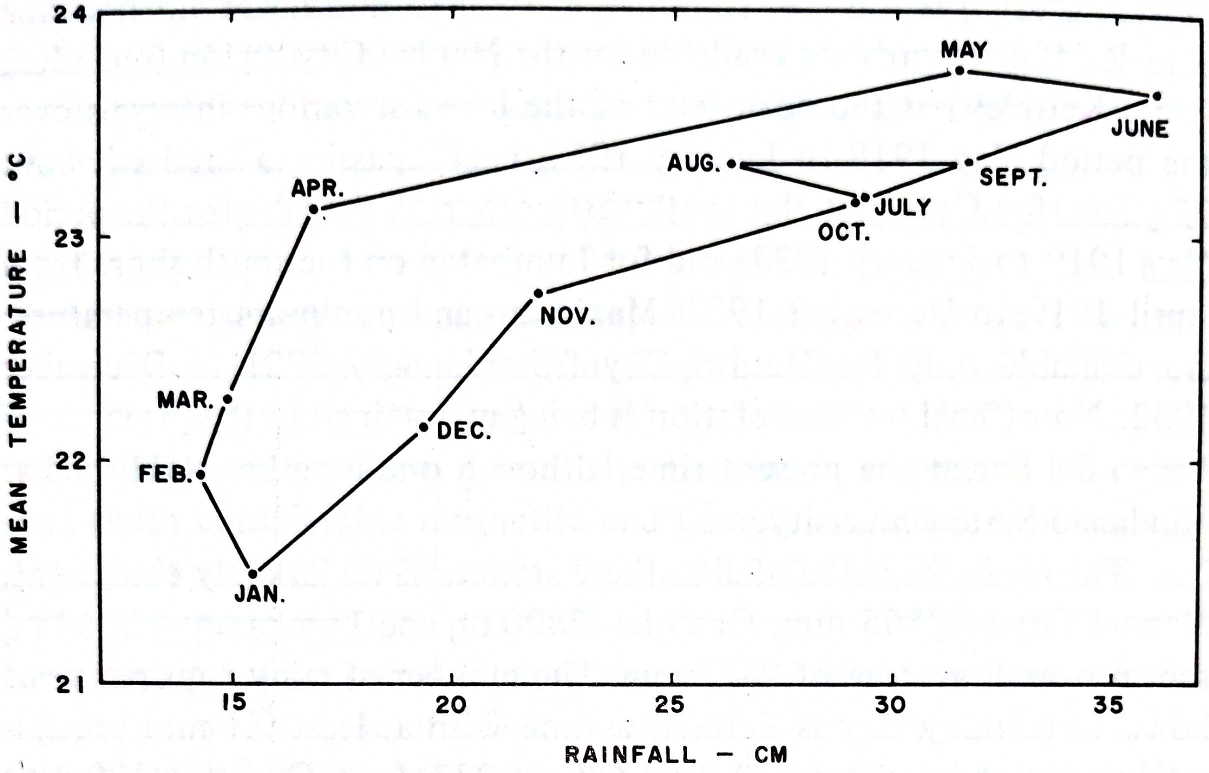

Fig. 2. Climatograph for Marawi City. Mean rainfall for the various months is based on 21 to 26 individual monthly totals over the period May 1918 to January 1954. Monthly mean temperatures are based on 8 to 10 averages for each month accumulated over the period January 1921 through December 1932. All data are from the records of the Weather Bureau, except rainfall data for July 1950 through January 1954, which are from the National Power Corporation.

although substantial peak in September.

Hydrology

The Lake Lanao-Agus River system is presently unregulated. When the lake level is high, more water leaves the lake than when the level is low. This results in a stable lake but an unstable river. Over 27 years of record, the mean annual variation of lake level has been only 0.8 m (range 0.3–1.5 m), with an extreme range of 2.09 m. On the other hand, the monthly mean discharge from the lake over this period has varied from 233.0 m^3/sec. in December 1955 to only 12.8 m^3/sec. in May 1958 and even less than this in March and April 1966.

Based on data generously made available by the National Power Corporation, over the periods 1932–40 and 1948–66 the mean lake level was 701.89 m. The time of occurrence of the annual maximum and minimum monthly mean lake levels corresponds closely to the annual cycle of precipitation: 53% of all maxima occurred during the months June through August, although each month of the year had at least one instance in which the annual maximum occurred in that month. Minimum lake level occurred 70% of the time in March and April, and the months July through October never had a minimum for any year of record.

During the period July 1938 through December 1940, discharge measurements were made on the Agus River where it leaves the lake at Marawi City, from which a rating curve was established for approximating discharge for any given lake level. During this period the mean monthly lake level varied from 701.60 to 702.29 m and the discharge from 73.38 to 160.14 m^3/sec. A least-squares analysis of these data, assuming a linear relationship between discharge and lake level, gave the regression equation $Y = 118.375\ X - 82{,}981.536$ (Y is discharge in m^3/sec. and X is lake level in meters), with a highly significant correlation coefficient of 0.960 for Y as a function of X. This rating curve is slightly different from the one derived by the National Power Corporation, having approximately the same y-intercept but a somewhat steeper slope. Both curves yield zero discharge at 701.00 m, and yet in March and April 1966 when the mean monthly lake levels were 700.94 and 700.95, respectively, there was still a small discharge from the lake (based on verbal reports of a number of persons at Mindanao State University). Hence, discharge as a function of lake level may be approximately linear over most of the expected range but apparently not at extremely low lake levels.

From the regression equation given above, the mean discharge from the lake (at a mean water level of 701.89 m) is 104.71 m^3/sec., which yields an average annual discharge of 3.304 billion m^3. Since the area of the total watershed above the source of the Agus River at Marawi City is approximately 1.680 billion m^2, each square meter of watershed surface (including the lake) contributes roughly 1.97 m^3 to the discharge from the lake. Assuming a mean precipitation of 2.873 m for the entire watershed (although it may well be substantially higher than this), the difference of 0.90 m must be accounted for by evapotranspiration and other losses from the system.

The Lake Lanao watershed can be resolved into the major components shown in Tab. 1 (see also Figs. 3 and 4).. Discharge measurements for the five major rivers draining the mountainous region to the east are available for the period September 1919 through June 1922. The discharge from the lake for this same period can be estimated from the discharge measurements of the Agus River made at Momumgan 23 km downstream from the lake. Tab. 2 shows that in general each watershed contributes to the total discharge from the lake in proportion to its area. The Masiu River and the Gata + Bacayawan Rivers (the Bacayawan is shown in Fig. 4 as the small elongated watershed – labelled S – between the Taraka and Gata watersheds) have a small excess contribution, the Ramain and Taraka a small deficient contribution. The excess of the Bacayawan itself is undoubtedly explained

Tab. 1. Breakdown of the Lake Lanao watershed into major components by area and percentage of the total area.

Watershed	Area km²	% of total
Lake Lanao	356.6	21.2
Bacayawan River	23.9	1.4
Gata River	208.3	12.4
Masiu River	347.0	20.7
Ramain River	162.4	9.7
Taraka River	285.6	17.0
Small marginal watersheds	296.5	17.6
Total	1680.4	
Agus River below Lake Lanao	254.1	

Tab. 2. Percentage distribution of total discharge for various periods of time, and comparison with the percentage distribution by area of the watershed involved.

Watershed	1920	1921	% discharge 1919 + 1922[1]	Total	% area[2]
Bacayawan	3.5	4.4	4.6	4.2	2.3
Gata	16.8	21.0	19.2	19.3	20.3
Masiu	37.5	34.2	35.8	35.6	33.8
Ramain	17.3	13.8	13.9	14.9	15.8
Taraka	25.0	26.5	26.6	26.0	27.8
Agus at Momungan	63.0	58.1	66.5	61.2	—
Agus at Marawi City[3]	69.1	63.7	72.9	67.1	61,1

[1] December 1919 plus January through June 1922.
[2] Determined by planimetry from 1 : 50,000 maps available from the Board of Technical Surveys and Maps, Manila.
[3] Flow at Momungan times 0.9117 (factor derived by Nation Power Corp.).

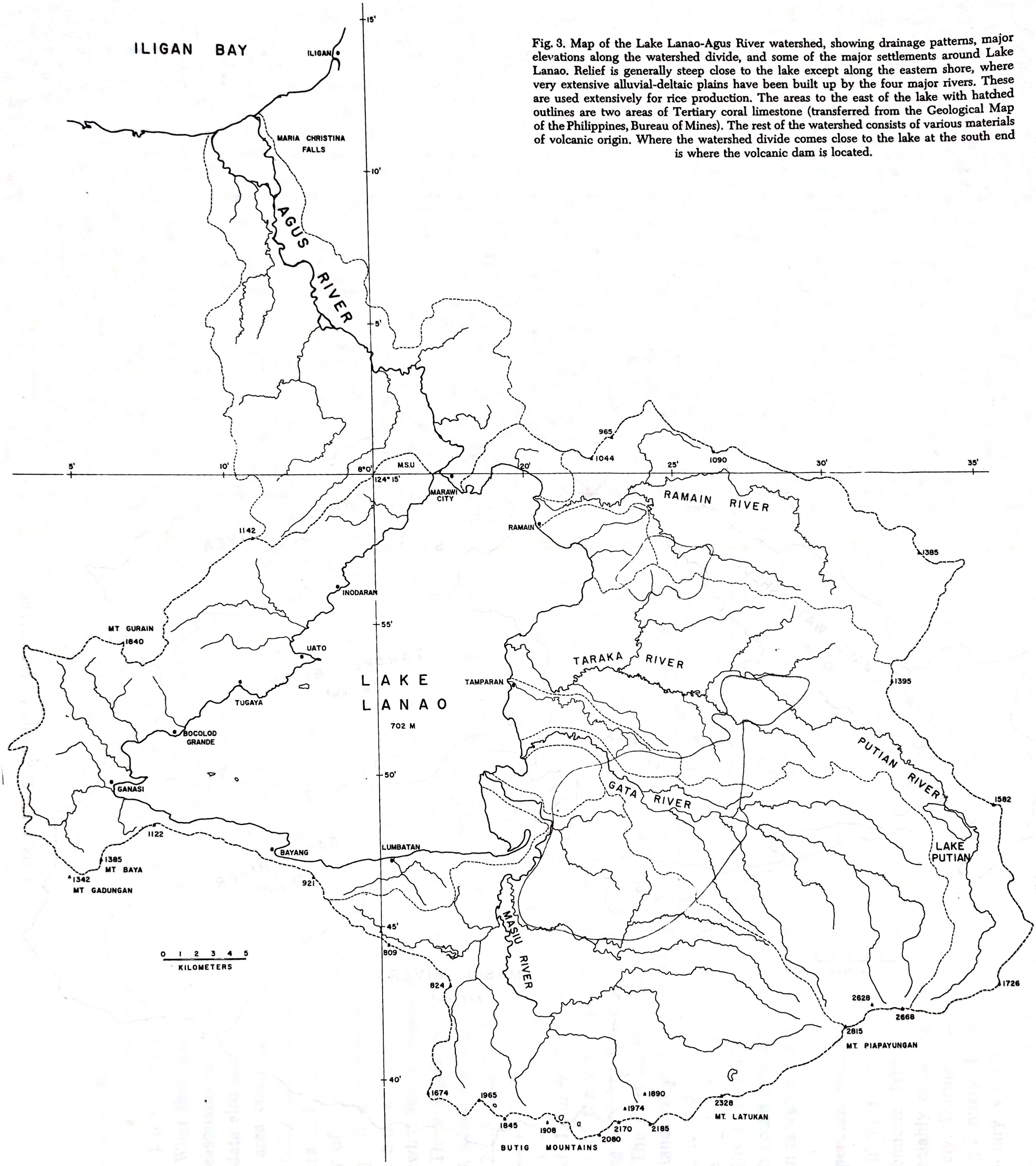

Fig. 3. Map of the Lake Lanao-Agus River watershed, showing drainage patterns, major elevations along the watershed divide, and some of the major settlements around Lake Lanao. Relief is generally steep close to the lake except along the eastern shore, where very extensive alluvial-deltaic plains have been built up by the four major rivers. These are used extensively for rice production. The areas to the east of the lake with hatched outlines are two areas of Tertiary coral limestone (transferred from the Geological Map of the Philippines, Bureau of Mines). The rest of the watershed consists of various materials of volcanic origin. Where the watershed divide comes close to the lake at the south end is where the volcanic dam is located.

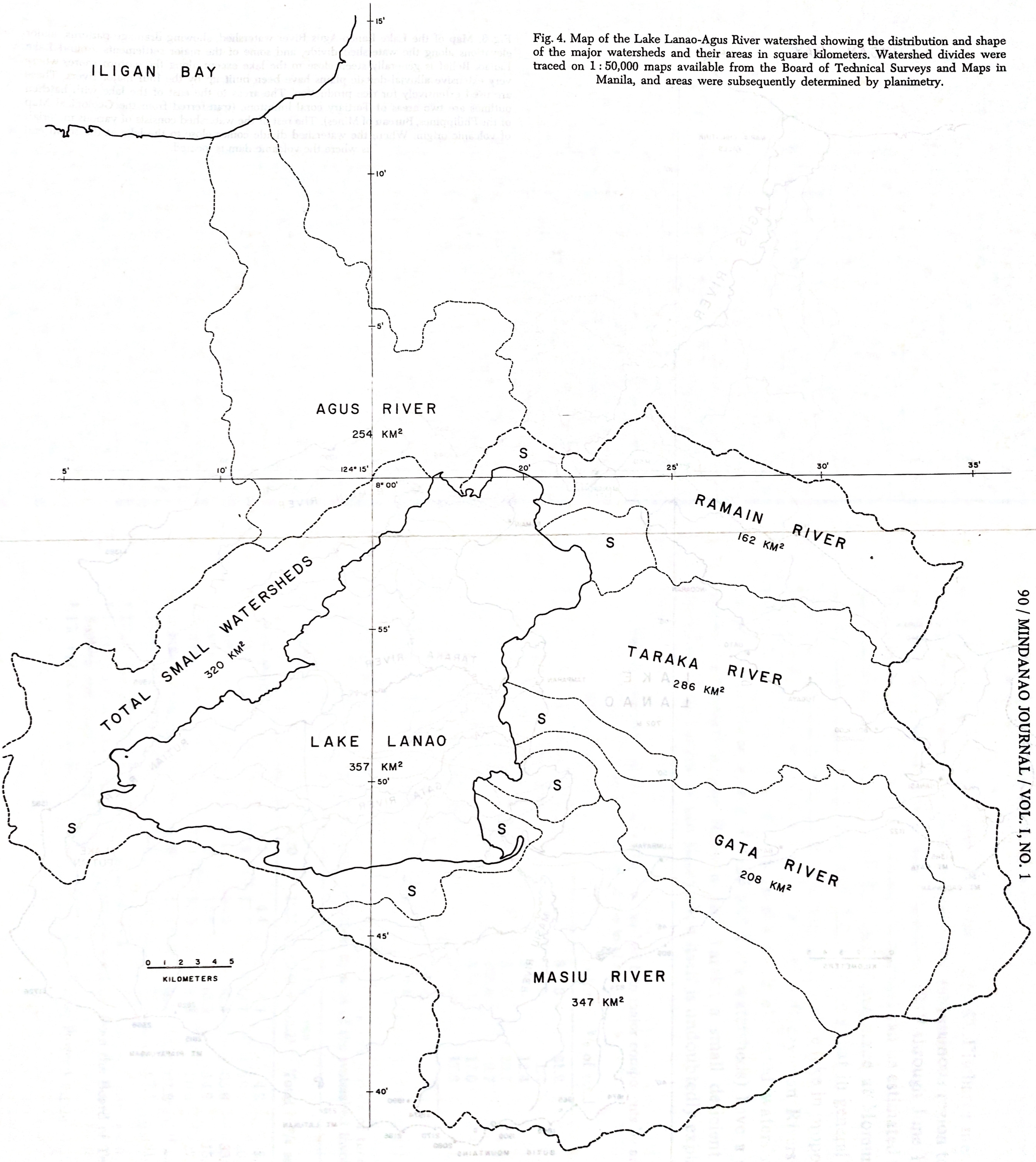

Fig. 4. Map of the Lake Lanao-Agus River watershed showing the distribution and shape of the major watersheds and their areas in square kilometers. Watershed divides were traced on 1 : 50,000 maps available from the Board of Technical Surveys and Maps in Manila, and areas were subsequently determined by planimetry.

by the water from the Gata River that flows into it through several distributaries where the river comes out of the mountains onto the Basak alluvial-deltaic plain.

What these data suggest is that the rainfall pattern and distribution are reasonably uniform over the entire watershed, at least the land area. The data also show that these rivers comprising 61% of the total watershed area contribute about 61% of the water leaving the lake. Undoubtedly the small marginal watersheds, which are largely in agriculture and grassland, experience a greater rate of evapotranspiration. Many of these small streams do not maintain surface flow during the dry portion of the year. Furthermore, because of its suppressive influence on atmospheric convection, the lake might be expected to have somewhat less precipitation than the land.

These suppositions are supported by the meager data at hand. In 1920, which was a relatively "dry" year (total precipitation at Marawi City 2685 mm), the five major rivers contributed 63% of the flow from the lake, whereas in 1921, a "wet" year (total precipitation 3262 mm), they contributed 58%. Furthermore, during December 1919 and the period January through June 1922, which encompasses the "dry" season of the year, the five major rivers contributed 73% of the flow leaving the lake at this time.

The Agus River is a high-energy stream, with a drop of 700 m over a distance of only 36 km. In order to develop a major portion of its hydroelectric potential of 750 megawatts, the Agus River would have to be regulated by the controlled release of water from the lake. Such stability in river discharge would be at the cost of stability in lake level, which could have severe economic and sociological repercussions on the region as well as marked influences on the limnology of the lake.

Temperature and light

If the 1967–68 year is representative, then Lake Lanao is a warm monomictic lake. The months December through March are so appreciably colder than the rest of the year (Fig. 2) that oligomixis is unlikely. During the year of study, the lake was actively circulating during January, February, and early March, interrupted by periods of temporary warming. From mid-February to mid-March the lake was essentially isothermal at 24.4°C. Over a three-week period from 10–31 March, coincident with the end of the winter foggy season, the uppermost 30 meters warmed rapidly to 26.5°, with a sharp thermocline between 21 and 23 m, which persisted through April (Fig. 5) at roughly the same depth. Such a sharp thermocline would be ideal for studying internal waves in the lake, except that during this period the winds apparently were not strong enough to generate seiches. A series of seven bathythermograph casts at roughly 2-km intervals along an east-west transect on 26 May gave almost precisely the same temperatures at corresponding depths. A Whitney thermistor was used for more precise temperature measurements of the uppermost 60 m.

During May and June the surface water warmed to almost 28°, which is probably near the maximum for the year. During this period also the thermal gradient moved downward and became less steep. However, temperatures at depths greater than 40 m remained at 24.3° or somewhat less throughout this period. In mid-August of 1967 when the first thermal profile of the lake was obtained, the temperature was 25.4° down to 30 m. Subsequently there was a minor warming of a few tenths of a degree in early October before the lake slowly cooled down to isothermal overturn in January.

Light was measured with a Whitney submarine photometer, which late in the study period was provided with a series of five Jena filters through the generosity of Prof. Heinz Loffler. The 1% level (without filters) varied from 11 to 25 m. Transparency was low during overturn, reached a maximum immediately after stratification was established in March, and then declined rapidly as a large bloom of nannoplankton developed (Fig. 5). Hence, the trophogenic zone is thick. Green light was transmitted best, followed in order by blue, orange, violet, and red. The approximate transmission maxima of the filters used are 420, 480, 530, 600, and 660 mμ. The Secchi disc reading on 7 May 1932 was 6 m, which made Lanao the most transparent Philippine lake of those studied during the Wallacea Expedition (Woltereck 1941).

Chemistry

Only the simplest chemistry could be studied because of the lack or non-delivery of equipment and supplies. Methyl-orange alkalinity averaged about 1.2 m.eq. and conductivity (K_{25}) about 120 micromhos. Neither of these parameters showed any systematic variation with depth during stratification. The Ramain, Taraka, and Gata rivers have con-

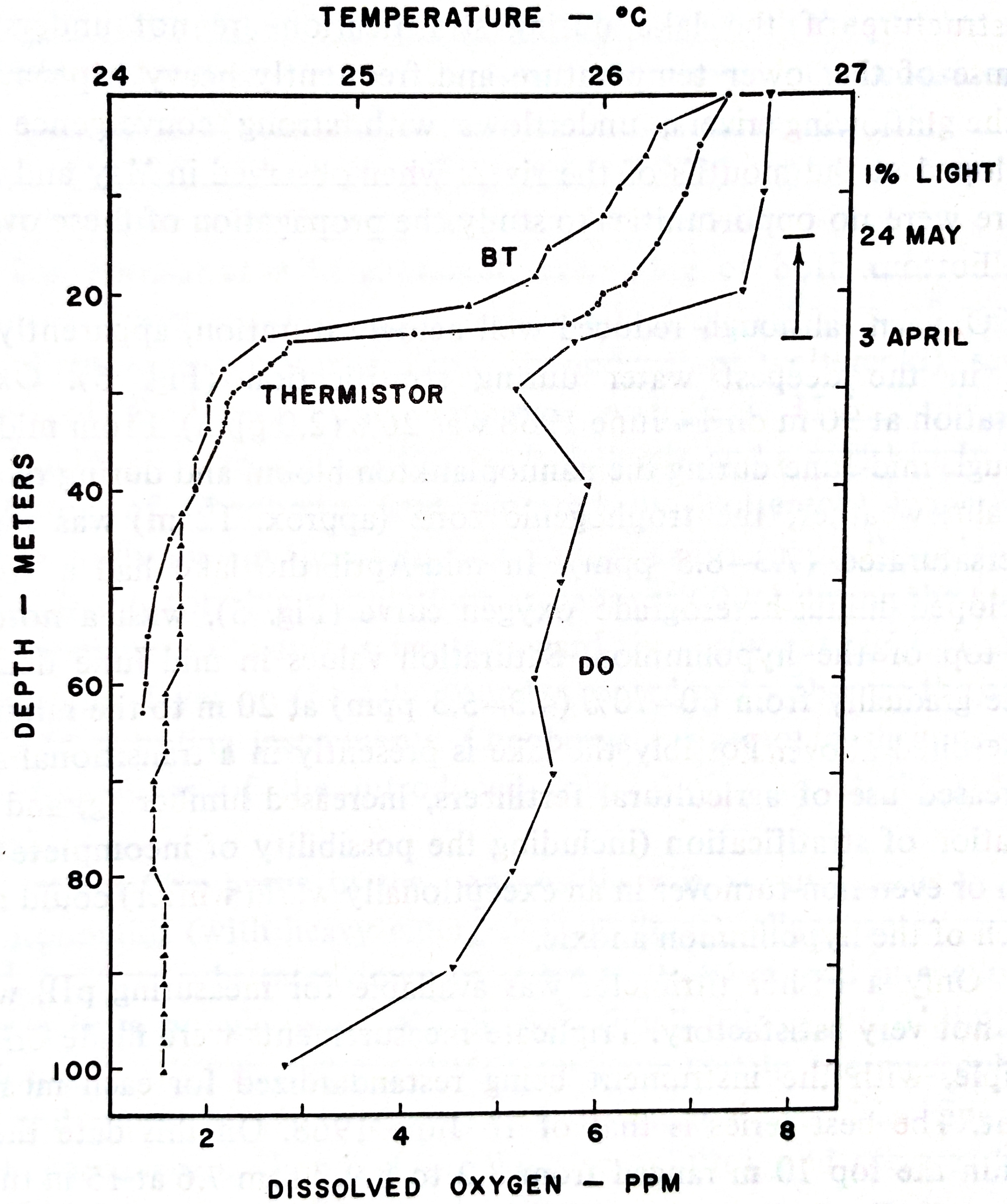

Fig. 5. Temperature and oxygen profiles in Lake Lanao on 19 April 1968. A Whitney thermistor and a Kahl bathythermograph were used for measuring temperature. The thermistor data are more reliable, as the instrument was standardized over its entire operating range against a calibrated mercury thermometer. Deepwater variations in the BT data are not significant because of the width of the stylus trace and the fact that the reading grid was not precisely drawn. Dissolved oxygen was determined by the unmodified WINKLER method. Because the temperature difference between top and bottom is so small, the saturation curve closely parallels the curve shown. The top 20 meters at this time were slightly supersaturated (106 % at the surface).

centrations less than this, the Masiu greater, (probably as a result of the Tertiary coral limestones in its watershed) so that the concentration in the lake is largely the resultant of these combined sources. The processes by which these inflowing waters become incorporated into the structure of the lake during stratification are not understood. Because of the lower temperature and frequently heavy tripton loads of the inflowing rivers, underflows with strong convergence lines developed at the mouths of the rivers when observed in May and June. There were no opportunities to study the propagation of these over the lake bottom.

Oxygen, although reduced well below saturation, apparently persists in the deepest water during stratification (Fig. 5). Oxygen saturation at 90 m on 14 June 1968 was 26% (2.0 ppm). From mid-May through mid-June during the nannoplankton bloom and during relatively calm weather, the trophogenic zone (approx. 12 m) was slightly supersaturated (7.3–8.5 ppm). In mid-April the lake had a weakly developed minus-heterograde oxygen curve (Fig. 5), with a notch at the top of the hypolimnion. Saturation values in mid-June declined quite gradually from 60–70% (4.3–5.3 ppm) at 20 m to the minimum value cited above. Possibly the lake is presently in a transitional state. Increased use of agricultural fertilizers, increased lumbering, and long duration of stratification (including the possibility of incomplete overturn or even non-turnover in an exceptionally warm winter) could make much of the hypolimnion anoxic.

Only a Fisher titrimeter was available for measuring pH, which was not very satisfactory. Triplicate measurements were made on each sample, with the instrument being restandardized for each measurement. The best series is that of 16 June 1968. On this date the pH within the top 10 m ranged from 8.2 to 8.9. From 7.6 at 15 m the pH the gradually declined to 7.2 at 45 m. These pH differences along with the oxygen saturation data give some indication of the intensity of photosynthesis at this time.

Biota

As the quantitative and taxonomic studies have not been completed, only general information can be presented. All specific names are from the report by Woltereck (1941), except as noted. There is very little net phytoplankton in the lake – chiefly **Botryococcus, Pediastrum, Melosira granulata, Ceratium,** and a filament that resembles **Leptothrix** very closely (not reported by Woltereck). Three radiocarbon runs on 26 May, 6 June, and 16 June, in the last two of which the plankton was fractionated by means of a 35 μ Nitex net, showed that considerably more than 80% of the photosynthesis at this time was being accomplished by nannoplankton. Woltereck (1941) noted many small flagellates in the centrifuge plankton on 7 May 1932.

The zooplankton is abundant, consisting of both calanoid and cyclopoid copepods (with at least one endemic species of each – **Tropodiaptomus gigantoniger** and **Thermocyclops wolterecki**), several species of Cladocera (**Diaphanosoma modigliani, Moina micrura**[1], **Bosmina longirostris,** and **Bosminopsis deitersi**), and a surprisingly large population of **Chaoborus** (not reported by Woltereck) living both planktonically and in the sediments. In terms of numbers the calanoids are dominant, forming populations as dense as 600/1 during the bloom of nannoplankton. Adults migrate toward the surface at night, forming such a dense layer on the echo-sounder record as to obscure the echos from the sampling instruments. **Chaoborus,** palaemonid shrimps, and small fingerlings of the introduced goby also occur at the surface at night.

Besides **Chaoborus** in the benthos there is a considerable variety of chironomids (with heavy emergences at times), oligochaetes, gastropods[2] on firm substrates down to at least 30–40 m, and in shallower water a large population of **Corbicula**[2]. Small palaemonid shrimp (7 species, according to Villaluz 1966) are abundant in the macrophyte zone and appear on the local markets in substantial quantities. Sponges and bryozoans are abundant on the macrophytes, and sponges have been found on gastropods as deep as 30 m.

The native cyprinids of the lake consist of approximately 20 species (perhaps more, but not yet described) of the genus **Barbodes** (also referred to as **Puntius** or **Barbus** by some authors) and several derived genera – **Mandibularca, Spratellicypris, Cephalokompsus,** and **Ospatulus.** Most of these are endemic to Lake Lanao, although at least four species also occur in Lake Dapao (Kosswig & Villwock 1965) about 5 km to the southwest of Lake Lanao and at an elevation about 100 m higher. Lake Dapao is presently in a different drainage system. Herre (1933) and Myers (1960) argued that all these species evolved from a single progenitor, **Barbodes binotatus,** although Kosswig & Villwock (1965) suggest there may have been several divergent populations of the species in the streams of the region before the lake was formed. They postulate that cyprinids (3, and possibly 4, genera) reached the southern Philippines from Borneo during one or more of the glacial lowerings of sea level. A matter of importance in the evolution of these fishes is whether the lake was already in existence at these times or was not formed until later.

A number of persons have collected (or, more commonly, purchased in local markets) specimens since Herre's time – W. L. Tressler in 1932 (Woltereck 1941: all these specimens have been lost, according to Kosswig, in correspondence), Angel Alcala in 1959 (Myers 1960), Charles E. Wood in 1962–63, Prof. Curt Kosswig and associates in 1963 (Kosswig and Villwock 1965), and ourselves in 1967–68. Wood (Wood & Wood 1963) has assembled a monograph of the cyprinid fishes of Lake Lanao (still unpublished), and Kosswig and colleagues (Kosswig, in correspondence) are still working on the systematics of the specimens they collected. Aside from Herre's original descriptions of the species, further taxonomic studies still underway, and speculations concerning the evolution of these fishes, virtually nothing else is known about them – their habitats (except for some general remarks by Herre & Kosswig), habits, behavior, food habits, and genetic relationships.

Those fishes endemic to the lake have evolved in the absence of any serious fish predators. Maria Cristina Falls about 57 m high and a correspondingly high falls on the Linamon branch of the Agus River have kept all predacious marine species – such as the gobies – from entering the lake. About 1962–64, however, the white goby (**Glossogobius giurus,** called kadurog locally) was accidentally introduced, presumably with milkfish fry planted by the Philippine Fisheries Commission (Villaluz 1966), and in the relatively few years since then has irrupted to a large population, which has made serious inroads on the populations of some of the endemic cyprinids as well as on the palaemonid shrimps. The situation is reminiscent of the havoc created by the sea lamprey **(Petromyzon marinus)** in the St. Lawrence Great Lakes. Changes are proceeding so rapidly in Lake Lanao, according to the fishermen, that some of the species may be threatened with extinction. Hence, any detailed studies on the species other than taxonomic may well have to be accomplished within the next few years if we are to get any reasonable understanding about this experiment in evolution.

Other species occurring in the lake, many of which have been introduced, are the following (Villaluz 1966): the silurid **Clarias batrachus**, the anabantids **Anabas testudineous**, and **Trichogaster pectoralis**, the anguillid **Anguilla mauritiana**, the ophiocephalid **Ophiocephalus striatus**, the ciprinid **cyprinid carpio**, the cichlid **Tilapia mossambica**, the centrarchid **Micropterus salmoides**, the chanid **Chanos chanos**, and **Glossogobius giurus**.

Productivity

Three radiocarbon series were run on 24 May, 9 June, and 16 June 1968. Light and dark bottles after inoculation with 1.89 μc of $Na_2{}^{14}CO_3$ each were incubated in situ at 0, 1, 3, 5, 7, 10, 15, 20, 25, and 30 m for three hours, approximately from 0900 to 1200 hours. On the second and third series two light bottles were run at each depth, one containing raw water and the other water that had been filtered through a 35 μ Nitex net to eliminate the macroplankton. The station utilized was off Nataron Point (the point just south of Inodaran in Fig. 3) in about 50 m of water. On all three dates the sky overhead was completely clear during the incubation period, so that photosynthesis should have been proceeding at near-maximum rates. On 24 May, which was a clear day at Mindanao State University where the pyrheliograph was located, the period from 0900 to 1200 comprised 67% of the morning insolation. If relationships in the afternoon were the same, the total insolation, and hence total photosynthesis, would be 2.98 times that of the exposure period. Because of usual afternoon clouds and haziness, however, the factor was arbitrarily reduced to 2.4 for estimating total carbon fixation during these days.

The results in Tab. 3 and Fig. 6 show the marked buildup in in phytoplankton over this period, both in terms of absolute amounts of carbon fixed and in the progressive upward displacement toward the surface of the zone of maximum (optimum) photosynthesis. On 24 May the 1% level of surface light occurred at 15.1 m, but only at 10.8 m

Tab. 3. Carbon fixation by phytoplankton, based on C^{14} uptake. The mg C/m²/day is an estimate, based on the light received during the 3-hour exposure period beng. approximately 1/2.4 of the total light-day (see text).

Date 1968	Incubation period	mg C $m^{-2}3hr^{-1}$	mg C $m^{-2}day^{-1}$	V/O ratio	Depth — meters: 1 % surface light	Depth — meters: Max. photo-synthesis
24 May	0905—1205	123	295	0.11	15.1	5
9 June	1015—1315	154	370	0.13	—	3
16 June	0930—1225	201	482	0.12	10.8	1—3

on 16 June. Fig. 6 shows that there was a fair amount of net photosynthesis (approximated by the C^{14} estimates) at depths below 10 m.

The V/O ratio proposed by Rodhe (1958) – the ratio of mg C/m³ at maximum to mg C/m² of lake surface – is approximately constant, as Rodhe also found for Swedish lakes. On 9 June 82% and on 16 June 88% of the total photosynthesis was accomplished by nannoplankton

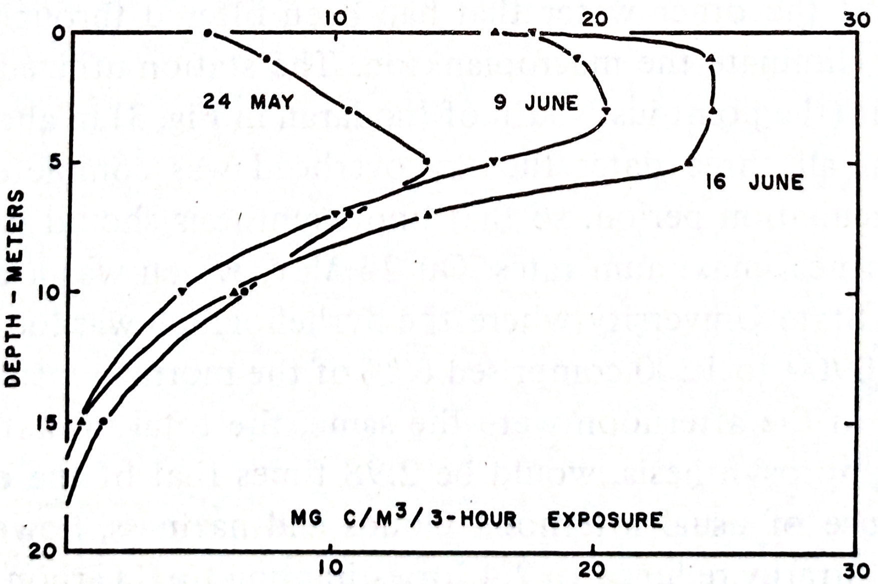

Fig. 6. Net photosynthesis, as calculated from C^{14} uptake. To convert to mg C/m³/day, the figures in the graph should be multiplied by the approximate factor 2.4 (see text). On 9 and 16 June more than 80 % of the total photosynthesis was accomplished by nannoplankton (< 35 μ). No larger algae were significantly active at depths of 7 m an greater.

(< 35 μ). Macroplankton (net plankton) was negligible in photosynthesis at depths of 7 m and greater.

One's subjective impression, based on benthos biomass, is that secondary productivity is quite high, although there are few substantiating data as yet. At irregular but rather frequent intervals except during the winter overturn, there were large emergences of midges, which could form windrows up to ½ inch thick on window sills at night when the wind was from the south. At times of such emergences the lake surface was densely populated with cast pupal skins and emerging adults. Fish were attracted toward the surface (recorded as blips on the echo sounder), and fishermen under these conditions fished their gill nets during the day rather than chiefly at night. According to the estimates of Villaluz (1966), more than 50 metric tons of shrimps and 200 metric tons of molluscs were caught in the lake in 1963–64.

Excluding these invertebrates, an estimated total of 1.7 million kg of fin fishes was caught in the lake in 1963–64, amounting to 48 kg/ha. The native cyprinids comprised 56.7% of the fin-fish catch. The mudfish (**Ophiocephalus**) and the carp (**Cyprinus carpio**) each made up 13.7% of the catch, **Glossogobius** 7.4% and **Tilapia** 6.3%. All together the introduced species comprised 27.7% of the total catch of fin fishes. Considering the high level of primary production and the apparently high level of secondary production of the invertebrate level, the fish harvest seems low. Undoubtedly there will be demands to introduce other species of fishes to utilize the food resources of the lake more effectively, but in light of what is happening to the native fishes since the accidental introduction of the kadurog, no further introductions should be permitted until the native fishes have been studied and the situation is better understood.

Large quantities of water hyacinth (**Eichornia crassipes**) grow on the lake surface. In clumps of various sizes up to large rafts they drift back and forth across the lake with changing winds and sometimes line up in distinct rows or bands along surface convergences. Removal of this material via the Agus River occurs continually, particularly when winds are from the southeast.

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AUTHOR'S NOTE: These studies were carried out while the author was a Ford Consultant at Mindanao State University. The Ford Foundation (through Educational Projects, Inc., in Pittsburgh) also provided a really extensive suite of limnological equipment, not all of which, regretfully, arrived during my period of residence in the Philippines. This research would not have been possible without the cooperation of many persons. Participating in field trips and helping collect data were my class in limnology and volunteers from among the students, faculty, Peace Corps Volunteers, and British Volunteers Service Overseas. I am particularly indebted to Asuncion A. An Lim and Rodrigo Calva, who, besides faithfully helping out during the academic year, served as full-time assistants from mid-April to mid-June, and to Dean Domiciano K. Villaluz of the College of Fisheries. Persons outside the University include Engr. D. C. Paz of the National Power Corporation, Dr. Froilan Gervasio of the Bureau of Mines, Mr. Felix E. Encina of the Weather Bureau, and Mr. Galo B. Ocampo of the National Museum. Dr. Robert G. Wetzel of Michigan State University kindly determined the activity of the C^{14} used and made counts on the membrane filters from the photosynthesis runs. The Research Center of Mindanao State University generously provided funds for rental of a boat and employment of the two full-time assistants in April—June. The Ford Foundation provided many services through its Manila office.

NOTES

1. This species was identified with the help of Goulden's 1968 monograph. Woltereck had reported the species as **M. microphthalma.**
2. Specimens sent to the National Museum in Manila have been provisionally identified as **Vivipara pagodula** Bartsch, **Vivipara mearnsi** Bartsch, **Vivipara** spp., **Pila ampullacea** Linné, **Thiara** spp., **Melania** spp., **Bulimus** spp., **Lymnaea** spp., and **Corbicula fluminea** Müller (correspondence from Mr. Galo B. Ocampo, Director, dated 30 July 1968). Hence, the fauna is quite diversified as well as abundant.

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