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Ecological Monographs, Volume 44, Issue 4 (Autumn, 1974), 377-409.

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PRIMARY PRODUCTION IN THE PLANKTON COMMUNITY OF A TROPICAL LAKE¹

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Abstract. The primary production of Lake Lanao, Philippines, was studied over a 15-month period by in situ application of C-14 and oxygen-difference techniques. Supporting data include weather, water chemistry, light penetration, and standing crop of both autotrophs and heterotrophs. A statistical treatment of production estimates precedes the presentation of data. Extensive comparison of the oxygen and C-14 methods indicates that the C-14 method as applied in Lake Lanao measures net primary production.

Data from time-course experiments show no evidence of diurnal rhythms in the efficiency of photosynthesis per unit area of lake surface. Heterogeneity studies based on transect data indicate that at low to moderate levels of production, the probability that production at an index station will differ from the average for the lake on a given date by more than 30% is less than .05, while the comparable probability for high levels of production is .35. There is no significant difference between stations in mean primary production for the study period.

Vertical profiles of photosynthesis exhibit light inhibition on all but the most overcast days. The threshold for inhibition at the surface is near 133 kerg/cm²·s during calm weather and somewhat lower in windy weather. The mean threshold for inhibition 1 m or more below the surface is lower than at the surface (101 kerg/cm²·s). The lake is exceptionally transparent (mean extinction coefficient, 0.38) considering its high productivity and has a vertical dispersion of production that is similar to temperate oligotrophic lakes. The characteristic is explained in terms of the low amounts of dissolved and suspended matter in the euphotic zone, high production per unit of standing crop, and great amount of mixing in the upper water column.

Net primary production averages 1.7 gC/m²·day, and gross primary production is 2.6 gC/m²·day. Autotrophs account for 80% of respiration in the euphotic zone. Factors controlling seasonal variation are related to resource supply rather than to temperature or biomass removal. Between 12 and 30% of seasonal variation in production can be accounted for by variations in incident light. Light limitation also occurs due to thickening of the zone of mixing during the circulation period and during storms. Nutrient supply is the dominant controlling factor during stratification. Nutrient depletion is relieved at frequent intervals by changes in the depth of mixing associated with storms. High sustained production on a low nutrient base is explained by rapid transfer of nutrients from the zone of decomposition back to the euphotic zone.

General conclusions are drawn concerning the relative importance of seasonal and aperiodic variation in regulating the resource supply of temperate and tropical plankton communities.

Key words: Plankton ecology; primary production; tropical ecology; tropical lakes.

INTRODUCTION

The marked contrast between temperate and tropical regions in annual variability of sunlight and temperature leads naturally to the hypothesis that the magnitude, efficiency, and variability of energy flow in biological systems must also differ greatly between these regions. Freshwater plankton communities are well suited for testing such a hypothesis because the productivity of lacustrine phytoplankton is well documented for the temperate zone, and because there is a great deal of taxonomic overlap in the composition of temperate and tropical plankton communities.

There is already some evidence that the tropical lakes of Africa are highly productive (Talling 1965a, 1966a). Experiments by Deevey (1955, 1957) in Central America, indirect evidence from Ruttner's (1931a, 1952) survey of Indonesian lakes and recent studies in the Philippines (Frey 1969, Lewis 1973c) suggest that tropical lakes are universally more productive than their temperate counterparts. The mechanisms by which high productivity is sustained in the tropics are still unclear, however, because of the lack of published comprehensive seasonal observations on tropical lakes other than Lake Victoria (Talling 1966a).

The present work provides an estimate of primary production in the plankton community of Lake Lanao, Philippines, and attempts to identify the factors controlling production. In recognition of tem-

¹ Manuscript received July 16, 1972; accepted December 18, 1973.

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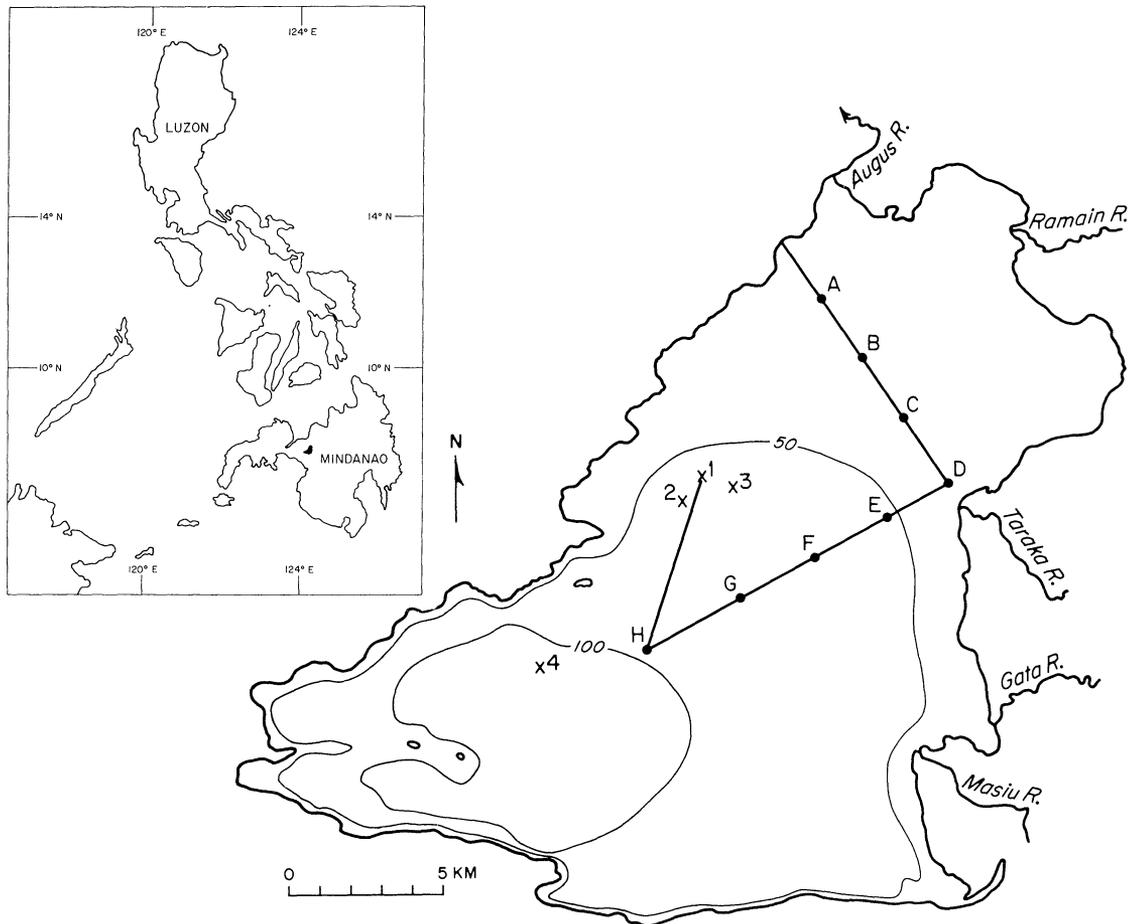


FIG. 1. Outline map of Lake Lanao showing the 50- and 100-m contours.

perate-zone findings, primary production is treated here as a quantity that is potentially variable on three linear axes and with time in both diurnal and seasonal patterns. A set of weekly depth profiles of carbon fixation over a 14-mo period provides the main data base. These profiles are evaluated in conjunction with several separate sets of experiments and observations that were designed to assess sources of variation that are not adequately accounted for by the weekly regimen of measurements. Controlling factors are evaluated on the basis of concurrent physico-chemical data and plankton census. Factors of general relevance to tropical lakes are separated from those that are unique to Lake Lanao wherever it seems justifiable to do so.

DESCRIPTION OF THE LAKE

Lake Lanao (8°N , 124°E) is located in the southern Philippines on Mindanao, 30 km inland from the Mindanao sea, 702 m asl (Fig. 1). The principal physical features of the lake as given by Frey (1969) are: maximum depth, 112 m; mean depth, 60.3 m; area, 357 km^2 ; replacement time, 6.5 yr.

As these statistics would indicate, Lake Lanao is sufficiently large and deep that the littoral community does not intrude noticeably upon the plankton community, which is quantitatively of much greater importance in determining the overall primary production of the lake. Allochthonous influences on the nutrient budget of the lake are likewise damped by the great volume of water relative to watershed size. Human impact on the nutrient budget is still trivial as there is a low population density and little intensive agriculture. More than half of the watershed is still forested.

The weather of the Lake Lanao region is cool and relatively dry from December through March. Mean temperatures for these months are generally between 21.5 and 22.5°C , and rainfall averages between 150 and 200 mm/month. April and November are transition months, and the remaining 6 mo are the warmest and wettest of the year with mean temperatures of 23.0° – 24.0°C and rainfall of 250–350 mm/month. Marked changes in daily insolation, temperature, and wind also occur at irregular

intervals in connection with typhoons moving east across the Philippines. Although 20 such storms originate in the average year, only five or six strongly affect the Philippines. Mindanao ordinarily experiences only the peripheral weather disturbance of these storms, whose main force passes to the north (Chaffee et al. 1969).

Thermal stratification is virtually absent in Lake Lanao during the last part of the cool season (January and February), which will be referred to here as the "circulation period." Exchange between deep and superficial regions of the lake is of course maximal during the circulation period. During most of the year the lake is thermally stratified. As explained in greater detail elsewhere (Lewis 1973a, b), the low ceiling on density difference across thermoclines at low latitudes and the reduced influence of the Coriolis force in the tropics results in the formation of a very thick epilimnion (40–60 m). Due to the thickness of the epilimnion and the small amount of solar heat needed to change the density of the warm epilimnetic water, the epilimnion splits into two or more layers during calm weather by the development of additional thermoclines. Significant amounts of primary production occur in only the uppermost of the epilimnetic layers. The lower, stagnant portion of the epilimnion receives senescent plankton and particulate organic matter from above, the decomposition of which leads to the accumulation of nutrients and depletion of oxygen. After an interval of a few days to several weeks, the epilimnion is once again homogenized by heavy winds. The homogenization of the epilimnion results in radical changes of water chemistry, notably nutrient concentrations, in the zone of production due to the chemical divergence of the epilimnetic layers during their separation. I have used the term "atelmixis" to refer to this mixing of chemically divergent layers during stratification (Lewis 1973b). Atelmixis occurs frequently in Lake Lanao, both by the epilimnetic-splitting mechanism just described and by a simple deepening of the primary thermocline, which results in the addition of nutrient-rich hypolimnion water to the euphotic zone.

In 1971 molybdate-reactive phosphate averaged 29 mg/m³ in the euphotic zone (0–15 m) and was always detectable. Soluble nitrate, which is probably limiting, averaged 9 mg/m³ and was frequently undetectable near the surface. Silicate averaged 9.2 mg/liter and never declined sufficiently to suggest limitation of diatom growth. Lake Lanao is moderately well-buffered (methyl orange, 51 ppm) and varies less than 10% in available carbon (12.2 mg/liter) over depth and time within the euphotic zone. The lake contains somewhat more sodium (5.0 mg/

liter) and less calcium (4.5 mg/liter) than one would expect considering the total ionic content of the water (105 μ mho) and the source of runoff. Transfer of some marine salts in rain during typhoons apparently leads to sodium enrichment (Lewis 1973a).

The phytoplankton community includes species belonging to the Cyanophyta (11), Euglenophyta (1), Chlorophyta (43), Chrysophyceae (2), Bacillariophyceae (4), Dinophyceae (3), and Cryptophyceae (2). The mean phytoplankton standing crop of the 14-mo study period, as determined by weekly cell counts, was 23000 mm³/m² (cell volume), of which 36.3% was due to diatoms, 31.3% to green algae, 19.3% to bluegreen algae, and 8.0% to cryptomonads. The five most important species as determined by mean standing crop are *Synedra radians*, *Dictyosphaerium pulchellum*, *Cryptomonas marssonii*, *Lyngbya limnetica*, and *Oocystis submarina*.

The zooplankton are dominated by *Chaoborus*, one cyclopoid copepod (*Thermocyclops hyalinus*), one calanoid copepod (*Tropodiatomus gigantiviger*), and rotifers of the genera *Conochiloides*, *Hexarthra*, *Keratella*, *Tetramastix*, and *Polyarthra*. Cladocera of the genera *Bosminopsis*, *Moina*, and *Diaphanosoma* are also present but are not so abundant as the other forms.

METHODS

Primary production in aquatic environments is measured most accurately by techniques that monitor the flux of metabolically labile molecules, especially oxygen and carbon dioxide. The most common of these techniques currently in use involve the differential metabolism in transparent and darkened bottles of either oxygen or C-14 labeled carbon dioxide. Both techniques have certain unique disadvantages that can be partially offset by using the two techniques in combination. Consequently, both the C-14 and oxygen-difference methods were used in this study for slightly different purposes and as independent checks on the overall production estimates. The details and limitations of these techniques that are not fully given below are outlined in IBP Handbook No. 12 (Vollenweider 1969).

C-14 technique

Incubations of water samples from Station 1 (Fig. 1) were made in situ at weekly intervals between 11 September 1970 and 22 October 1971. Reagent bottles containing 125 cm³ and ranging less than 5% in volume were used in the incubations. The bottles were rinsed thoroughly with distilled water and heated overnight prior to use at 150°C to prevent bacterial buildup on the glass. The bot-

tles were flushed and filled in the field from a 2-liter plastic Van Dorn sampler. Depth distribution of the samples in meters was usually 0, 1, 2, 3, 4, 5, 6, 7, 8, 10, 14, 18, 22. Two light (transparent) bottles were filled from each depth. A partitioned box with light-excluding lids for individual bottles protected the samples from light damage while they were on deck. A dark (blackened) bottle was also filled from depths 0, 2, 4, 6, 8, 10, 14, 18, and 22 m.

The C-14 inoculum consisted of a sterile (amplified) $\text{Na}_2^{14}\text{CO}_3$ water solution with an activity of $3.32 \mu\text{Ci}/\text{cm}^3$. As the activity of the inoculum was determined in the gas phase it can be regarded as highly accurate. In all cases 1.00 cm^3 of the solution was administered to the bottles with an automatic syringe of the type described by Goldman (1963). The delivery range of the syringe was checked periodically and remained less than 2% for a series of 20 inoculations.

After inoculation with C-14 the incubation bottles were shaken to mix the label and were suspended at the depths from which they had been taken. The suspension device was floated by two gallon jugs joined with a $\frac{1}{4}$ -inch steel crossbar. A floating surface rack supported the two light bottles and one dark bottle for 0 meters with about half of each bottle submerged during calm weather. The deeper samples were attached to Plexiglas plates mounted on a rope attached to the crossbar. Open-ended conduit clips held the bottles perpendicular to the rope. Horizontal bottles suspension is advantageous (Ohle 1958, Elster and Motsch 1966), and the conduit clips have the additional merit of reducing handling time on deck. The incubations always began near 0800 and terminated after about 3 h. The samples were returned to the dark box at the end of the incubation and taken immediately to the laboratory for filtration.

In the laboratory, samples were removed singly from the dark box, shaken, and subsampled (50 cm^3). The subsample was filtered at 0.5 atm vacuum onto 47-mm Millipore HA filters ($0.45 \mu\text{m} \pm 0.02 \mu\text{m}$) and rinsed twice with water to remove noncellular label. The wet filters were transferred to a scintillation vial containing 12 cm^3 of dioxane cocktail (Schindler 1966), capped, and shaken. Schindler and Holmgren (1971, *pers. comm.*) report significant losses of label through Millipore HA filters and suggest a correction procedure based on an extrapolation to zero volume. The extrapolation was made for each of the Lanao incubations, but it did not reveal any significant loss of label through the filter. The correction factor for this source of error is therefore set at unity in the calculations.

The radioassay was done with an ambient scintillation counter and the vials were individually quench-corrected by the channels-ratio method. Counting efficiencies were in the 60%–70% range.

The dpm figures that were computed from the quench and cpm were converted to mgC/m^3 assimilated by Steemann Nielsen's (1952) original procedure. The available CO_2 was estimated from the tables of Saunders et al. (1962) using pH and CO_2 content of water from the same depths as the incubated samples. The estimation in this case presents no serious threat to the accuracy of the C-14 technique because available carbon is not particularly low in Lake Lanao (11.5–13.0 mg/liter). The customary isotopic discrimination factor of 1.06 was also used in the calculations (Steemann Nielsen 1952, Sorokin 1959).

Incubation experiments with C-14 that supplemented the weekly vertical series included transects and time-course incubations, both in situ. The transects were designed to assess heterogeneity of primary production over the lake surface, and the time-course experiments were designed to expose any diurnal trends in photosynthetic efficiency.

The transect experiments were preceded by a number of tests using three stations (1, 2, and 3) as checks on variation of C-14 uptake between sites. Later the transect was lengthened to include stations A through H along a 30-km path over the lake (Fig. 1). In both the earlier (3-station) and later (9-station) versions of the transect experiment the incubation itself was carried out at Station 1 and was concurrent with a vertical series at that station. Samples were taken along the transect at a single depth nearest the depth of maximum fixation the previous week (usually 3 m) and stored in the dark box. The samples were triplicated at each station instead of duplicated as in the vertical series. The three samples from each station were inoculated at the same time as the vertical series and placed on holders suspended from a bar at the depth from which they had been taken. The transect was run backward alternately to avoid order effects on stations. The bottles were also scrambled for incubation purposes to eliminate position effects. Since the research vessel was fast, processing time for transect samples was not excessive (running time for the transect, 1 h).

Time-course incubations split the day into four equal time periods for which the C-14 fixation was separately measured by vertical series incubations at Station 1. The procedure on these days was the same as for the ordinary vertical series, except that four consecutive vertical series of equal duration covered the entire period of daylight.

The oxygen-difference technique

Thirty-two of the weekly C-14 vertical series were accompanied by a concurrent oxygen-difference incubation. The oxygen-difference incubations were carried out in 500-cm³ bottles to provide a greater volume for titration. These bottles were rinsed in weak thiosulfate to clear them of iodine, then rinsed with distilled water and heated to dryness before they were used. Two to four light bottles and an equal number of darks (usually three of each) were incubated at one precisely located depth in the lake. The depth was always near the depth of maximum fixation (2 or 3 m). One Van Dorn sample was used to fill one each of the C-14 light bottles, oxygen light bottles, oxygen dark bottles, and initial-oxygen bottles (also triplicated). The initial-oxygen bottles were immediately fixed with manganous sulfate and alkaline iodide, and the others were suspended at the depth from which they had been taken. The suspension apparatus for the oxygen bottles held the light and dark oxygen bottles at the proper depth until the C-14 incubation period was terminated, then they were fixed with Winkler reagents and returned to the lab for titration. Since a short time was required to install and remove the C-14 series, the oxygen and C-14 incubations were about 10 min out of phase. To prevent systematic error, separate starting and finishing times were recorded for each series, and the sunlight integrals for each time period were obtained separately.

The oxygen titrations were made on duplicate 250-cm³ aliquots of each bottle with N/80 thiosulfate. Duplicate titrations seldom differed by more than 0.02 cm³ of titrant, the equivalent of 0.008 mg/liter of oxygen. The results of the titrations were converted to gross oxygen production (light bottle — dark bottle), net oxygen production (light bottle — initial), and respiratory oxygen uptake (initial — dark bottle).

Bottle effects

Since all of the productivity data to be presented here are derived from incubation techniques, the final estimates are vulnerable to those errors that arise from the confinement of samples in bottles. These bottle effects include differences in turbulence and light climate and the existence of a solid substrate inside the bottle. Turbulence and gross circulation patterns, of course, influence the supply of light and nutrients reaching individual cells and the sedimentation rate of cells. Turbulence is known to affect the productivity of plankton cultures (e.g., Ohle 1961), but the exact relevance of this knowledge to in situ incubations is difficult to guess. The suspension apparatus used on Lake Lanao is very

TABLE 1. Comparison of carbon uptake in bottles of different size, all incubated at 3-m depth for 4.5 h. Means are not significantly different

	Bottle volume (cm ³)			
	125	300	500	1000
Light bottle				
Mean, mgC/m ³	206	234	234	210
Light bottle				
95% limits	158–254	186–282	208–260	192–228
Dark bottle				
Mean, mgC/m ³	15	12	12	12
Dark bottle				
95% limits	7–23	0–26	1–23	5–19
Surface (cm ²)				
per volume (cm ³)	1.32	0.87	0.79	0.63

responsive to wave action, so that the amount of water movement inside the bottles was undoubtedly related rather closely to the turbulence outside. Bottles may also screen some of the shortest wavelengths (Findenegg 1966) and thereby alter the light climate, especially at the surface. Still other effects could potentially arise from bacterial or plankton growth on the walls of the vessel, although some recent work indicates that such effects are unimportant (Qasim et al. 1972).

Bottle effects were subjected to a short investigation as a precaution against misinterpretation of incubation data. A test was designed whose null hypothesis is that bottles of the same shape with greatly different volumes should show the same C-14 uptake per unit volume. If the hypothesis had been rejected, a relation could be inferred between fixation rates and surface area of bottle per unit volume of sample. The test was accordingly formulated to fit an analysis of variance, completely randomized design, with bottle size constituting the variable of classification. Four sizes of light bottle were taken into the field, filled in random order with water from 3-m depth, inoculated with identical C-14 per unit volume, and incubated at 3 m for 4.5 h. The volumes of these four bottle types were 125, 300, 500, and 1000 cm³. Concurrently, the corresponding sizes of dark bottle were incubated in the same way. There were four replicates of each bottle size for both light and dark categories. Filtration and counting were as described for the C-14 vertical series. The results of the incubations are given in Table 1.

Experimental variances, probably due to some unforeseen difficulties in bottle manipulation, are larger than would be expected for the two smaller bottle sizes. The main effect is insignificant at the 0.05 level. The statistical implication is that the ratios of substrate area to volume were not significantly different in their effect, if any, on C-14

uptake during short incubations. This supports the validity of the incubation technique as it was applied in Lake Lanao, and suggests particularly that substrate effects were negligible.

Measurement of insolation

A Belfort pyrhelimeter located on the northeast portion of the watershed 5 km from the water's edge provided the sunlight data used in this study. Two types of data were obtained by planimetry from the intensity traces on the pyrhelimeter chart: (1) the total insolation per day for each of the 490 days spanned by the study, and (2) the exact amount of insolation during each of the incubation periods. The integration method itself produces negligible error. Planimeter readings were made in duplicate and ordinarily ranged less than 1% of the mean reading.

Potential sources of error in the sunlight data include change in sensitivity of the instrument, improper initial calibration, and variable cloud cover over the lake. The pyrhelimeter that was used on Lake Lanao is designed on the principle of differential expansion of reflective (silvered) and absorptive (dark) metal bars in response to solar heating. Instruments of this type lag slightly in their response to rapid changes in sunlight, but this is not a critical deficiency for present purposes. It was not difficult to verify the stability of the instrument because seasonal changes in maximum intensity of radiation are slight at the latitude of Lake Lanao. Systematic comparison of the midday intensity under cloudless conditions on different days thus provided assurance that the instrument was stable.

The scale accuracy of the pyrhelimeter was verified by comparing the readings for cloudless days with theoretical figures derived from the tables and constants compiled by List (1951). An example is the record for the cloudless day of 15 December 1970, for which the pyrhelimeter gave an integrated value of 565 cal/cm². During this part of December the amount of sunlight reaching the outside of the atmosphere is near 755 cal/cm². When correction is made for losses to ozone and water vapor 685 cal/cm²·day is the theoretical insolation at the earth's surface. This figure is uncorrected for transmission losses due to scattering. At a transmission coefficient of 0.7, List's tables give 430 cal/cm²·day of direct sunlight, which if corrected to the altitude of Lake Lanao would be near 473 cal/cm²·day. Assuming an equal probability of scatter in any direction, diffuse sky radiation is half the difference between the figure that was uncorrected for scatter (685 cal/cm²·day) and the direct light (473 cal/cm²·day), or 105 cal/cm²·day. The total theoretical light at the surface with the stated as-

sumptions is therefore 578 cal/cm²·day, 18% of which is diffuse and 82% direct. The total compares closely with the instrument reading of 565 cal/cm²·day. Since both the transmission coefficient and percent scattering implied by this treatment are well within the range of reasonable values for cloudless days, the pyrhelimeter reading seems quite realistic.

One final consideration related to the sunlight data is the variability of cloud cover over the lake. If the usual afternoon cumulus buildup can be figured as random over the lake and watershed, overall light values for the weather station will be typical of the lake surface. This is not always the case, since the clouds may appear first over the land, especially high ground, and move out over the lake. Under some circumstances a cloud window persists over the lake (Frey 1969) so that the watershed is shaded more extensively by cumulus clouds than is the lake surface. On a yearly basis, this effect is probably minor, but it is of potentially greater importance in the comparison of C-14 uptake to sunlight during the incubation periods. The incubation periods were scheduled to terminate before noon so that this effect was minimized. Observation indicated that radiation patterns at the incubation site were generally not significantly different from those at the weather station, which is visible from Station 1. In two instances the cloud window did result in noticeably differential clouding and the intensity trace on the pyrhelimeter chart was smoothed in the critical places for integration purposes. This amounted to a correction of around 10%.

Photosynthetically useful wavelengths comprise only 46%–48% of the total incident light (Talling 1957c, Westlake 1965, Steemann Nielsen and Willems 1971). This figure could be slightly different over Lanao because of the lower average optical air mass at 700 m altitude and correspondingly greater amounts of the short wavelengths. The percentage must also change with time of day and with season, but these sources of variation are of least importance in the tropics because the optical air mass varies over narrower limits. The proportion of photosynthetically available radiation is here assumed not to differ significantly from the values previously cited for sea level.

Biomass and nutrients

At weekly intervals, four replicate samples were taken a few meters apart at both Station 1 and Station 2 (Fig. 1). All samples were taken with an integrating tube sampler over the 0–15-m depth interval, which closely corresponds to the euphotic zone in Lake Lanao. An inverted microscope was

used to obtain the numbers of protozoa, bacteria, and all phytoplankton species present in these samples. The cell volume of each species was obtained from mean cell dimensions determined at various times of the year. This information was used to compute the total autotroph standing crop as live cell volume for each week. The specific gravity of protoplasm was assumed to be 1.0 in the conversion of total cell volume to total wet weight.

Amounts of nitrate, phosphate, silicate, and total dissolved solids in integrated samples from the 0–15-m layer were determined at approximately bi-weekly intervals. All determinations were made at more than one station. Dissolved solids assay was conducted on fresh samples that were filtered on washed Millipore HA filters and dried at 105–115 °C for 12 h. Since the range of dissolved solids from replicate stations exceeded 10% of the mean only once, results are reported simply as means. Nitrate and phosphate samples were filtered on washed Whatman GF/C (about 2.0 μm pore size) glass fiber paper and frozen in polyethylene bottles shortly after collection. Thawed samples were later analyzed for free nitrate by reduction to nitrite as described by Wood et al. (1967), followed by nitrite determinations using the method of Bendschneider and Robinson (1952). Nitrite was never detected in unreduced samples. Phosphate determinations were conducted by an ascorbic-acid molybdenum blue method (Golterman and Clymo 1969). Silicate samples were not filtered, and the analysis followed Armstrong and Butler (1962).

STATISTICAL PROPERTIES OF PRODUCTION ESTIMATES

Some caution is required in comparing oxygen-difference data with C-14 uptake data because of the difference in sensitivity and limits of variation of the two methods. For the oxygen-difference method in particular, experimental error may be large compared to measurable differences. It is thus desirable to establish the limits within which any of the production estimates can be interpreted.

Oxygen bottles

Let A_1 be set of all possible light-bottle oxygen values that could be obtained by the titration of an unlimited number of replicate bottles for a single field trip. A_1 is thus an infinite set composed of elements that can be denoted $a_{1,1}, a_{1,2}, a_{1,3}, \dots$. Population A_1 will have a variance that reflects the sampling variance (differences in composition or quantity of phytoplankton in replicate bottles at the beginning), experimental variance (differences in the treatment or initial condition of the bottles), and measurement variance (variance in titration

methods). The corresponding sample population, A_1 , is composed of elements $a_{1,1}, \dots, a_{1,i}$ where $i = 2$ or 3 depending on the number of replicate incubation bottles for the experiment represented by A_1 . The parent population is treated as normal and estimates of its parameters are derived from A_1 . The theoretical populations of light-bottle values for other field trips can be denoted as A_2, A_3, \dots , and corresponding populations of dark bottle values as B_1, B_2, \dots .

A simplified analysis of all the oxygen-bottle productivity data is possible if all the theoretical light- and dark-bottle populations are assumed to have the same variance, even though their means are certain to differ. In experimental terms, this means that the variation in light- and dark-bottle readings is independent of the oxygen levels themselves. This is a very reasonable assumption regarding the experimental and measurement components of variation. It may not be strictly true for sampling variation, but any relationship between oxygen values and variance of oxygen values for light or dark treatments is weak at best. A test of linear correlation between $|a_1 - a_2|$, $|b_1 - b_2|$ and $(a_1 + a_2)/2$, $(b_1 + b_2)/2$ showed no significant relationship ($p \gg 0.05$, $df = 61$). The assumptions are further justified by the narrow limits of variation in oxygen values over the year.

If variances are equal for all theoretical populations, then the sampling populations A_1, A_2, \dots and B_1, B_2, \dots can be treated as a unit in the determination of dispersion. The first sample populations to be considered are those that represent field trips on which only two light and two dark bottles were incubated. As an elaboration of the assumption that A_1, A_2, \dots and B_1, B_2, \dots are normal with equal variances, the confidence limits for gross oxygen production, net oxygen production, and respiratory oxygen uptake can be established from the ranges $|a_{1,1} - a_{1,2}|, |a_{2,1} - a_{2,2}|, \dots, |a_{k,1} - a_{k,2}|$ and $|b_{1,1} - b_{1,2}|, |b_{2,1} - b_{2,2}|, \dots, |b_{k,1} - b_{k,2}|$ where k is the number of trips on which two light and two dark bottles were incubated. The properties of the statistic,

$$\bar{w} = \sum_{j=1}^k (|a_{j,1} - a_{j,2}| + |b_{j,1} - b_{j,2}|) \quad (1)$$

can be derived from tabulations of w and σ for various sample sizes (Dixon and Massey 1957, Table 8b(1)). Treatment of data from field trips on which three light and three dark bottles were incubated is fully analogous.

For the complete set of oxygen data, $\bar{w} = 0.0307$ ppm, or 9.58 mgC/m³. The confidence limits of the standard error as mgC/m³ are $p(7.07 < \sigma < 10.61) = 0.95$. Setting $\sigma = 10$ mgC/m³ as a conservative measure, 95% confidence limits for individual determinations of the oxygen content of light

or dark bottles will be $\pm 20 \text{ mgC/m}^3$. For dual light and dark bottles, 95% limits on the means, expressed as mgC/m^3 , are $(a_{j,1} + a_{j,2})/2 \pm 14.1 \text{ mgC}\cdot\text{m}^3$ and $(b_{j,1} + b_{j,2})/2 \pm 14.1 \text{ mgC}\cdot\text{m}^3$. For triple light and dark bottles, 95% limits fall within $\pm 11.5 \text{ mgC/m}^3$ of the mean.

Calculation of net primary production (PN_p) and respiration of the primary producers (R_p) requires subtraction of two oxygen determinations. Variances of PN_p and R_p are consequently double the amount for a single determination (the covariance term is zero). The 95% limits for triple-bottle estimates are thus PN_p or $R_p \pm 14 \text{ mgC/m}^3$. Gross primary production (PG_p) is obtained by subtraction of light from dark bottle oxygen concentrations. In this case a nonzero covariance term must be added to account for significant correlation ($r = 0.80$) between PN_p and R_p . The 95% limits for triple-bottle estimates are thus $PG_p \pm 19 \text{ mgC/m}^3$.

Carbon-14 bottles

A treatment of the same kind that was used for oxygen can be applied to C-14 light bottles, but is somewhat more complex. A test for linear correlation between the mean and range of dual light bottles shows a weak positive but highly significant relationship ($r = 0.36$, $p \ll 0.01$, $df = 715$). This relationship would probably show up in the oxygen-bottle data as well if the sensitivity of the method did not limit its application to the most productive region of the euphotic zone and thereby restrict the range of means. It is noteworthy that Efford (1967) found a relationship of the same type in Marion Lake. The biological implications of this trend, if any, are enigmatic without more comparative information.

Whether it be of biological or technical origin, the correlation of dispersion with mean carbon fixation in the Lanao data requires that the data be partitioned according to fixation level before further evaluation. Because of the rather weak correlation, separation of the data by 25 mgC/m^3 increments in the mean produces subpopulations of ranges that are essentially homogeneous.

Beginning with paired light-bottle figures that average between 0 and 25 mgC/m^3 , subsets of the C-14 data are separately treated in a manner exactly analogous to the treatment of the oxygen-bottle determinations. Each pair of values within the subset is assumed to be drawn from a distinct theoretical population, so that the data consist of a number of samples of size, two from different populations. These populations have different means but identical variances. The variances of populations from different subsets are not the same, however, and must be estimated from the values within their own

subsets. The result of these estimations are given in Table 2. The dark-bottle values cannot be treated fully, since they were not paired. There is no reason to suspect, however, that levels of variation would exceed light bottles of a comparable fixation level. The data for light bottles imply a standard error for single dark bottles of $2\text{--}3 \text{ mgC/m}^3$. Whenever corrections are made for dark uptake at a specific depth, the dark-bottle variance must be added to the light-bottle variance derived from Table 2 to obtain the total variance of the net uptake estimate.

Depth integrals

Net primary production (PN_p) per unit area is the most frequently used summary statistic in the following data analysis. Confidence limits for this depth integral are not obvious from the above treatment of variation in C-14 fixation per unit volume of water. An upper bound can be calculated for the areal PN_p , however, and is useful as an assurance of accuracy in the C-14 technique.

Areal PN_p is obtained by mechanical integration of the photosynthesis-depth curve, which for present purposes is equivalent to the summation of areas of successive rectangles whose lengths are equal to PN_p per unit volume at successive depths and whose heights are equal to the increment between depths. The variance of PN_p per unit volume can be obtained for each depth from Table 2. The depth increment is a constant equal to 1 m over the middle portion of the profile, 2 or 4 m near the bottom of the vertical series where the bottles were more widely spaced, and 0.5 m at the top of the profile because there is no fixation above the water surface. The variance of the area of each rectangle is equal to the square of the depth increment times the variance of the PN_p per unit volume.

The variance of a sum can be obtained only if individual variances and covariances are known. Part of the variance of areal PN_p can be calculated by summing variances for each rectangular component of area. The standard deviations corresponding to such a summation for 62 PN_p profiles on Lake Lanao range between 16 and 25 mgC/m^2 . These figures are, of course, below the true standard deviations of areal PN_p because the covariance terms have not been added.

The covariance component for areal PN_p can be obtained indirectly. Since 13 rectangles must be summed in each case to obtain the areal PN_p , there are 156 possible nonzero covariance terms. Each term can be calculated as the product of the standard deviations of area in two different rectangles and the product-moment correlation coefficient for the areas of rectangles separated by a specified distance on the depth profile. The standard deviations

TABLE 2. Limits of variation for some production statistics, expressed as mgC/m³. Estimates of the variances are made from the ranges of paired samples with the assumptions detailed in the text. Correcting for dark uptake will add about 2–3 mgC/m³ to the mean standard error for C-14 production

	Cases	Standard Error Single bottle		Standard Error Mean of two bottles		Standard Error Mean of three bottles	
		Mean SE	95% Limit	Mean SE	95% Limit	Mean SE	95% Limit
Oxygen -3m							
<i>PN_p</i> , <i>R_p</i>	63	12.0	10.1–14.8	8.5	7.1–10.5	6.9	5.8– 8.5
<i>PG_p</i>	63	16.3	13.5–19.9	11.5	9.6–14.1	9.4	7.8–11.5
Carbon-14							
0–25 mgC/m ³	250	3.0	2.7– 3.3	2.1	1.9– 2.3	1.7	1.6– 1.9
25–50	178	3.8	3.4– 4.2	2.7	2.4– 3.0	2.2	2.0– 2.4
50–75	114	4.6	4.1– 5.4	3.3	2.9– 3.8	2.7	2.4– 3.1
75–100	55	5.2	4.4– 6.5	3.7	3.4– 4.6	3.0	2.5– 3.8
100–125	20	6.0	4.5– 8.9	4.2	3.2– 6.3	3.5	2.6– 5.1
125–150	19	5.8	4.3– 8.8	4.1	3.0– 6.2	3.3	2.5– 5.1
150–175	18	7.8	5.8–11.9	5.5	4.1– 8.4	4.5	3.3– 6.9
175–200	13	8.9	6.3–15.1	6.3	4.5–10.7	5.1	3.6– 8.7
200–225	16	6.3	4.6– 9.9	4.5	3.3– 7.0	3.6	2.7– 5.7
225–250	11	10.0	6.9–18.1	7.1	4.9–12.8	5.8	4.0–10.5
250–275	9	9.1	6.1–18.1	6.4	4.3–12.7	4.1	3.5–10.4
275–300	5	16.3	9.8–48.4	11.5	6.9–34.2	9.4	5.7–27.9

of rectangle area can be calculated in the manner previously described. The difficulty lies in obtaining the correlation coefficient matrix.

To estimate the correlation between areas of rectangles separated by a given depth increment, it must be recognized that variance of PN_p increases somewhat as PN_p increases (Table 2). The data must therefore be divided into homoscedastic subpopulations by increments of 25 mgC/m³ PN_p before correlation. The matrix of coefficients thus consists of rows representing different subpopulations and columns representing increasing degrees of separation between rectangles. The correlations are significant in two limited portions of the matrix: (1) At fixation levels of 25–75 mgC/m³, fixation at a given depth is significantly correlated with fixation in bottles 1, 2, or 3 positions below. The values of the coefficient are relatively low, however ($r = 0.18–0.33$). (2) At fixation levels of 250–300 mgC/m³, fixation at a given depth is significantly correlated with fixation up to 5 positions below. The coefficients in this case are higher ($r = 0.40–0.65$).

Both groups of correlations are meaningful in terms of the depth distribution of photosynthesis. Any bottle yielding low fixation is very likely to be below the depth of maximum fixation on the day in question, and a steady decline of production due to light attenuation is to be expected on this portion of the profile. The highest fixation levels are likely to be equal to or very near the depth of maximum fixation on a given date and will consequently yield higher fixation than any bottle at greater depths. Intermediate fixation levels, how-

ever, are found on the portion of the curve where light inhibition and light extinction interact to produce a rise and subsequent decline in PN_p with depth. The position of any particular incubation bottle with respect to the maximum on a given date is therefore unpredictable unless the fixation is either very high or very low.

It will be sufficient here to calculate the maximum probable variance of areal PN_p instead of making separate estimates for each depth series. The largest of the summed variances, 625, is thus used as the variance component of areal PN_p . Of the 156 possible terms in the covariance component, at most one quarter will be significantly different from zero even if the criterion for significance is relaxed ($\alpha = 0.10$). The number of nonzero terms can thus be safely set at 36. The maximum value in the correlation coefficient matrix is 0.65, and the vast majority of standard deviations for rectangle area are below 5.0 mgC/m². Each of the 36 covariance terms is thus conservatively set at $(0.65) \cdot (5.0)^2 = 16.3$. The covariance component for areal PN_p is therefore at most $(36) \cdot (16.3)$, or 587. Adding the variance and covariance components gives 1212, maximum probable variance of areal PN_p .

Since areal PN_p must be corrected for dark uptake of C-14, dark-bottle variance must be added to the estimate. When treated in a manner analogous to that used for the light bottles, dark bottles yield a maximum probable variance component of 162, or a total variance of 720 for dark fixation per unit area. The dark-corrected areal PN_p thus has a maximum variance of $1212 + 540$ or 1752, assuming that light and dark fixation are independent.

There is actually a significant relationship between the two, which adds a covariance component of 418 for a total of 2190. The maximum probable 95% confidence interval for areal PN_p corrected for dark uptake is thus $PN_p \pm 90 \text{ mgC/m}^2$, or about $\pm 15\%$ of PN_p for the average incubation period. Since this estimate is extremely conservative, the areal PN_p figures unquestionably provide a firm statistical foundation for interpretation.

RELATION OF TRUE NET PRODUCTION TO C-14 UPTAKE

Assuming that C-14 uptake rates inside the incubation bottles accurately reflected the uptake potential of the phytoplankton outside, there remains the problem of converting C-14 uptake to production. Gross production can be defined here as the total amount, measured as carbon or as energy, of organic compounds synthesized by phytoplankton from sunlight, oxygen, and carbon dioxide. Furthermore:

$$PG_p = PN_p + R_p + E_p, \quad (2)$$

where PG_p = gross primary production, PN_p = net primary production, R_p = respiration of the primary producers, and E_p = excretion of the primary producers. From the most elementary consideration of photosynthesis (excepting autotrophs that use substrates other than CO_2), it is plain that the uptake of C-14 will occur at a rate very nearly proportional to PG_p . It is equally obvious that when the carbon label has entered the cell, there is a probability that it will be affected either by R_p or E_p , and thus will leave the cell. For this reason, the measurable quantity, C-14 content of phytoplankton cells, cannot without risk be assumed to represent either PG_p or PN_p . Some evidence indicates that the C-14 method very nearly represents net production for short incubations (Vollenweider 1969). For the Lanao study, the separation of PG_p into its components was of sufficient interest to warrant a systematic calibration of the C-14 method with oxygen-difference incubations.

The experimental plan was to use C-14 techniques extensively to measure variation of production with time, depth, and location, and thus profit from the great sensitivity of the technique and the extent to which it can be automated. The accompanying study of production by the oxygen-difference technique at one location near the surface, as described in the methods section, was intended to calibrate the C-14 data and provide a means of separating PG_p , PN_p , and R_p . It is thus assumed that certain deficiencies of the oxygen method are not critical. For example, increase of plant biomass in the light bottle during the incubation may result in a slight

increase in R_p that does not occur in the dark bottle, or dark bottles may show slightly excessive respiration because they are protected from short wavelengths of light (Ryther and Vaccaro 1954). The separation of R_p from heterotrophic respiration is dealt with in the subsequent data analysis.

The photosynthetic quotient

In order to make conversions between oxygen-difference and C-14 uptake measurements, some average values must be established for the relative fluxes of oxygen and carbon dioxide through the phytoplankton. The stoichiometry of this relationship would be static if synthetic processes always resulted in the same proportions of compounds. Since the proportion of highly-reduced compounds varies, the photosynthetic quotient (O_2/CO_2 , molar) also varies. Nutritional status is known to affect the quotient (Fogg 1965).

The photosynthetic quotient of Lake Lanao phytoplankton was measured on one occasion. Four light and 4 dark 500- cm^3 bottles were incubated at 3 m for 3.5 h on 20 November 1970. Two light bottles and 2 dark bottles were fixed with Winkler reagents and titrated with thiosulfate, but the other 4 bottles were titrated to an electrometrically checked endpoint for CO_2 (200 cm^3 , N/88 H_2SO_4). The results are as shown in Table 3. The photosynthetic quotient for these data is 1.26, very close to the value of 1.25 judged by Strickland (1960) to be a good average. The agreement is somewhat deceptive, however, in that the methods used here could not establish the quotient to any great degree of accuracy in a single set of determinations. More on the strength of Strickland's recommendation than this particular experiment, all calculations calling for the conversion of oxygen to carbon are based on the quotient 1.2.

Comparison of oxygen-difference and C-14 production estimates

In order to establish the relationship between C-14 uptake and true net production, carbon fixation as estimated by the C-14 technique can be compared with the production figures that were obtained by the oxygen-difference method. A comparison is best made after correction for the slightly different incubation times of the oxygen and C-14 bottles. The C-14 estimate of carbon fixation per unit sunlight is therefore compared with the carbon equivalent of net oxygen production (PN_p) per unit sunlight on the same day at the same depth.

Carbon-14 fixation is virtually identical to net production as measured by oxygen-difference. A nonparametric pairing-design test, the Wilcoxon Signed-Rank Test, indicates no significant difference

TABLE 3. Concentrations of oxygen and carbon dioxide in light and dark bottles after a 3.5-h midmorning incubation at Station 1

	Light ppm	Dark ppm	Differ- ence ppm	Differ- ence μ moles/ liter
Oxygen	8.43	7.74	0.69	21.5
Carbon dioxide	48.50	47.75	0.50	17.0

between PN_p and C-14 uptake ($z = -0.57$, $n = 32$). Variances of areal PN_p or areal dark fixation are not so highly dependent on fixation rate as are the variances of PN_p per unit volume, hence the relationship of the two variables can be expressed as a linear correlation. The overall mean production as determined by the C-14 techniques is 0.533 mgC/m^3 per cal/cm^2 of incident sunlight. The comparable figure for the concurrent oxygen incubations is 0.523. The correlation coefficient for these two independent measures of production is 0.95 and highly significant ($t = 16.9$, $df = 30$).

The analysis suggests that for the Lanao data it is safe to equate carbon fixation estimated from C-14 uptake with net production determined by the oxygen-difference method, which is in turn presumed to be an accurate measure of PN_p . This relation will be assumed as valid for all sampling dates and all depths.

A second interesting implication of the analysis is that E_p , excretion by primary producers, must be quite small on the average. The C-14 uptake method should greatly underestimate PN_p if much of the C-14 label is released in organic form from cells, as would occur if E_p were large. The assumption that E_p is trivial compared to PN_p therefore seems justified.

DIURNAL VARIATION IN PRIMARY PRODUCTION

Since the C-14 vertical series were always incubated at the same time of day, precautions must be taken against the possibility that the resulting values are not typical for the entire day. Potentially the most disturbing influence on the data would be a persistent diurnal rhythm in production that could cause the ratio of production to sunlight for any particular time of day to be either consistently above or below average for the day. Such a rhythm would also be of direct biological interest.

The details of two complete Lake Lanao time-course incubations are given in Fig. 2 and Table 4. The great difference in magnitude of PN_p and sunlight from one time period to another suggests that small differences in the ratio of production to sunlight should not be considered significant. The two

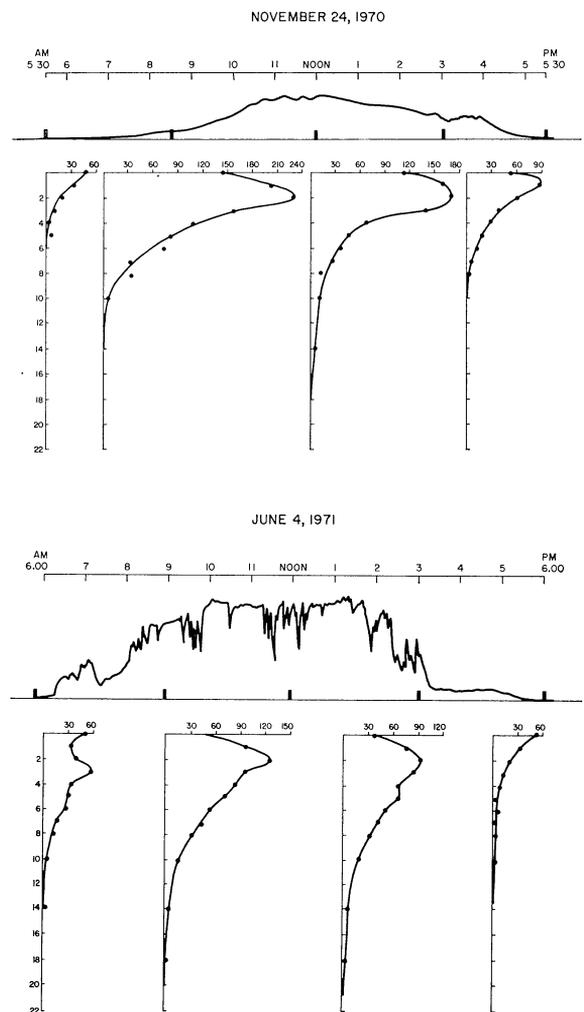


FIG. 2. Curves for sunlight and primary production (dark-corrected) for two time-course experiments on Lake Lanao. Each day is divided into four equal time periods covered by separate vertical series incubations at Station 1.

days that were chosen for the experiments differed greatly in total sunlight and mean level of productive efficiency. November 24 was an overcast day with a relatively smooth daily change in insolation. The upper water column at this time had been recently recharged with nutrients by *atelomixis*. June 4 was a partly cloudy day with rain and heavy cloud cover during the fourth period (Fig. 2), and was scheduled during a period of marked nutrient depletion. No obvious rhythm of productive efficiency is visible in the data for either of the experiments. A third experiment was done on 26 March under intermediate conditions and gave similar results, but is not detailed here because the first two incubations were lost.

Numerous studies have demonstrated diurnal

TABLE 4. Distribution of primary production, sunlight, and photosynthetic efficiency over the day in two time-course experiments on Lake Lanao

Date	Measurement	Time Period				Total or Mean
		1	2	3	4	
24 Nov. 1970	Time	0530-0830	0830-1200	1200-1500	1500-1730	
	PN_p (mgC/m ²)	87.0	1012.0	777.0	293.0	2169.0
	% of Total	4.0	46.6	35.8	13.5	100.0
	Sun (cal/cm ²)	6.5	91.9	90.5	24.6	213.0
	% of Total	3.0	43.0	42.4	11.5	100.0
	PN_p /Sun	13.5	11.0	8.6	11.9	10.2
	PN_p %/Sun %	1.33	1.08	0.84	1.17	1.0
4 June 1971	Time	0600-0900	0900-1200	1200-1500	1500-1800	
	PN_p (mgC/m ²)	282.0	721.0	624.0	127.0	1754.0
	% of Total	16.1	41.1	35.6	7.3	100.0
	Sun (cal/cm ²)	92.7	236.5	227.2	30.5	587.0
	% of Total	15.8	40.3	38.7	5.2	100.0
	PN_p /Sun	3.0	3.1	2.7	4.2	3.0
	PN_p %/Sun %	1.02	1.02	0.92	1.40	1.0

changes in the photosynthetic potential of natural phytoplankton assemblages by incubating samples taken at different times of day under fixed artificial illumination (Doty and Oguri 1957, Yentsch and Ryther 1957, Shimada 1958, Ryther et al. 1961, Lorenzen 1963, Newhouse et al. 1967, Kalf 1969). There is typically, but not always (Newhouse et al. 1967), a morning peak in photosynthetic potential. Studies in situ under natural, variable light conditions both by incubation (Vollenweider and Nauwerck 1961) and by observation of diurnal changes in the dissolved gases of the water column (Verduin 1957) also suggest the existence of diurnal patterns. Beyers (1963) has repeatedly documented respiratory and photosynthetic rhythms in experimental microcosms. Interpretation of this evidence is difficult, since the observed patterns almost certainly are effected by multiple influences on primary production.

The immediate point of interest in converting relatively short C-14 incubations to day-rate estimates is the amount of variation over the day in production per unit area for a unit of incident sunlight. Most studies of photosynthetic potential contribute little to the solution of this problem because they deal with only a portion of the community (e.g., a specific depth) or do not include quantitative sunlight data. Although the response of algae to constant light does provide information about their physiological state or the limiting conditions of the medium at a particular time, the phytoplankton at any specific depth in the water column can experience this light climate for only a few brief periods during the average day. There are also certain obvious limits on the potential light climate at any given

time of day or depth that may override the productive capacity of the phytoplankton.

The photosynthetic rate of phytoplankton is maximum at some intensity between the extremes of midday irradiance at the surface and relative darkness at the bottom of the euphotic zone. The precise diurnal pattern of areal photosynthesis in a theoretical plankton community without any diurnal rhythm whatever is therefore not obvious. Talling (1955, 1957a) has given theoretical arguments in favor of an approximately logarithmic relationship between areal PN_p and incident radiation in such a community, whereas other models (Sverdrup 1953) assume a linear relationship. If diurnal rhythms are a superimposed source of variation, as they appear to be in nature, the probable relationship between areal PN_p and light becomes even more obscure.

While there is little doubt that diurnal productivity patterns are widespread in planktonic systems, it is thus unclear whether there is always an accompanying diurnal variation in the ratio between areal PN_p and light per unit surface area. Since a variety of intrinsic factors (endogenous physiological rhythms, cell division cycles, light adaptation) and extrinsic factors (zooplankton migration, nutrient exhaustion, photo-oxidation) must operate simultaneously in nature, one rhythm could easily obscure or moderate another. The only realistic evaluation of the areal relationship of PN_p to sunlight is therefore empirical.

Few simultaneous determinations of sunlight and areal primary production in situ for discrete intervals over an entire day are reported in the literature. Goldman (1960, 1963) refers to the use of such data in evaluating his incubations and notes that at

least in Castle Lake, California, amounts of production during the first and second halves of a day are little different. Tilzer (1973) reports no significant diurnal variation in the ratio of sunlight to primary production in a mountain lake. The most extensive study was done by Vollenweider and Nauwerck (1961) on Lake Erken. This study has been frequently cited as evidence of diurnal asymmetry of photosynthetic efficiency. The Lake Erken data were originally used to document the effect of incubation duration rather than diurnal variation and are refigured alongside the Lanao data in Table 5 to stress diurnal variation in PN_p . The appearance of high photosynthetic efficiencies both early and late in the day on 30 May suggests a weakness in the analysis that has not been previously considered. Vollenweider and Nauwerck apparently did not correct for nonphotosynthetic fixation of C-14. Since the bottles of the first and last periods remained in near-darkness for much of the incubation period, dark fixation could obviously have given inflated photosynthetic efficiencies. If a true rhythm were involved, one would expect a low evening efficiency. It therefore seems that a diurnal rhythm of photosynthetic efficiency has never been satisfactorily documented in a natural plankton community. The absence of a marked rhythm in photosynthetic efficiency in Lake Lanao (Table 5) is thus not so surprising as it first appeared to be from the literature.

It would be unwise to draw categorical conclusions about the diurnal pattern of photosynthesis in Lake Lanao on the basis of present information. Since the production per unit sunlight was found to be constant for any particular day, however, the correction of incubation rates to day rates will be made in this work on the basis of direct proportion from sunlight values. The error of estimating PN_p over the whole day of 24 November 1970 using the incubation data of only the second period and the sunlight for the whole day is +8%. The comparable error for 4 June 1971 is +3%.

AREAL HETEROGENEITY OF PRIMARY PRODUCTION

Primary production may vary over the surface of a lake as the phytoplankton respond to local variations in sunlight, nutrients, cropping, and other factors. Areal heterogeneity of primary production in Lake Lanao was assessed first on the basis of C-14 data from three stations and subsequently from a nine-station transect of the lake.

The first test for heterogeneity consisted simply of a comparison of C-14 fixation at stations 1, 2, and 3 in the manner previously described. The stations were situated 1 km apart in a triangle (Fig. 1). Comparison of the stations on 2 October, 6

TABLE 5. Ratio of net production per unit area to incident light in Lake Erken, as calculated from the data of Vollenweider and Nauwerck (1961), and in Lake Lanao. Time periods divide the day into equal portions beginning with sunrise and ending with sunset. More time periods were required for Lake Erken because of the greater day length (17 h) than on Lake Lanao (12 h). Blanks for Periods 1 and 2 on 26 March are due to difficulties that delayed the start of the experiment

Time period	Lake Erken		Lake Lanao		
	30 May 1956	1 July 1956	24 Nov. 1970	26 Mar. 1971	4 June 1971
1	2.92	1.39	13.5	—	3.0
2	1.86	1.07	11.0	—	3.1
3	0.94	0.83	8.6	8.4	2.7
4	1.07	1.04	11.9	8.5	4.2
5	2.31	1.09			

November, and 25 December 1970 showed only trivial differences. The coefficients of variation in C-14 uptake between stations were 3.5% in October, 3.7% in November, and 1.8% in December. Such variation is so low as to be virtually indistinguishable from variation between replicate samples at a fixed location.

Since the preliminary work provided some assurance that C-14 data from Station 1 would be highly representative of a rather large area in the vicinity of the station, a more elaborate study of variation was designed to cover a much larger portion of the lake. The size of PN_p at a fixed depth near the point of maximum fixation is assumed to be representative of productivity at each of the nine stations (A-H) on the sampling transect. The rather close relationship between areal PN_p and PN_p at the depth of maximum fixation will be demonstrated in a later section. It seems valid on both theoretical and empirical grounds to assume that areal PN_p will be no more variable, and will probably be considerably less variable, than PN_p at a fixed depth (3 m) near the depth of maximum fixation.

Variability in PN_p along the transect at various times of the year is illustrated in Fig. 3. Since all of the samples were incubated at Station 1, all variability is due to the phytoplankton themselves or to the chemistry of the water from which they were taken, and not to variation in light. Previous statistical considerations (Table 2) show that some of the between-station differences on particular days are significant. The 95% limits for fixation in the 50 mgC/m³ range are approximately ± 5 mgC/m³, and in the 150 mgC/m³ range, about ± 8 mgC/m³ from the mean.

There are few really striking differences between stations. The first two transects were made during the preliminary phases of stratification and probably reflect variations in the degree of mixing at various

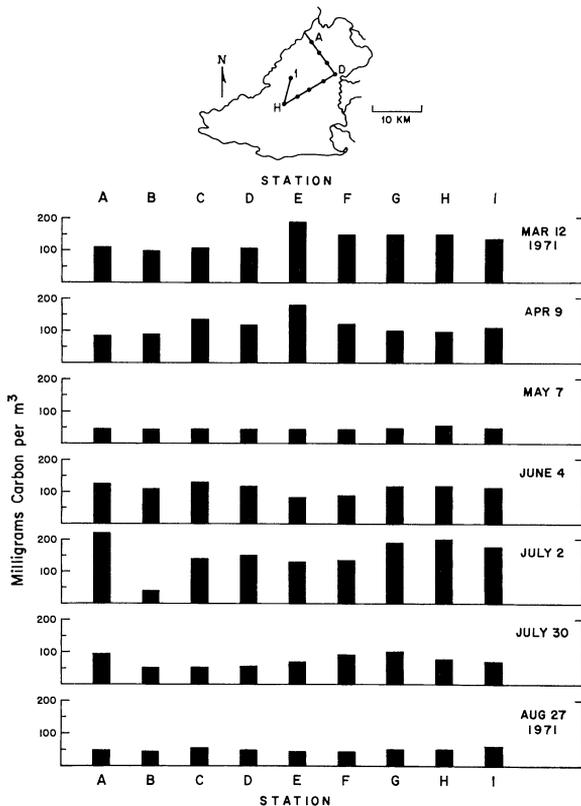


FIG. 3. Areal heterogeneity of net primary production on seven sampling dates at nine stations. Bars indicate the amount of light-bottle carbon fixation at 3-m depth for a 3-h incubation. Each bar is the mean of triplicate bottles. Confidence limits for the means are as given in Table 3.

locations. Transects for 7 May and 27 August were both made at times of nutrient depletion and show remarkable uniformity. The transect for 2 July followed some important June storms that caused atelomixis. The marked difference in productivity between stations A and B on this date suggests that the stormy weather generated some heterogeneous water masses at the surface. Station A may have received a charge of nutrients that were dislodged from the nearby littoral zone during the period of

heavy southerly winds, or internal waves may have caused upwelling in this area.

Table 6 summarizes the level and variation of production for the 7 transect dates. The differences in mean PN_p between days are of course highly significant, but their explanation can be deferred pending the discussion of seasonal variation in PN_p . The chief implication of Table 6 is that heterogeneity of primary production over the lake surface is greatest when PN_p is high. This is not to be confused with the earlier finding that variability of PN_p for replicates at the same station increases as PN_p increases.

The hypothesis of equal variances for all sampling dates can be tested using the maximum F -ratio statistic. The tabulated value of F_{\max} (Bliss 1967) at $df(7,9)$, $\alpha = 0.01$ is 13.1. The F_{\max} statistic from Table 6 is 85, implying a highly significant difference between variances. The exponential nature of phytoplankton growth during favorable periods undoubtedly magnifies the importance of all types of local variation, and thereby results in greater divergence of water masses during these periods.

The rate of primary production at Station 1 seems on the whole to be a highly reliable indicator of productivity at other points on the lake. It is of course impossible to make a precise statement without gridding the entire lake, but the transects intentionally followed a path that would invite variability. The data suggest that at low to moderate levels of PN_p , the probability that a measurement of PN_p at Station 1 would lie within 30% of the mean for the lake is greater than 0.95, and at moderate to high PN_p the probability is greater than 0.65.

The foregoing considerations have left open the possibility that certain regions of the lake are consistently more productive than others, even though no such difference is obvious in Fig. 3. The means and variances for the nine stations of the transect are given by Table 7. Testing for the equality of means in this case requires that variances be equal for each station. The maximum F -ratio test shows no significance differences between the variances of

TABLE 6. Means and variances for net primary production at 3-m depth on 7 different dates. Means are for 9 stations, 3 bottles for each station and date

Date ('71)	Mean	Rank	Variance	Rank	Coefficient of variation, %	Rank
12 March	133.2	2	922	2	23	4
9 April	111.9	3	805	3	25	2
7 May	42.9	7	34	6	13	6
4 June	109.3	4	259	5	15	5
2 July	151.9	1	2907	1	36	1
30 July	72.4	5	292	4	24	3
27 August	47.8	6	27	7	11	7

TABLE 7. Mean, rank, and variance for net primary production at 3-m depth for 9 stations on Lake Lanao. Means represent 7 incubation dates for each station, 3 bottles for each station and date.

Station	Mean	Rank	Variance	Rank
A	102.4	4	3557	2
B	66.7	9	916	9
C	92.4	7	1796	8
D	89.4	8	1813	7
E	103.8	3	3786	1
F	93.8	6	1850	6
G	106.7	1	2830	4
H	106.0	2	2897	3
I	99.6	5	2041	5

PN_p at these nine stations ($s_{\max}^2/s_{\min}^2 = 4.12$; $F_{\max, .05(9,7)} = 13.5$). The comparison of means is most appropriately carried out with a one-way analysis of variance, randomized complete block design, model 1. The overall PN_p is known to vary between days, and this source of variation is removed as a block effect. Table 8 shows that there is no significant difference in PN_p between stations.

The absence of any substantial differences between stations also implies that the precision of long-term productivity estimates for the lake greatly increases with the number of C-14 incubation dates on which they are based. This would not necessarily be true if variability between stations were high.

DEPTH DISTRIBUTION OF NET PRIMARY PRODUCTION

Perhaps the most thoroughly explored aspect of primary production is its distribution with depth. Early theoretical investigations, which began in oceanography, have been reviewed by Patten (1968). The intensive application of production-depth models to lakes originated with Talling (1957a, 1957c), who developed a successful means of predicting areal photosynthesis on the basis of a light saturation curve and a minimum extinction coefficient. Vollenweider (1965, 1970) subsequently added a more realistic photosynthesis response curve (cf. Steele 1962) and analytical methods for integration over depth and time, which have since been interpreted numerically for easy application (Fee 1969). None of the models is particularly suited for the overall analytical purposes of this work, hence the Lake Lanao data are not fitted to a model. The concepts and terminology of the Talling and Vollenweider models are particularly useful for the treatment of vertical distribution of PN_p , however, and are used below for this purpose.

Light inhibition

Selected profiles of PN_p in Lake Lanao are given in Fig. 4 to illustrate the annual variation in vertical

TABLE 8. Analysis of variance for station effects on primary production, randomized complete block design

Source	Degrees of freedom*	Sum of squares	Mean square
Blocks (trips)	6	95707	15951
Treatments (stations)	8	8742	1092
Error	48	33231	692
Total	62	137681	—

* $F = 1.58$; $df = 8,48$; $F_{.05(8,48)} = 2.2$.

distribution of PN_p . All but two of the 62 weekly incubations showed suppression of photosynthesis near the surface. This is a familiar feature of the photosynthesis-depth relation in lakes and is usually attributed to light inhibition. Ryther (1956) has convincingly demonstrated the vulnerability of marine phytoplankton to light inhibition under nearly natural conditions, and the inhibition phenomenon has long been recognized in culture work (Rabinowitch 1951). However, Talling (1965a) has emphasized that sedimentation may play a role in the suppression of photosynthesis near the surface of lakes. The problem is further complicated by the adaptation of plankton cells to their light climate (Rabinowitch 1951, Fogg 1965). The limits within which these adaptations are possible and the speed with which they occur cannot be specified even in general terms for natural communities. The persistence of the subsurface maximum in PN_p for Lake Lanao suggests, however, that light inhibition is in fact the major explanation for a suppression of surface rates, and that the intensity of light at the surface even on partly overcast days exceeds the compensatory abilities of the phytoplankton.

Approximate boundary conditions can be established for photoinhibition at the surface of Lake Lanao using the 62 weekly profiles and daily records of sunlight. Photosynthesis was highest at the surface only on 25 December 1970 and 9 July 1971. The average insolation for incubation periods on these two dates was low—0.26 cal/cm²·min for 25 December and 0.38 cal/cm²·min for 9 July. On four other incubation dates insolation was below 0.40 cal/cm²·min, but on each of these dates there was some surface suppression of PN_p . There is a clear distinction between these 4 days and the 2 days when PN_p was maximum at the surface. The weather on 25 December and 9 July was calm, whereas the other 4 days were either windy (white-caps) or extremely windy (storm). Since winds of this strength occurred on fewer than 25% of the incubation days, there is some reason for inferring a causal relationship between wind and surface PN_p .

When the weather is windy, a plankton sample at the surface of the lake is likely to contain a high

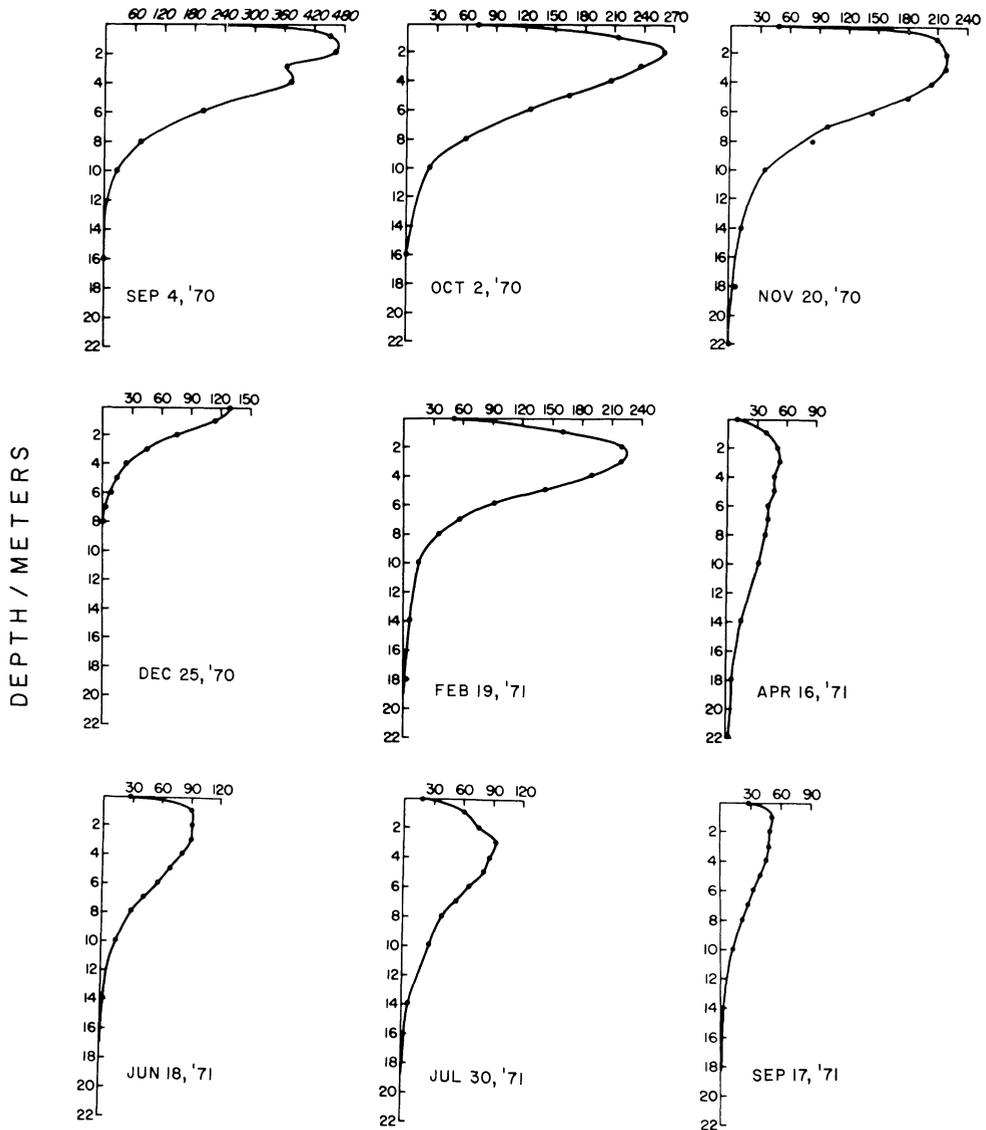
MILLIGRAMS CARBON PER M³

FIG. 4. Depth distribution of primary production for the selected incubation dates of the study period. Production is expressed as mgC/m^3 for a 3-h incubation, corrected for dark fixation. Each point is the mean of two determinations. All plots have the same scale except 4 Sept. 1970, which is double the others.

proportion of cells that have only recently been transported by turbulence to the surface. These cells would be adapted to very low light intensities and could suffer from light inhibition if they were trapped in a bottle and held at the surface, as during a C-14 incubation. On a calm day at the same light intensity, a surface sample is likely to contain many cells that have been near the surface for long periods and have adapted to the light climate as fully as they are able. The threshold of

light inhibition is therefore likely to be higher on a calm day than on a windy day. This is the simplest hypothesis that accounts for the results, although by no means the only one.

Low sunlight thus appears to be a necessary but not a sufficient condition for preventing light inhibition of PN_p at the surface of Lake Lanao. The best approximation from the data of the minimum irradiance that will cause light inhibition in calm weather is $0.40 \text{ cal}/\text{cm}^2 \cdot \text{min}$. Since this figure rep-

resents surface irradiance (I_0), compensation must be made for reflection and photosynthetically inactive wavelengths. Reflection can be set at 5% and the photosynthetically active portion of the remaining light (I'_0) can be set at 0.46 according to the rationale of Talling (1957c, 1965a). The threshold of photosynthetically active radiation for light inhibition at the surface is thus 0.19 cal/cm²·min (133 kerg/cm²·s) during calm weather and somewhat lower in windy weather. Talling (1957c) notes that he and a number of other workers have placed the inhibition thresholds between 100 and 150 kerg/cm²·s for a wide variety of phytoplankton. The inhibition threshold for Lake Lanao cannot therefore be considered particularly high despite the high average irradiance at such low latitudes.

Sunlight must fall below the inhibition threshold each day during the first and last hours of daylight. The approximate threshold of inhibition and the daily sunlight data can in fact be used to calculate the proportion of production on Lake Lanao that occurs under noninhibiting light conditions. Insolation usually first exceeds 0.40 cal/cm²·min between 0700 and 0800 and remains above this level until afternoon. Because of the usual afternoon clouding and rain, intensity drops below 0.40 cal/cm²·min by 1300 to 1400 and remains low until sunset. In a sample of 20 days drawn at random from the study period, the mean interval between sunrise and the time insolation first reaches 0.40 cal/cm²·min is 1.95 h. The average interval between the last occurrence of 0.40 cal/cm²·min and sunset is 3.70 h. The estimated portion of the light day for which light inhibition is insignificant is therefore about 5.65 h, or nearly half the average day. The average amount of sunlight delivered during this period is about 0.20 cal/cm²·min or a total of 68 cal/cm²·day. This is 17% of the daily average sunlight (399 cal/cm²·day, 1 November 1970–31 October 1971). Production profiles showing light inhibition therefore account for at least 83% of the total PN_p on Lake Lanao.

If the calculation of inhibition thresholds is extended to include dates when inhibition occurred well below the water surface, the extinction of light within the water column must be accounted for as well as the incident radiation. The observed depth of maximum fixation (z_{opt}) is only an integrated measurement for the incubation period. The depth of the PN_p maximum might furthermore be affected by unequal vertical distribution of phytoplankton biomass. It will be assumed that irradiance is a direct correlate of z_{opt} for a given incubation period, and that biomass is not so unequally distributed as to invalidate the calculations. Because of the brevity of the incubations and the relatively high turbulence

TABLE 9. Statistics related to light inhibition of photosynthesis in Lake Lanao. The depth at which the maximum volume rate of photosynthesis occurred (z_{opt}) was obtained from plots of PN_p against depth for the dates listed. Mean insolation (I'_0) is the total amount of sunlight delivered to the water surface during the incubation, less 5% to correct for reflection, divided by the length of the incubation period (usually 180 min). The extinction coefficient for green light was obtained on each date with a submarine photometer and Schott filter (525 nm peak). The last column lists the total photosynthetically available radiation at z_{opt} as calculated from the other columns by the method described in the text

Date (1971)	z_{opt} (m)	Mean I'_0 cal/cm ² ·min	η'_{min} (Green)	I''_{opt} , 300–700 nm kerg/cm ² ·s
Feb 19	2.4	1.15	.446	98
Mar 19	2.0	0.33	.283	56
Apr 2	4.0	1.14	.281	91
Apr 22	3.0	0.74	.238	102
Apr 30	3.5	0.68	.253	73
May 7	5.0	1.33	.252	87
May 21	4.0	1.11	.257	98
Jun 11	1.3	0.56	.353	109
Jun 17	2.0	0.99	.394	122
Jul 2	2.5	0.83	.375	84
Jul 23	2.5	0.72	.292	95
Jul 30	3.0	1.04	.279	109
Aug 13	4.0	1.19	.288	91
Aug 27	4.5	1.10	.228	123
Sep 3	3.5	1.30	.255	136
Sep 17	4.0	1.10	.293	81
Sep 24	3.0	0.98	.262	126
Oct 22	2.5	1.23	.342	130

near the water surface, these assumptions seem reasonable.

The range of z_{opt} for the 62 weekly incubations is 0.0–5.0 m, and the mean is 2.6 m. The inflection of the PN_p curve at z_{opt} is taken as the onset of light inhibition. On certain of the incubation dates, a full set of color filters was used to determine the optical properties of the water. The amount of photosynthetically available energy reaching z_{opt} on these dates can be determined by Talling's procedure (1957c, 1965a), which can be summarized as

$$I''_{opt} = (0.95) \cdot (0.46) \cdot I_0 \cdot \exp(-\eta'_{min} \cdot z_{opt}), \quad (3)$$

where I''_{opt} is the photosynthetically available (400–700 nm) radiation at the depth of maximum fixation, I_0 is the incident radiation, η'_{min} is the extinction coefficient at the wavelength of maximum transmission times a correction factor of 1.33 (Talling 1957c), and z_{opt} is the depth at which PN_p is maximum. The results of the calculations are given in Table 9.

The mean value of the threshold for light inhibition from Table 9 is 101 kerg/cm²·s. There is some tendency for higher values of I''_{opt} to accompany higher mean values of I_0 . The exceptionally low value of I''_{opt} on 19 March, for example, oc-

curred on an overcast day. This trend may reflect the compensatory abilities of the phytoplankton. The threshold values are somewhat lower than the threshold obtained previously for plankton at the lake surface. This is entirely reasonable, since the autotrophs deeper in the water column may in many instances be acclimated to lower average light intensities. The two analyses concur in their implication that the inhibition threshold is not exceptionally high for the phytoplankton of Lake Lanao.

Profile shape

Most of the PN_p -depth profiles conform to the pattern of a smooth curve with a maximum at only one depth (z_{opt}) in accordance with the expected interaction of light inhibition and light attenuation acting on a uniformly distributed autotroph biomass (Fig. 4). A few profiles (e.g., 4 September 1970) are slightly dichotomous. Production curves with multiple maxima are relatively common in small lakes (e.g., Schindler and Holmgren 1971) and occasionally appear in larger lakes as well (e.g., Rodhe 1965). Findenegg (1964) has recognized that dichotomous curves are characteristic of certain lakes, although it is equally clear that the form of the production curve can change seasonally in any lake. There is no obvious relationship between thermal and chemical conditions of the water column and the occurrence of double maxima in Lake Lanao. The uppermost thermocline is almost always too deep to split the euphotic zone as it does in some lakes, so the divergence of communities separated by a thermal discontinuity is not common. Convolutions of the production-depth curve must therefore represent unstable divergences of a temporary nature or random heterogeneity in the water column and are apparently of no great significance to the productivity of the lake.

The most striking seasonal change in shape of the production-depth curves is the disappearance of marked production maxima between 15 April and 1 June and the concurrent deepening of the production profile. This type of curve apparently accompanies severe nutrient depletion and essentially amounts to a truncation of the PN_p per unit volume in accordance with the nutrient shortage. The lower levels of PN_p near the surface are associated with lower volume-specific standing crop and higher transparency, which partially relieves the light limitations on production deeper in the epilimnion. The mechanism by which nutrient depletion occurs and its effect on areal PN_p are treated in connection with seasonal changes in primary production.

In view of the high levels of production that are

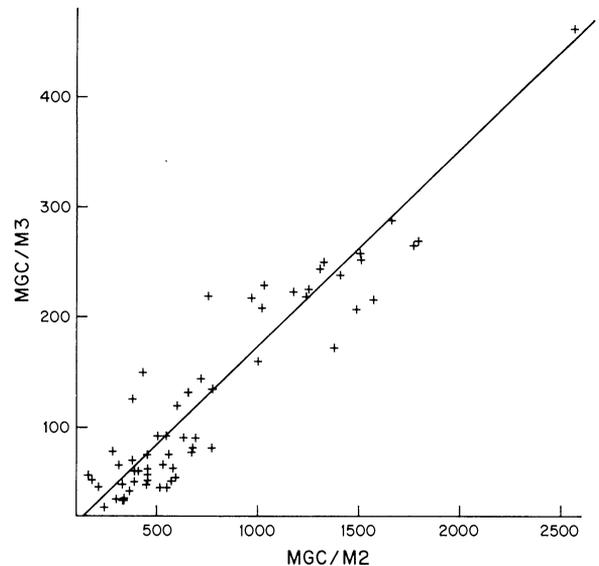


FIG. 5. Relation between production per unit surface area (x) and production per unit volume at the depth of maximum fixation (y). Each data point represents one incubation period of about 3 h. All uptake rates are corrected for dark fixation.

evident in Fig. 4, the extinction coefficients of Table 9 and the high mean value of z_{opt} (2.6 m) indicate that Lake Lanao is surprisingly transparent. The distribution of production with depth is more reminiscent of a transparent oligotrophic temperate lake than a eutrophic lake with its typically compressed euphotic zone. An ingenious means of measuring the shape of PN_p -depth profiles was invented by Rodhe (1958) and is useful in evaluating this apparent peculiarity of Lake Lanao. Rodhe has demonstrated that lakes differ greatly in the vertical distribution of PN_p and that individual lakes can be characterized by a line relating maximum production per unit volume (V , Volumen) to total production per unit area (O , Oberfläche). Because Rodhe's lines are based on 24-h incubations, part of the difference between lakes is masked by underestimation of high PN_p . The lakes that Rodhe treats are nevertheless distinguishable on the basis of their V/O ratio. The eutrophic lakes, Erken and Gorvaln, have high V/O ratios, while the oligotrophic lakes, Kultsjon and Ransaren, have a more diffusely distributed production and a consequently lower V/O ratio.

Rodhe does not report slopes or regression analysis. My calculations from his Fig. 4-7 indicate the following slopes for plots of maximum production per unit volume (y) against production per unit area (x): Kultsjon, 0.20; Ransaren, 0.18; Erken, 0.30; Gorvaln, 0.38. All regressions are significant

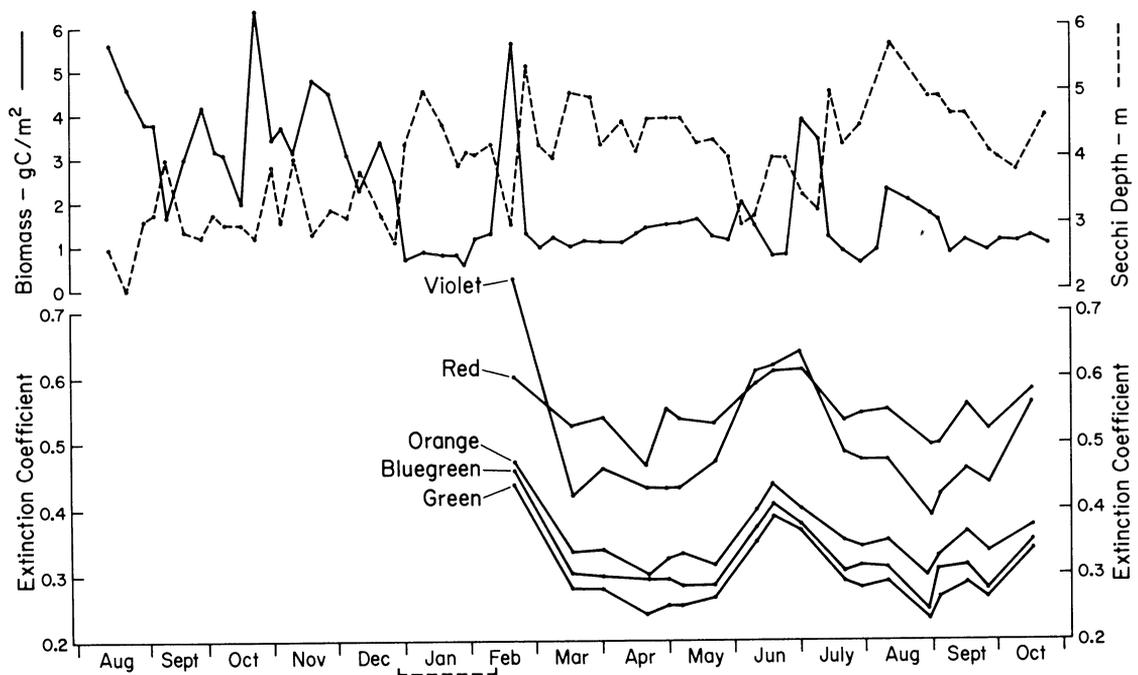


FIG. 6. Distribution of standing crop and light penetration over the study period on Lake Lanao. Standing crop for the euphotic zone (0–15 m) was obtained by phytoplankton census, and is expressed as gC/m² on the assumption that 10% of the fresh weight is carbon (Strickland 1960). The spectral breakdown of penetrating light was accomplished with Schott filters having transmission maxima of 660, 600, 525, 520, and 370. Extinction coefficients are means for coefficients at 1-m intervals from 1 to 14 m.

at $\alpha = 0.05$. The V/O ratio for Lake Lanao is derived from Fig. 5. The regression is highly significant ($t = 15.7$, $df = 60$), with a slope of 0.18 (95% limits, 0.156–0.200). Lake Lanao thus falls within the range of Rodhe's oligotrophic lakes from Lappland, despite the fact that its annual productivity greatly exceeds that of eutrophic Lake Erken.

Three factors contribute to the simultaneous occurrence in Lake Lanao of a low V/O ratio and a high level of primary production. (1) The attenuation of light in the water column is minimally affected by dissolved substances and nonautotrophic suspended matter. (2) The production per unit of standing crop is high. (3) The uppermost portion of the euphotic zone is thoroughly mixed by nocturnal cooling, and the epilimnion is exceptionally thick.

(1) The contribution of nonautotrophic particles (principally detritus, bacteria, protozoa) and dissolved matter to light extinction is difficult to quantify. If light extinction is minimally affected by nonautotrophic components, however, the dependence of light penetration on standing crop of autotrophs must be high. A comparison of autotroph standing crop and light extinction can thus be formulated to test the hypothesis.

Figure 6 illustrates the changes of standing crop

and transparency over the study period. The most penetrating component of light, which was green on all dates, is accepted as the fairest representation of total light penetration (Talling 1957c), and need not be multiplied by a correction constant for purposes of regression analysis. Standing crop is an approximate measure of pigment concentration. Since absorbance and concentration are linearly related according to Beer's Law, the relation between standing crop and extinction coefficient should be linear. A linear correlation between standing crop and extinction coefficients for green light is highly significant ($p \ll 0.01$) but only moderately strong ($r = 0.61$). About 38% of the variation in light penetration is thus accounted for by changes in standing crop. Although truly comparative data are difficult to obtain, the dependence of light climate on standing crop in Lake Lanao appears to be stronger than in many temperate lakes, but perhaps weaker than in marine environments (Platt 1969, Schindler and Holmgren 1971, Talling 1971). Weekly phytoplankton census counts confirm that nonliving material is a negligible component of the seston in Lake Lanao. Talling (1965a) has noted the relatively high transparency consistent with high standing crop in Lakes Victoria and Nyasa, and Lewis (1973c) has observed the same phenomenon

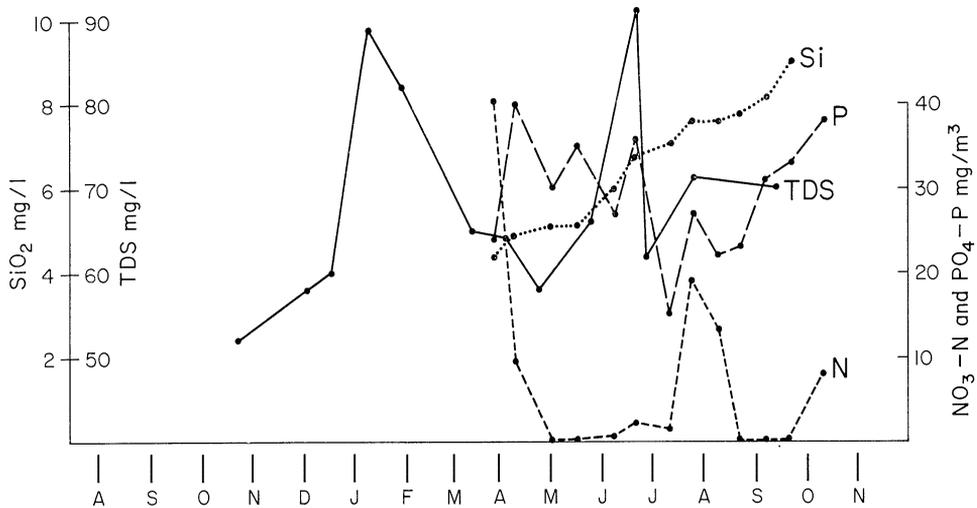


FIG. 7. Variation of nutrient and dissolved-solids concentrations in Lake Lanao. Concentrations apply to integrated samples of the euphotic zone (0–15 m).

in another Philippine Lake. Tropical lakes may prove to be so efficient in the degradation of organic compounds that they are generally more transparent for a fixed standing crop and hence have thicker euphotic zones.

A close examination of Fig. 6 shows that identifiable factors other than standing crop are related to transparency. The increase of extinction coefficients, particularly of the shorter wavelengths, during June 1971, for example, is coincident with storms causing atomixis and a consequent rise in the dissolved solids component of the upper water column (Fig. 7). Similar events occurred during October 1971.

(2) If production per unit of standing crop (PN_p/B_p) ("bioactivity," Ohle 1956) is high, less transparency is sacrificed for a unit of production than if PN_p/B_p were low. High bioactivity is thus likely to increase the vertical dispersion of PN_p , and thereby decrease the V/O ratio.

Methods for the evaluation of PN_p/B_p have not yet been standardized for lakes. If PN_p per incubation period or per day is used to compute the ratio, the variation in incident light, which is not under biological control, will be reflected in the result. The efficiency of PN_p , expressed as PN_p per unit of incident light, is not subject to this criticism. Justification for the use of the efficiency to typify production on a given day comes from the observation discussed in a previous section that PN_p per unit surface area on a specified day is approximately proportional to incident sunlight. The biomass portion of the PN_p/B_p ratio can be equated with the standing crop of the euphotic zone, which is here defined as the upper 15 m of the water column, or approxi-

mately the depth at which photosynthesis balances respiration in Lake Lanao. Standing crop is expressed as gC/m^2 with the assumption that wet weight can be converted to carbon at a rate of 10% (Strickland 1960).

The relationship between efficiency of PN_p and B_p is illustrated in Fig. 8. Productivity increases with standing crop, and efficiency of PN_p is predictable to a surprising degree from B_p on the basis of a simple linear model. Linear correlation is highly significant ($p \ll 0.01$) and rather strong ($r = 0.77$). Direct biological implications of the correlation are rather limited, however, because of the multiplicity of factors affecting the ratio. Marked nutrient depletion, for example, partially inactivates phytoplankton biomass so that PN_p/B_p ratios for such periods fall consistently below the regression line regardless of the standing crop. In Lake Lanao nutrient depletion is due to disappearance of available nitrogen from the euphotic zone during extended periods of calm weather. The marked reductions of PN_p/B_p ratios for two such periods, late April through early June 1971 and late August through late September 1971 (Fig. 7), are indicated in Fig. 8.

The PN_p/B_p ratio is perhaps most meaningful intuitively when it is expressed as a biomass-turnover rate, or a finite rate of change in biomass over a 1-day period measured as the exact number of days required to replace the standing crop at the time of census. Each of the points in Fig. 8 can be converted to a turnover time by multiplying the ordinate by the total sunlight for the average day (399 cal/cm^2), converting the abscissa to mgC , and dividing the abscissa into the ordinate. The use of an average sunlight figure is intended to remove

the nonbiological source of variation from the PN_p/B_p ratio, but the results are not qualitatively different if individual sunlight measurements are used instead.

The turnover rates for Lake Lanao are compared with those of other lakes in Table 10. The range for Lake Lanao is perhaps deceptively broad because of a single turnover measurement exceeding 4 days. The next highest measurement was only 2.35 days. The highest value was obtained during a period of severe nitrogen depletion (3 September 1971), however, and is probably not due to measurement errors. Variability in turnover rates is surprisingly moderate (C.V. = 55%). The mean turnover rate of Lake Lanao is obviously very high although temperate lakes during summer may have turnover times as short as the shortest for Lake Lanao. Comparisons must be made with caution because of the seasonal bias of data from the temperate zone. The Canadian values are probably deceptively high because the lakes are sufficiently shallow to have truncate euphotic zones. The darker portions of the productive layer are thus selectively eliminated from the euphotic-zone average for these lakes.

The turnover times in Lake Lanao are obviously sufficiently short to account partially for the simultaneous occurrence of high transparency and high productivity.

(3) Nocturnal cooling of tropical lakes causes a great amount of turbulence in the upper portion of the euphotic zone because of the rapid change of water density with temperature at high temperatures. Accumulation of biomass near the surface is thus unlikely to occur in Lake Lanao and other tropical lakes, except those which are very shallow. Accumulation of standing crop near the surface (at z_{opt}) would be likely to increase the V/O ratio,

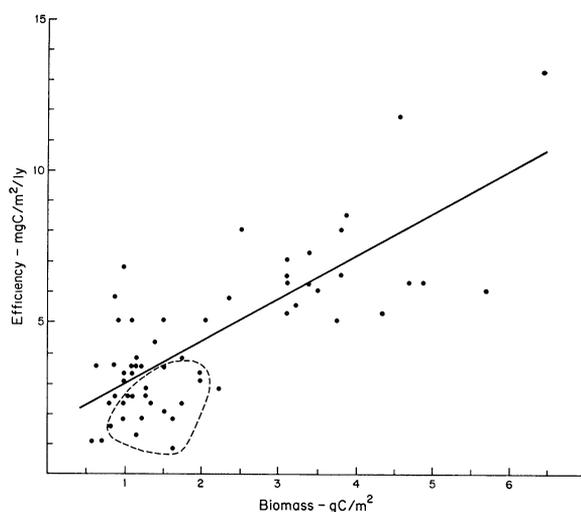


FIG. 8. Relation of standing crop to photosynthetic efficiency in Lake Lanao. Standing crop (0–15 m) is given as carbon with the assumption that carbon accounts for 10% of fresh weight. Efficiency is given as PN_p per unit total incident light (langley). The efficiency figures can be doubled to obtain efficiencies for the photosynthetically active wavelengths only (400–700 nm). The dashed line encloses all points representing two extended periods of documented nutrient depletion.

hence the nocturnal cooling must be a factor increasing the dispersion of PN_p .

The mixing effect of wind on Lake Lanao, and on tropical lakes in general, is greater than on comparable temperate lakes, for reasons that are given in detail elsewhere (Lewis 1973b). The homogeneity with which B_p is distributed through the upper water column and the vertical distance over which a given wind strength effects this distribution are thus likely to be greater in Lake Lanao than in a temperate-zone counterpart. Vertical rarefaction

TABLE 10. Turnover rates for various lakes and lake districts. Biomass is in all cases derived directly from phytoplankton census and cell volumes and converted to carbon at a rate of 10%. Productivity is in all cases computed from C-14 uptake. Variability indicated by the range is directly affected by meteorological conditions for all data except Lanao. Note that ranges are not strictly comparable due to differing numbers of samples represented

Locale	Season	Source	Turnover rate (days)			Number
			Max	Min	Mean	
Swiss lakes	Spring, autumn	Findenegg (1965)	7.1	0.23	6.08	12
Lake Erken	Jan.–July	Nauwerck (1963)	33.3	0.59	2.90	13
Carinthian lakes	Spring, autumn	Findenegg (1965)	4.8	0.77	2.55	12
Lake Mainit (Philippines)	Aug., Nov.	Lewis (1973c)	1.8	1.4	1.60	2
Canadian lakes	July, Aug.	Schindler and Holmgren (1971)	2.8	0.44	1.21	15
Lake Lanao	Weekly, 15 mo		4.9	0.35	1.24	61

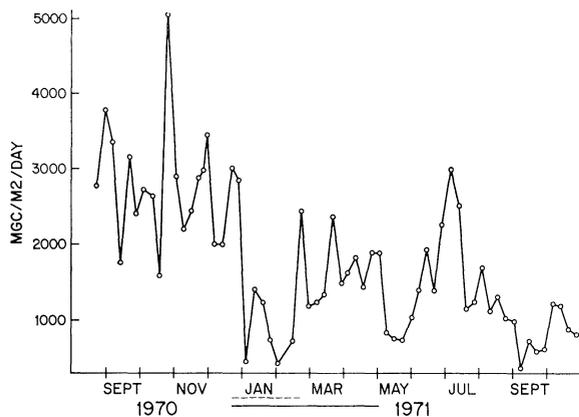


FIG. 9. Net primary production per unit surface area on Lake Lanao for the study period. Points were obtained by (1) integration of weekly production profiles, (2) division of areal photosynthesis so obtained by the total light for the incubation period, (3) multiplication of the ratio of production to light times the total sunlight for the days represented by the incubation (usually the day of incubation plus the three preceding and the three following days), (4) division by the number of days. Note that the ordinate begins at 300 mgC/m²·day instead of 0 mgC/m²·day. The dotted line on the abscissa marks the period of minimum water temperatures and deepest seasonal mixing. The solid line marks the period when the lake lacks a stable thermocline.

of B_p can in turn be expected to result in low V/O ratios.

SEASONAL VARIABILITY OF PRIMARY PRODUCTION Net production

The distribution of net primary production over the study period is illustrated in Fig. 9. The annual net primary production calculated from these values is 690 gC/m² between 26 August 1970 and 25 August 1971. Since the data cover a period exceeding 12 mo, it is worthwhile to consider the overlapping annual values in making the final estimate. The annual PN_p for the period 26 October 1970 to 25 October 1971 is 550 gC/m². The lower estimate in this case reflects a difference in conditions during the 1971 stratification period. The mean of these figures provides the final estimate of annual PN_p , 620 gC/m², or 1.7 gC/m²·day.

Since incubation periods are relatively short they introduce sources of variation that are of no biological interest whatever. A plot of primary production against time is subject to error if either the sunlight or the response of the plankton community to a unit of sunlight during the incubation period is atypical of the time block represented by the incubation period. It is not feasible to monitor algal response to sunlight continuously, but sunlight can be recorded continuously, totalled for each time

block, and used in the final data presentation (Fig. 9) to remove artifacts in the data that would appear if only the sunlight of the incubation period were considered. Figure 9 thus shows the annual pattern of primary production with minimal interference from atypical sunlight measurements.

The following features of Fig. 9 are noteworthy: (1) Primary production is low during January and February while the lake is isothermal. (2) High primary production is typical of the transition from circulation to stratification (March through April 1971). (3) Primary production for the stratification period of 1970 (prior to 30 December) is greater than for the stratification period of 1971 (subsequent to 1 May). (4) Peaks of productivity (e.g., October 1970) are not followed by a fully compensatory crash. Production characteristically stabilizes at a relatively high level following a peak. (5) The steady rise of primary production during June of 1971 and rather steady decline through early September 1971 indicates a change from generally favorable to unfavorable conditions during the stratification period.

The two outstanding features of the results are the extremely high level of primary production and the evenness of its distribution over the year.

Respiration and gross production

Although respiration of phytoplankton was measured much less extensively than net production, an annual mean can be calculated from the oxygen-difference data. The annual mean oxygen consumption within dark bottles was equivalent to 3.4 mgC/m³·h ($n = 32$, 95% limits 2.6–4.3). This is not a direct estimate of R_p , however, since the heterotrophic components of the plankton contributed to the total oxygen decrease within the bottles. Separation of trophic levels can be achieved either by filtration of the samples or by complete census of heterotrophs and autotrophs followed by individual estimation of their respiratory rates based on their body size. The latter procedure was adopted because filtration gives incomplete separation and is traumatic to the plankton.

The metabolic rate of organisms varies with size, thus

$$R_1 = aW_1^b, \quad (4)$$

where R_1 is respiration of an autotroph biomass unit, and W_1 is the size of that unit. The respiratory rate for heterotrophs of a given size relative to autotrophs of a given size is therefore

$$R_2/R_1 = a'W_2^{b'}/aW_1^b, \quad (5)$$

where R_2 is the respiration per unit time and W_2 is the size of heterotroph.

The estimation of R_2/R_1 demands two approximations. First, mean body sizes must be assigned to autotrophs and heterotrophs despite their variation in size. Important autotrophs in this case vary in volume between about 30 and 700 μm^3 , although some rare species fall outside this range. The weighted seasonal average is near 500 μm^3 , which will be used here. Important heterotrophs are more variable and must be treated as three groups. These groups with their approximate weighted mean body sizes are: microcrustacea and rotifers, 300,000 μm^3 ; protozoa, 1,000 μm^3 ; bacteria, 0.1 μm^3 . The second approximation demanded by the estimate is that $a = a'$ and $b = b' = 0.75$ for both autotrophs and heterotrophs. These assumptions can be tested using maximum probable limits of error for interspecific comparisons (Hemmingsen 1950, 1960) and both prove to be inconsequential to the ultimate conclusions following from these calculations.

The assumptions permit equation (2) to be converted to a form that is soluble given the data at hand:

$$\log(R_2/R_1) = 0.75 \log(W_2/W_1). \quad (6)$$

The ratio R_2/R_1 for the zooplankton-rotifer component of heterotrophs is 120, for the protozoa the ratio is 1.7, and for the bacteria it is 0.0053.

The size of R_2/R_1 only indicates the relative heterotroph-to-autotroph respiratory rate on an individual basis. The relative respiratory rate per unit biomass is more meaningful. To obtain relative respiratory rate per unit biomass, R_2/R_1 is multiplied by W_1/W_2 . Thus the consumption of oxygen by equal weights of autotrophs and heterotrophs is compared. For crustacea and rotifers, the respiratory rate of a unit of biomass relative to a unit of autotroph biomass is 0.20. For protozoa, the rate is 0.85, and for bacteria it is 26.

Autotrophs comprised 67% of the mean ($n = 66$) standing crop of living plankton and heterotrophs comprised 33%. Of the heterotrophs, crustacea and rotifers made up 20% of total standing crop, protozoa 12%, and bacteria 0.1%. From the proportion of biomass in each of the four plankton categories and the relative respiratory rate of each category as derived above, 80% of the total 3 $\text{mgC}/\text{m}^3 \cdot \text{h}$ respiration can be attributed to phytoplankton, 5% to crustacea and rotifers, 12% to protozoa, and 3% to bacteria.

If the respiration data are approximately representative of the entire euphotic zone, the mean annual phytoplankton respiration (R_p) within the top 15 m of Lake Lanao is 860 $\text{mgC}/\text{m}^2 \cdot \text{day}$. More than 95% of the annual mean PN_p , or 1700 $\text{mgC}/\text{m}^2 \cdot \text{day}$, is also produced within this layer. Annual mean gross production of phytoplankton (PG_p) is

TABLE 11. Statistics related to respiration within the euphotic zone of Lake Lanao (0–15 m). Data for crustacea and rotifers is applicable only to the midday periods when respiration was measured, since the vertical distribution of these organisms changes diurnally. Basis of computations given in text

	Mean volume, μm^3	Relative metabolic rate	% Total biomass	Respiration $\text{mgC}/\text{m}^2 \cdot \text{day}$
Phytoplankton	500.0	1.00	67.0	860
Crustacea and rotifers	300,000.0	0.20	12.0	54
Protozoa	1,000.0	0.85	20.0	130
Bacteria	0.1	26.00	0.1	32

thus 2560 $\text{mgC}/\text{m}^2 \cdot \text{day}$, of which 34% is lost to respiration. The results of computations on respiration are summarized in Table 11.

CONTROLLING FACTORS

The preceding sections have suggested some of the formal causes for high annual PN_p in Lake Lanao. High productivity per unit standing crop, high sustained standing crop per unit area, and maximum transparency per unit of production are all related to high production. At the level of material causation, however, certain key questions remain unanswered. It is critical to determine to what extent the magnitude and variation of total PN_p can be explained by resource supply or other factors, and what mechanisms exist to sustain the high average level of resource supply that must accompany a high average level of primary production.

Factors that might affect seasonal variation of primary production in Lake Lanao are listed below, the most important with an asterisk.

I) Resource supply

A) Light

- *1) Seasonal and aperiodic variation in incident light.
- *2) Effects of circulation depth on light availability.
- 3) Time-lag effects of aperiodic variation in incident light.
- 4) Effects of standing crop on light penetration.

B) Nutrients

- *1) Frequency and extent of atelomixis or full circulation.
- 2) Variation in recycling rates of nutrients within the euphotic zone.

II) Temperature

- A) Temperature dependence of photosynthesis.
- B) Temperature dependence of decomposition.

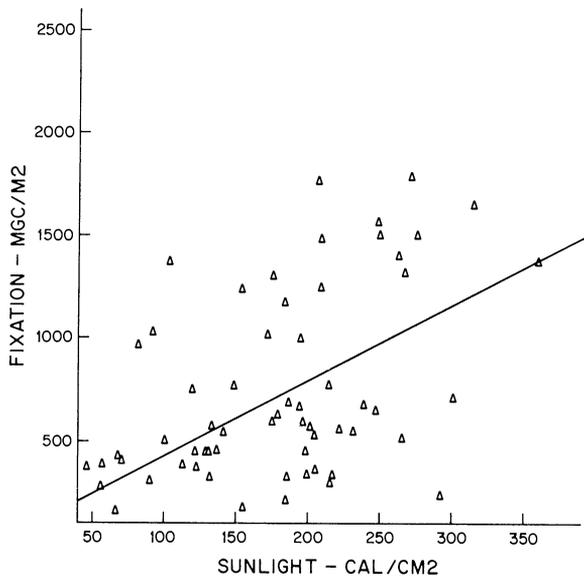


FIG. 10. Relation between sunlight (cal/cm^2) and areal rate of net primary production (mgC/m^2) for the duration of the incubation period. The regression is $Y = 3.69X + 106$, and is highly significant.

III) Biomass removal

- A) Sedimentation rates.
- B) Zooplankton grazing.

Most of the following discussion is concentrated on those sources of variation that were identified in the course of data analysis as accounting for most of the variation in primary production. Certain items on the list may exercise important feedback effects that are not obvious from the data at hand, and others are important but do not have effects of sufficient magnitude to allow discussion here. Certain factors, notably temperature, are important in distinguishing between tropical and temperate lakes but do not account for much seasonal variation in Lake Lanao. These factors are treated in a subsequent section.

Light

Time-course experiments on Lake Lanao showed that a nearly linear relation exists between areal PN_p and incident light for portions of a day. Changes in total daily incident light must similarly affect the level of PN_p from one day to the next. The analysis of light as a source of variation over a period of days or weeks is of course hindered by concurrent changes in standing crop and in the response of a unit of algal biomass to a unit of light. Two approaches nevertheless offer a partial definition of light as a controlling factor of PN_p : (1) correlation techniques, (2) assessment of residual

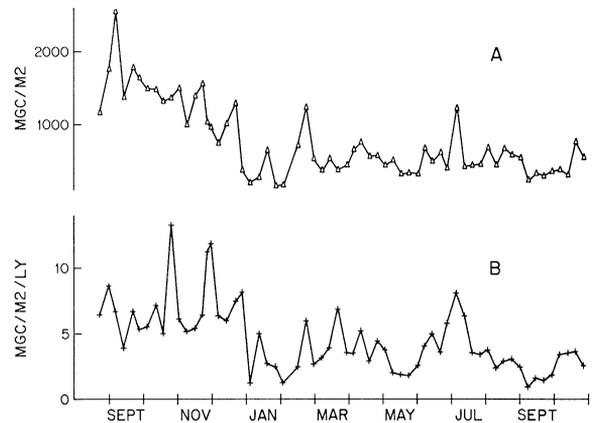


FIG. 11. The variation of primary production with time on Lake Lanao. (A) The fixation rates, expressed as mgC/m^2 for the incubation period. (B) The same data divided by the amount of light during the incubation period to give a measure of productive efficiency.

variation in a productivity index that is insensitive to variations in sunlight.

A product-moment correlation can be tested for sunlight per incubation period (x) and areal PN_p for the same period (y) with the assumption that they do not depart greatly from bivariate normality. The variables are related as shown in Fig. 10. The correlation is highly significant ($p \ll 0.01$, $df = 60$) but not particularly strong ($r = 0.54$). This suggests that about 30% of the variation in PN_p between incubation periods can be accounted for by variation in sunlight. There is no basis for concluding that all of the correlation is attributable to the direct dependence of the photosynthetic mechanism on sunlight, however. Among the most important sources of spurious correlation are: (a) a tendency for the highest production to occur when the circulating layer is shallow—most likely at times of intense sunlight, and conversely, (b) a tendency for deep mixing—most probable at times of weak sunlight—to reduce production by dilution of the standing crop in the euphotic zone. Still other factors have the opposite effect and thus mask the correlation: (a) nutrient depletion during long sunny periods, and (b) nutrient enrichment of the euphotic zone in connection with stormy, overcast weather. Because these and other influences on production are less quantifiable than light, it is not justifiable to pursue a multivariate statistical model.

The direct effect of sunlight on PN_p can be removed from the data by conversion of PN_p to an ecological efficiency. The efficiency of the plankton community in using sunlight, expressed as $\text{mgC}/\text{m}^2 \cdot \text{ly}$, is graphed in Fig. 11 as a function of time. A dimensionless efficiency could be obtained by the

conversion of mgC to its approximate caloric equivalent (10 cal/mgC: Winberg 1971), but the units mgC/m²·ly are more useful for present purposes and differ only by a proportionality constant from the true efficiency. The efficiency used in Fig. 11 is based on total sunlight. The efficiency figures can be uniformly doubled to correct for a 5% loss to reflection and presence of photosynthetically unavailable wavelengths. Since the efficiency based on total light varies between 1 and 13 mgC/m²·ly, the dimensionless energy: energy equivalents of the values shown in Fig. 11 vary between 0.1% and 1.3% (mean 0.44%) or 0.2% and 2.6% (mean 0.89%) if incident light is halved to correct for unavailable light. Feedback effects related to sunlight are of course not removed by conversion to efficiency.

The efficiency-time relationship is a mainstay of the following analysis, since it characterizes condition of the phytoplankton community rather than the weather conditions of the incubation period. A comparison of the two curves in Fig. 11 shows that some marked peaks that appear on the efficiency curve are either absent or reduced on the fixation curve above it. This signifies a change in production brought about primarily by a change in productive efficiency of the phytoplankton. Peaks on the fixation curve that do not appear on the efficiency curve can be attributed primarily to an increase of incident radiation rather than to changes in the phytoplankton community itself.

The relative range ($\log [\max] - \log [\min]$) of the data is reduced in passing from the fixation curve (1.4) to the efficiency curve (1.0). The coefficient of variation is likewise less for the efficiency of production (C. V. 57%) than for production (C. V. 65%). The relative change in coefficient of variation is thus 12%.

The two methods of analysis concur in their implication that variability of incident sunlight is an important but not overwhelming cause of variation in primary production. More than one-tenth and less than one-third of the total variation in PN_p appears to be directly attributable to variation in incident sunlight.

The availability of light may change with the depth of circulation even when incident light is constant. Since phytoplankton cannot (with some qualification for the phytoflagellates) readily maintain a position in the water column, the light that each cell receives depends upon its movement in relation to the light profile of the water column. When the wind is actively circulating the epilimnion, the average cell can be assumed to spend half its time above and half below $z_e/2$, if z_e is the depth of the epilimnion. As z_e increases, R_p and PG_p converge for the phytoplankton cells. When a certain

“critical depth” of circulation is reached, $PG_p = R_p$, which prevents the accumulation of biomass. Sverdrup (1953) introduced the critical-depth concept in connection with certain evidence that great turbulence in the ocean suppresses phytoplankton growth. Patten (1968) has explored theoretical alternatives to Sverdrup’s critical-depth concept, but for present purposes it is instructive to apply Sverdrup’s original concept to Lake Lanao.

Let a hypothetical phytoplankton assemblage of biomass B_p (dimensionally, M/L^2) have a fixed photosynthetic response to sunlight. If B_p is distributed uniformly over z_e , the depth of an actively-circulating epilimnion, any increase in z_e will obviously reduce the amount of light that the average cell receives. Considering the ranges of z_e , B_p , light intensity, and light extinction coefficients for Lake Lanao, an increase in z_e must in most cases result in a departure from optimal light climate for the average cell. Thus PN_p is reduced if B_p is unchanged. The initial depression of PN_p may be offset eventually by compensatory change in B_p or in the quality and composition of the phytoplankton.

In Lake Lanao the mean extinction coefficient for light (η) is about 0.38. Under these conditions, 1% of incident light, corresponding approximately to the level at which $PN_p = 0$, penetrates to 12 m. If B_p is evenly distributed through z_e by turbulence, a change in z_e from 12 m to 24 m will reduce the light exposure of B_p by about one-half. In general, a change from z_e to z'_e will change the light exposure of evenly-distributed B_p by a factor of z_e/z'_e , provided that $z_e > 12 < z'_e$. The minimum value of z_e/z'_e for Lake Lanao is about 12/60 or 0.20. Light reaching the average plankton cell may thus be reduced as much as five fold as the depth of mixing increases in response to storms (Fig. 12).

Strictly theoretical treatments of the critical depth problem are likely to be unrealistic for lakes because surface turbulence ranges widely over short time intervals. The depth of mixing by wind can easily vary from negligible to many meters in the course of a day. It is not uncommon on Lake Lanao for a windless morning with little water movement to give way to a breezy afternoon during which phytoplankton cells are moved rapidly through a great range of light climates.

The effects of mixing depth on light availability in Lake Lanao are most easily observed at times of radical thermocline depression and accompanying uninterrupted windy weather lasting at least several days. The onset of seasonal circulation of the entire lake in late December seems to provide a clear case history. The efficiency of primary production at this time declined more radically than for any other week except one. The level of incident light is

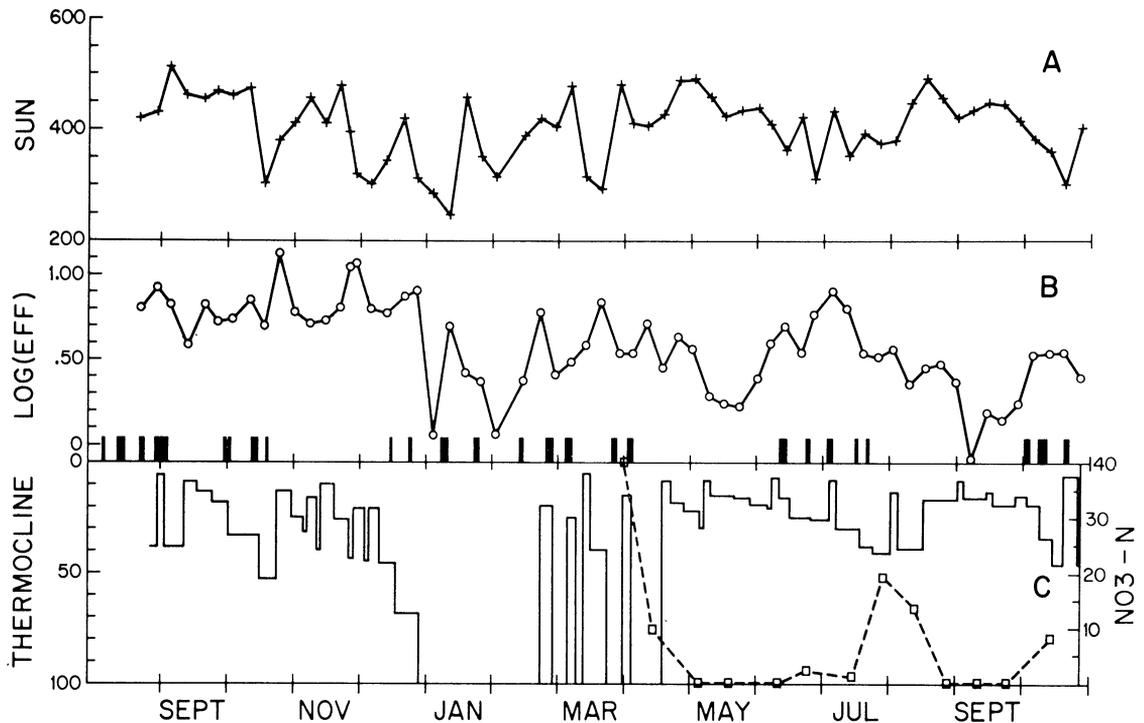


FIG. 12. (A) The line connecting the plus symbols shows the time course of the incident light component of the light exposure history for the phytoplankton community. Each point is the mean daily sunlight ($\text{cal}/\text{cm}^2\cdot\text{day}$) for 7 days prior to and including its position on the abscissa. (B) The line connecting the ovals shows the time course of efficiency of primary production ($\log[\text{mgC}/\text{m}^2 \text{ per incubation period divided by } \text{cal}/\text{cm}^2 \text{ sunlight for the same period}]$). The efficiency is expressed as a logarithm only to emphasize the relative importance of changes. (C) The broken line shows the free nitrate concentration (mg/m^3) of the top 15 m. (D) The solid line shows the depth (m) of the uppermost thermal discontinuity. Typhoons and storms are marked along the middle abscissa. Size of the bars indicates the duration, not the severity, of the storms. Winds lasting less than 24 h are not included.

insufficient to explain the change in efficiency, since comparable levels of light at other times were not accompanied by marked declines in efficiency. Nutrients were at optimal levels because of the mixing. Deep circulation had the dual effect of diluting the biomass per unit volume in the lighted portion of the water column, and, more important, reducing the availability of light by continued mixing to such a depth that little or no restoration of biomass could occur. This hypothesis is supported by weekly cell counts for the same period, the lowest for the year (Fig. 8).

A thermal barrier to mixing is sufficient but not necessary in preventing circulation from exceeding the critical depth of the phytoplankton community. This is well illustrated by a partial recovery in productive efficiency during January, despite the absence of a thermocline during this month. Calm weather prevailed during the week following the crash of production at the end of December, and although sunlight was so low that no thermocline could be established, phytoplankton were not re-

moved from the surface because there was no wind. The consequent buildup of biomass in the illuminated water near the surface permitted a marked recovery in productive efficiency. The efficiency of PN_p during the remainder of the circulation period bears a very obvious relation to the amount of mixing for similar reasons. The formation of weak, temporary thermoclines (Fig. 12C) with calm weather during this period was always associated with a rise in efficiency of PN_p , regardless of the absolute levels of incident sunlight.

A third potential set of light effects could be connected with trends in incident light just prior to the measurement of PN_p . These are best described as time-lag effects of sunlight and might involve either a change in standing crop or a change in productive capacity per unit standing crop. For example, a phytoplankton population that is not nutrient-limited could respond to increased light by an increase in biomass, which could in turn increase the efficiency of the phytoplankton community in using incident sunlight. Alternatively, certain kinds

of light history could be expected to maximize fixation rate per unit biomass. If such effects are important, they should be expressed as a relation between the efficiency of the phytoplankton community and its immediate past history of exposure to sunlight.

Figure 12 shows the efficiency of PN_p beneath the mean daily sunlight for the 7 days prior to each incubation. A visual inspection reveals no obvious relation between these two lines. Both sunlight and efficiency can be scored each week as having increased or decreased from the previous week. In 32 of 61 cases, the two measurements trend in the same direction (*A*), while in 29 cases they trend in the opposite direction (*B*). Since $p(A \geq 32) \approx .50$ in a chance association between the variables, there is no evidence whatever for a causal relation between efficiency at a point in time and history of illumination over the previous week.

The final aspect of light availability is the self-shading effect, which is a complex feedback problem common to all photosynthetic systems (Talling 1970). Self-shading is not truly a source of variation, since it is directly related to standing crop and generally acts as a damper on the productivity of the plankton community. The effects of standing crop on transparency and the depth distribution of primary production have already been discussed, and it is clear how an increase in biomass associated with high PN_p can be retarded by declining light penetration. The operation of the feedback mechanism on Lake Lanao is difficult to judge empirically and will be passed over here on the grounds that its principal effect is to suppress variation.

Nutrients

The depth of mixing during the stratification period, as reflected by the depth of the uppermost thermocline, bears a definite relation to primary production because of the great potential for nutrient depletion as strong thermal barriers begin to isolate the deeper portions of the lake during this hottest part of the year. The efficiency of PN_p peaks dramatically only when the thermocline is high, but high productive efficiency cannot always be inferred from a high-lying thermocline. Figure 12 shows that two conditions must be met before efficiencies reach their highest levels: (1) circulation must be limited to the upper water column (ca. 25 m) to provide an optimal light climate, and (2) nutrients must have been recently brought to the surface by atelomixis or circulation. These two conditions most often occur simultaneously when a period of calm weather succeeds a long storm. The peaks of October 1970 and November 1970 are examples of maximum productivity occurring under

such conditions. Abrupt decline from peak values occurring without any change in the depth of mixing implies nutrient depletion.

The mechanism by which productive efficiencies increase and are sustained at moderately high levels is actually of greater importance than the conditions required for the brief periods of truly exceptional productivity. Here too the effect of mixing on nutrient supply is of obvious importance. The key portion of Fig. 12 is the 1971 stratification period (data subsequent to 1 May 1971). The persistence of calm weather from the onset of stratification at the end of April until the end of May depressed productive efficiency as available nitrate fell to undetectable levels. Under these conditions the supply of recycled nitrogen must also have been steadily reduced by continuous loss from the nitrogen pool via sedimentation through the thermal barrier. Such losses are of course aggravated by the lack of turbulence. June through middle July 1971, however, was a period of recurrent storms, which generated great turbulence and resulted in repeated episodes of atelomixis. Production efficiencies rose steadily in response to this enrichment. The worst storms had stopped by the last half of July, and efficiencies declined somewhat but did not crash, presumably because nutrient supply remained adequate. Nitrate in fact peaked during this period at a time exactly coincident with a pronounced disruption of the thermocline that apparently resulted from internal seiches (Lewis 1973*b*). This particular nitrate pulse therefore probably reflects upwelling. As calm weather continued, the formation of a more superficial thermocline and the consequent depletion of nitrate led to a decline of photosynthetic efficiency.

From the sequence of events during 1971 it is clear why the efficiency of PN_p was unexceptionably high from late August through December 1970. The absence of extended calm periods such as the one that occurred during the 1971 stratification prevented the extremes of nutrient depletion. Comparison of data for the same months of these 2 yr indicates the potential variation of the yearly pattern of production, which depends upon the distribution of storms during the stratification period.

The above analysis has stressed the role of turbulence in the transport of nutrients from deeper to more superficial layers, especially by atelomixis. One alternative or supplementary mechanism of euphotic-zone enrichment should also be mentioned. During storms the shoreline on the north side of the lake is pounded by waves, sometimes to the extent that virtually all rooted vegetation and *Eichornia* is destroyed. The waves raise a very noticeable band of seston some 0.5 km wide parallel to the shore.

This suspended matter consists partly of the rich littoral muds, which receive decaying portions of senescent macrophytes. The water in this zone must consequently be rich in nutrients. Some portion of these freed nutrients could be distributed over the lake surface by return currents or by a shift in the wind after the storm. This mechanism of nutrient supply would coincide with *atelomixis* and have similar effects. Because of the great surface area of the lake, however, *atelomixis* is undoubtedly the dominant mechanism by which nutrient depletion is relieved during stratification.

Other factors

Light and nutrients seem to account for most of the variation in primary production on Lake Lanao. There are a few other sources of variation that deserve mention here, although they may not be recognizable as discreet influences on primary production.

Seasonal temperature change apparently affects the composition and overall metabolic efficiency of temperate phytoplankton communities (Hutchinson 1967). Although the annual temperature variation of Lake Lanao is comparatively low, it nevertheless deserves some consideration as a direct source of variation in PN_p . A test was made for linear correlation between productivity per unit volume at the depth of maximum fixation (z_{opt}) and the temperature at z_{opt} . The test showed that no significant relationship exists ($p > 0.10$) despite the relative large number of points ($df = 59$) available for testing.

The range of temperatures at z_{opt} for the study period is 24.3–27.1°C, and the mean is 25.77°C. Recent values of the photosynthetic Q_{10} for natural phytoplankton communities range from 1.4 (Megard 1972) to 2.1 (Talling 1966b). Even if the phytoplankton of Lake Lanao had a Q_{10} of 2.0, photosynthesis at z_{opt} would range less than 25% due to the annual temperature changes, and areal PN_p would change even less. Since no statistical relationship between temperature and production can even be demonstrated, it seems that even the small potential temperature effect is not manifested because of the overwhelming influences of light and nutrients on PN_p .

Seasonal variations in temperature cause parallel trends in water viscosity, which affect the sinking rate of the phytoplankton. Since viscosity is not highly variable with temperature in the 25°C range, however, variation over the year in sedimentation rates is probably of minor importance to primary production.

Zooplankton can affect the efficiency of primary production by heavy cropping. Because zooplank-

ton populations vary in density on a longer time scale than phytoplankton populations they tend to exercise a rather steady cropping pressure despite week-to-week variations in primary production. Thus zooplankton do not "cause" the rapid peaks and declines in photosynthesis so much as they accentuate or damp trends that are attributable to other factors. Preliminary analysis of the zooplankton data shows that cropping pressure is almost absent during circulation, but is a major sink for plant biomass during the stratification period. Since biomass and production are not directly linked, however, the role of the zooplankton is not obvious. The data strongly imply that variation in PN_p is much more under the control of resource supply than biomass removal, but the final resolution of zooplankton effects must be deferred pending the complete analysis of zooplankton census data.

Factor interaction summary

The cool season is characterized by low illumination and deep circulation. The combined effect of these trends is to create an unfavorable light climate for photosynthesis. Nutrients are at optimal levels at this time of year but cannot be used fully because of the limitations on light. Thus during the cool season the community should be regarded as light-limited.

During the period of stratification, incident light may fluctuate and create parallel trends in primary production. Limitations on light caused by deep circulation may also exist when thermoclines are lowered during the strongest storms. Except in cases of extreme light limitations, however, the major controlling factor of the stratification period appears to be nutrients, specifically nitrogen.

During calm sunny weather, nutrient depletion occurs rapidly. Three conditions often coincide at such times to accelerate the depletion of nutrients: (1) Maximum sunlight promotes the rapid uptake of nutrients by phytoplankton. (2) High-lying secondary thermoclines limit the total nutrient pool to a relatively small volume of water and promote the loss of nutrients from the pool by minimizing the sedimentation distance necessary to remove seston from the pool. (3) Forces promoting the horizontal and vertical exchange of nutrients are minimal.

Storms stimulate primary production by returning nutrients to the euphotic zone after they have been lost by sedimentation, and since storms occur frequently, nutrients are delivered in frequent pulses to the plankton community throughout the stratification period. The timing of storms is essentially random, so that calm periods of more than a month can occur. These are marked by declining primary production caused by nutrient depletion. The stimu-

TABLE 12. Production statistics for plankton communities to be used for general comparative purposes. The estimates, especially the ranges, should be interpreted with particular attention to the number of measurements upon which they are based. Only in situ studies are included

Lake	Source	Total sun ^a kcal/m ² ·yr	Net production ^b gC/m ² ·yr	Range mgC/m ² ·day	Incubation dates number
Victoria	Talling 1965 ^a	1.54×10^6	640	1700–3800	14
Lanao		1.49×10^6	620	400–5000	62
Sylvan	Wetzel 1966	1.2×10^6	570	9–4950	33
Minnnetonka	Megard 1970, 1972 ^d	1.1×10^6	300	?–4140	11
Clear	Goldman & Wetzel 1963	1.2×10^6	160	2–2440	14
Erken	Rodhe 1958 ^e	0.83×10^6	104	20–1200	36
Aegean Sea	Becacos-Kontos 1968 ^f	1.3×10^6	64	70–330	20

^a Only Victoria, Lanao, Erken based on measurements. Others are my estimates based on latitude.

^b Carbon-14 in all cases except Victoria and Minnetonka, which are represented by O₂ data.

^c Talling reports a mean near 7 g O₂/m²·day gross production for 14 dates over 10 mo. I have converted to carbon using a PQ of 1.2 and subtracted 25% to convert gross to net.

^d Data from Megard's (1972) Table 8, mean of 3 localities, gross oxygen converted to net carbon as with Talling's data; no winter minimum was measured.

^e Production is underestimated because of long incubations.

^f Referred to as gross, but probably nearer to net production.

lating effect of storms is of course directly related to the unique thermal characteristics of tropical lakes, which include the formation of semistable nutrient traps within the upper water column.

COMPARISON WITH OTHER LAKES

Lake Lanao is compared to other lakes of known productivity in Table 12. As the table shows, the two tropical lakes, Lanao and Victoria, are among the most productive that have been studied. Both Minnetonka and Sylvan Lake are considered hyper-eutrophic, and by temperate standards Clear Lake and Lake Erken are both very productive. Victoria and Lanao markedly exceed these lakes in productivity, but they lack many of the pronounced eutrophic characteristics such as low transparency, high volume-specific standing crop, and high nutrient levels. Talling (1965a) has reviewed more fragmentary data for other tropical lakes in Africa, all of which appear to be very productive.

One potential explanation for the high annual production of tropical lakes is the greater amount of sunlight at low than at high latitudes. The primary production of Lake Lanao is some 5 to 10 times greater than its temperate counterpart in transparency and nutrients, but the total sunlight that it receives is less than double the expected amount at 45° north latitude. Obviously some additional explanation is needed to account for the high efficiency of the tropical plankton community in using sunlight.

Nutrients are present only in small amounts in Lake Lanao, but are probably recycled at much higher rates than in temperate lakes. Recycling really involves three separate phenomena: (1) the rate at which organic matter is degraded to a re-

usable form within the euphotic zone (epilimnion), (2) the rate of the same process below the euphotic zone, and (3) the frequency and extent of the mixing of the water of the euphotic zone with the richer water beneath it.

The total nutrient pool of the euphotic zone consists of a fraction that is unavailable for use because it is incorporated in living and nonliving organic matter and a smaller fraction that is either inorganic or sufficiently simple in structure to be absorbed and used by the phytoplankton. The unavailable nutrients of the seston can be lost from the nutrient pool either by sedimentation or grazing, or can be degraded to a form that is useful to phytoplankton. The rate at which this degradation proceeds in the epilimnion may well be higher in the tropics because of the higher water temperatures. Even during the productive summer season of the temperate zone, water temperatures of the epilimnion are generally lower than in lowland tropical lakes, and this difference may be important in regulating the recycling rate of limiting nutrients.

The contrast between deep-water temperatures in temperate and tropical lakes is even greater than for the upper layers. Organic matter may therefore decompose more rapidly after leaving the euphotic zone of a tropical lake, and will be available in greater quantity for recycling when the layers are mixed. The significance of this fact is augmented by the greater amount of mixing that occurs in tropical lakes.

Temperate lakes frequently suffer from extreme nutrient depletion after stratification stabilizes in the spring. Although some interchange between layers does occur, there is a steady drain on the nutrient pool that is not offset until the fall circulation. On tropical lakes stratification is not so stable, and

atolomixis may occur rather frequently during the stratification period. The nutrient pool of the euphotic zone is enriched by this process with decomposition products that would ordinarily remain unavailable in a temperate lake until the end of the stratification period. This is probably the most important single factor accounting for the difference in productivity between temperate and tropical lakes.

In a comparison of Lake Windermere and Lake Victoria, Talling (1965*b*) speculates that the high productivity of Victoria and other tropical waters (Talling 1957*b*, Prowse and Talling 1958, Vollenweider 1960, Talling 1965*a*) may be due largely to the great dependence of photosynthesis on temperature. There are two weak points in this theory: (1) conclusions drawn from specific plankton communities about the dependence of photosynthesis on temperature do not apply by simple extrapolation to communities that are adapted to greatly different temperature ranges, and (2) nutrient and light limitations are not relieved by temperature optimization.

Since biochemical reaction rates are catalytic they can be maximized by genetic change within reasonable limits. Metabolic rates can consequently be expected to differ much less between communities than would be predicted by the simple application of Q_{10} values to temperature differences. In a hypothetical example, a temperate and a tropical plankton community with identical resources, each having Q_{10} of 2.0, may metabolize at exactly the same rate even if their mean temperatures differ by 10°C. Extrapolating the effect of the 10°C-temperature difference from the Q_{10} would falsely indicate the metabolic rates in the tropical community were about two times higher. Although adaptation is not likely to produce identical efficiencies for all thermal regimes, it will tend to minimize the role of mean temperature in regulating metabolic rates.

Even if higher average temperatures are to some degree more favorable to photosynthesis, the limitations on primary production that are imposed by nutrients and light would often, perhaps nearly always, render the temperature effect unimportant in greatly changing annual production. The productivity patterns of temperate lakes are dominated by the seasonal enrichments of the euphotic zone that accompany circulation, and in most cases show evidence of marked nutrient depletion for much of the summer. Accelerating the photosynthetic rates during such periods would simply shorten the time required for nutrient depletion. The difference in mean temperature between temperate and tropical lakes is thus likely to be more important in its effect on metabolic processes that govern nutrient recycling than on photosynthesis itself.

CONCLUSIONS

At the most general level, the key contrast between temperate and tropical lakes is in the variability of resource supply. As is generally true of temperate lakes, the productivity of Lake Lanao appears to be principally limited by two resources—sunlight and a nutrient. It seems conceptually accurate to regard the primary production of lakes at any latitude as being markedly affected at almost any specified time by one or the other of these factors. The contrast between temperate and tropical lakes is thus not in the identity of controlling factors, but rather in their mode of operation.

Sunlight supply at the water surface is independent of biological control and in the temperate zone governs the supply of nutrients by determining the timing of interchanges between the trophogenic and tropholytic zones of lakes. For this reason the maximum supply rates for these two resources are precisely out of phase. A seasonal trend in the tropics toward lower light intensity also forces an opposite trend in nutrient supply, but seasonal variation is much reduced. The difference in magnitude of variation has two implications, both documented here: (1) both limiting resources will be used more efficiently in the tropics because of the greater equitability of their distribution over time, and (2) nonseasonal effects on resource supply will be more important in the tropics and will tend to uncouple the seasonally-based phasing of resources so that optima of the two resources are more likely to occur together.

The total annual supply of two limiting resources can be regarded as representing a maximum potential productivity that would be realized only if the resources were distributed over time in such a way as to minimize the difference in their average availability at any particular instant during the year. For example, if sufficient sunlight is available for the use of all nutrients present, sunlight in excess of this amount can be considered as wasted. For present purposes it is feasible to define resource waste as the inequitability in time distribution of one limiting resource with respect to another.

The distribution of limiting resources with time is illustrated schematically in Fig. 13 for simplified hypothetical temperate and tropical situations. Resource waste is greater for the temperate lake either as a proportion of the total resource or in absolute amount. Nonseasonal variations control resource supply in the tropical lake because of the damped seasonal influence, and cause the resource variability to be expressed as frequent pulses of smaller size and more irregular phasing than for the temperate lake. Sunlight is used more efficiently in the tropics because high delivery rates are less likely to

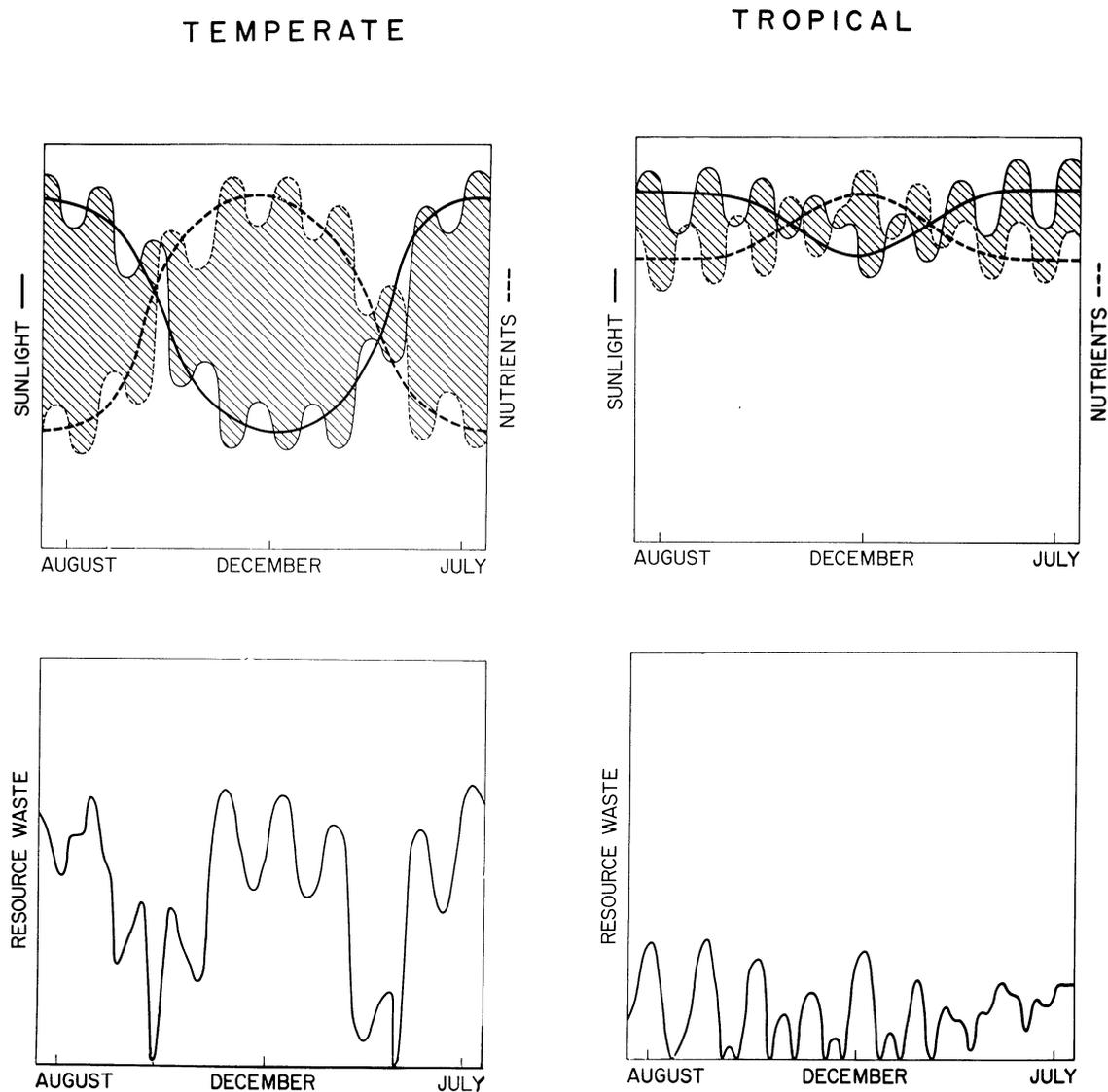


FIG. 13. Schematic representation of variation over time for the limiting resources of a temperate and a tropical lake, and the resulting resource waste. The seasonal-sunlight curves are properly scaled for 10° and 40° latitude, and the seasonal curve for nutrients is realistically phased but arbitrarily scaled. Aperiodic variations about the seasonal lines are hypothetical and are phased at random. The resource-waste curves were derived empirically from the resource-supply curves.

coincide with extremes of nutrient depletion. Nutrients are used more efficiently because of the greater frequency of controlling (aperiodic) variations, which distributes them more equitably with regard to sunlight and simultaneously permits them to be cycled more rapidly.

ACKNOWLEDGMENTS

I am especially indebted to D. W. Schindler of the Freshwater Institute at Winnipeg for providing the details of his liquid scintillation C-14 assay methods and for much other useful advice. Robert Wetzel of Kellogg Biological Laboratory guided me through the C-14 amputation procedure using his own facilities and checked

the activity of my C-14 inoculum. Rodrigo Calva aided me in all of the field work, and Lili Silva gave me much valuable help in the laboratory. I benefitted much from the previous Philippine experience of D. G. Frey, who has given help of every kind throughout the course of this study. I would also like to thank Mr. E. C. Pidduck of the New Zealand Government and Mr. Vernon Skaar of Maranao Timber for helping to make mechanical failures more bearable.

All phases of this work were greatly facilitated by the generous backing and services of the Ford Foundation Manila Office under the direction of Clark Bloom. Mindanao State University provided laboratory facilities and numerous services through the cooperation of its president, Mauyag Tamano, and my liaison with the University, Mila Medale.

This work is from dissertation research supported by National Science Foundation Grant GB 16054 to D. G. Frey, Indiana University. Certain aspects of manuscript preparation were also aided by contract AT(38-1)-310 between the United States Atomic Energy Commission and the University of Georgia.

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