

THE THERMAL REGIME OF LAKE LANAO (PHILIPPINES) AND ITS THEORETICAL IMPLICATIONS FOR TROPICAL LAKES

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ABSTRACT

A study of temperature profiles, climatic records, and chemical data for Lake Lanao, a low-altitude tropical lake, over 14 months shows that the annual pattern of heat distribution depends partly on a seasonal air temperature minimum and partly on nonseasonal climatic changes. The lake circulated during January and February at the time of seasonal cooling was intermittently stable during March and April, and was stratified during all other months. During stratification the principal thermocline achieved equilibrium with storm winds at 40-50 m. Secondary and tertiary thermoclines repeatedly split the epilimnion into an upper turbulent layer and a lower stagnant layer for periods up to 2 months, but were displaced or dissipated at irregular intervals by storms. The term *atelomixis* is proposed to denote the mixing of chemically divergent layers during stratification.

Changes in the shape of thermal profiles in Lake Lanao include sharpening of thermoclines by wind and convection, smearing of thermoclines by internal water movements, unstable thermal inversions due to cooling at the surface, and stable thermal inversions on the bottom that result from heat retention during cool weather.

Tropical limnology has accumulated many survey data and some significant intensive studies since the exploratory ventures of Juday (1915) and Ruttner (1931a). There are nevertheless more gaps in our knowledge of tropical lakes than one would expect, partly because of an understandable bias in data collection. The African lakes have provided the bulk of information for the lowland tropics. Apparently no first-class lake of the Asian or American tropics has been studied intensively for an extended period. The distinctive morphometry, history, and chemistry of the large African lakes have in some respects

hindered generalization, and other lakes have only recently received comparable attention.

The need for comparative data is nowhere more evident than in the study of heat distribution in tropical lakes. Hutchinson and Loffler (1956) recognized that tropical high-mountain lakes are likely to mix more than once per year (polymictic) and that lowland lakes might not mix on a yearly basis (oligomictic). Most of the lakes that have been investigated to date do not belong in either of these categories. Talling's (1969) recent review of thermal studies on African lakes suggest that a strong annual periodicity of the thermal regime is nearly universal in the African tropics. Although Hutchinson (1957) has theorized on the conditions associated with each of the tropical lake types, a general lack of information for the Asian and American tropics has left considerable doubt about the distribution of these types and the comparative significance of factors not incorporated in the classification scheme. My study contributes thermal information on a lake of the Asian tropics and illustrates the potential importance of nonseasonal weather changes to the thermal regime of tropical lakes.

A thorough description of Lake Lanao is given by Frey (1969); its maximum depth is 112 m; mean depth 60.3 m; area, 357 km²; replacement time 6.5 years. Lanao is a first-class lake in the sense of Birge (1915), since its morphometry permits maximal absorption of radiant energy. Altitude of the lake surface is 702 m. It lies well within the tropics, but somewhat north of the equator (8° 00' N, 123° 50' E), about 25 km from the nearest coast.

Methods

Daily weather records and weekly thermal profiles cover the period June 1970–December 1971. Supplementary thermal profiles demonstrate the responses of the lake to specific weather conditions. Scheduled thermal profiles are from station 1 (Fig. 1), where the water depth is 45 m. The station was relocated each week by means of an anchored buoy. Profiles were also taken at station 4 over the deepest part of the lake whenever changes in deep water were likely.

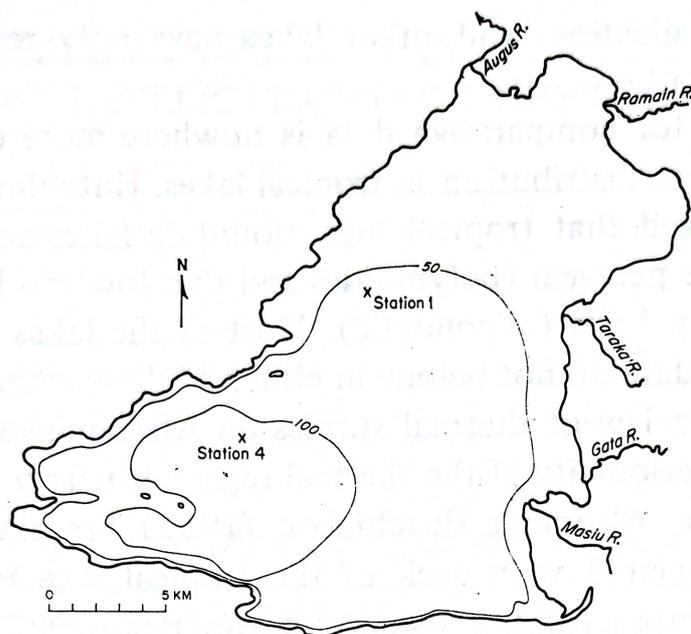


Fig. 1. Map of Lake Lanao with 100- and 50-m contours, showing location of principal stations. True depth at station 1 is 45 m, indicating a slight error on the placement of the 50-m contour (modified from Frey 1969).

Temperature was measured with a YSI 46TUC thermistor (November 1970–January 1971), Whitney CTU 3A thermistor (June–August 1970), or Kahl bathythermograph was calibrated with a mercy thermometer (reading to 0.02°C) at some depth along the most vertical portion of the temperature profile to avoid the inaccuracies of surface calibration. Oxygen was measured by the unmodified Winkler method at intervals of 1 m in the top 8 m and below that 2-, 4-, or 5-m intervals to the bottom at station 1. Daily weather records include solar energy measured by a Belfort pyrliometer (planimetrically integrated), maximum and minimum temperatures, rain by a wedge gauge, and subjective records of wind strength and direction. The weather station was located 3 km north of the lake and 100 m above it.

Results

The major features of heat distribution in Lake Lanao (Fig. 2) are due partly to a seasonal temperature minimum that induces full circulation and partly to aperiodic cycles of heat accumulation and loss that result from nonseasonal weather changes.

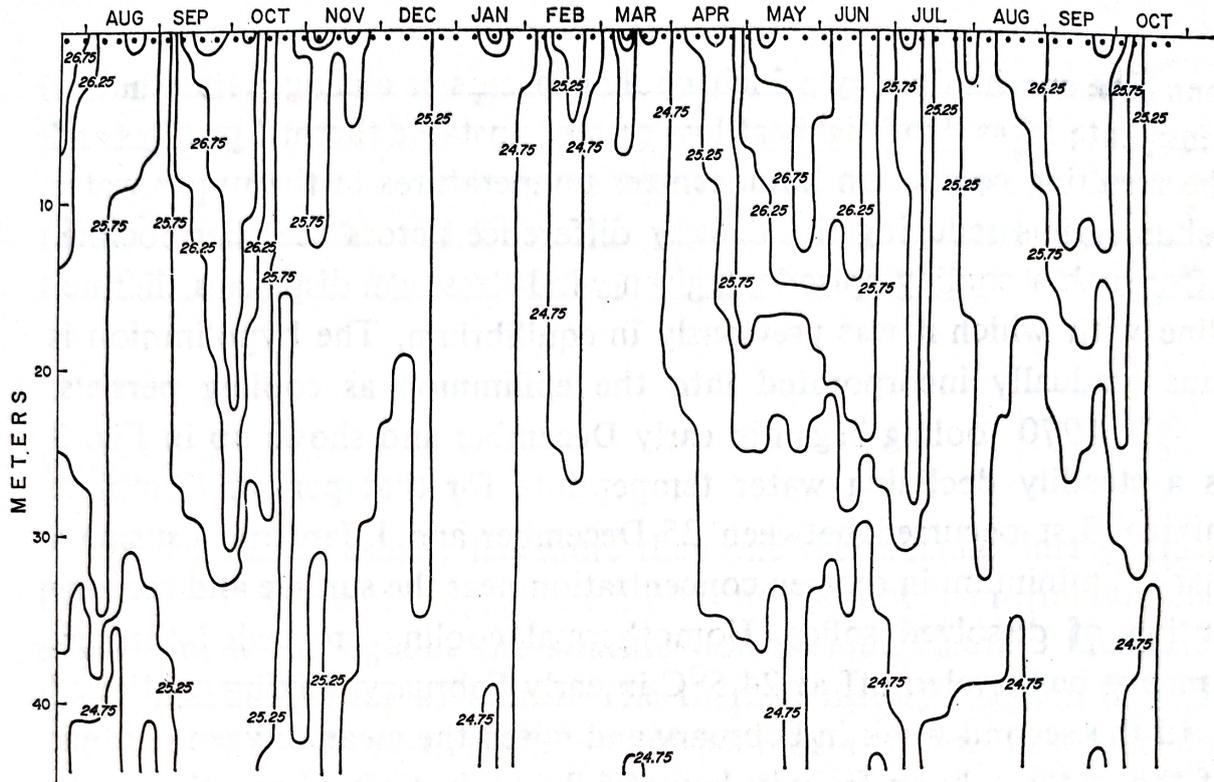


Fig. 2. Time-depth diagram for water temperature over the study period. Exact dates of the profiles are indicated by dots. Isotherms are at intervals of 0.5°C.

Circulations

Temperatures reach their minimum during a yearly cool period that lasts from December to March (Table 1). The temperature minimum results primarily from increased cloud cover which affects maximum temperatures to a greater extent than minimum temperatures, so that the temperature range for the average day during the cool season is smaller. Because day-time air and water temperatures are about the same during the coolest months, most of the seasonal heat loss occurs at night. This differs from temperate lakes, which may cool rapidly during the day.

Table 1. Summary of weather data for Lake Lanao. Data for 1921–1932 are as summarized by Frey (1969). Ranges are between monthly mean maximum and minimum temperatures (°C). Data for October–December are for 1970, other months for 1971

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1970-1971 cal cm ⁻² day ⁻¹	356	414	388	453	430	396	381	457	432	398	409	359
1921-1932 maximum	25.0	26.0	26.6	27.9	28.1	27.7	26.7	26.9	27.1	27.1	26.6	25.8
minimum	18.0	17.9	18.0	18.3	19.4	19.6	19.6	19.8	19.6	19.2	18.9	18.5
range	7.0	8.1	8.6	9.6	8.7	8.1	7.1	7.1	7.5	7.9	7.7	7.3
1970-1971 maximum	24.8	25.7	25.4	28.1	28.7	27.7	27.7	28.4	28.4	28.2	28.4	25.8
range	7.6	7.1	6.9	9.1	8.9	8.2	8.1	9.5	8.9	8.6	9.7	7.2

The mechanism by which cooling occurs is analogous to that of temperate lakes. Surficial heat loss creates unstable thermal profiles and the resulting convection homogenizes temperatures in the upper water column, thus reducing the density difference across the thermocline. After such a cooling episode, a given wind stress can displace a thermocline with which it was previously in equilibrium. The hypolimnion is thus gradually incorporated into the epilimnion as cooling persists.

In 1970 cooling began in early December and shows up in Fig. 3 as a steadily declining water temperature for that period. Complete mixing first occurred between 25 December and 1 January, causing a marked minimum in oxygen concentration near the surface and redistribution of dissolved solids. Homothermal cooling proceeded through January but leveled off at 24.5°C in early February. Mixing continued until the second week in February and raised the mean oxygen content of the water column from its low of 4.3 ppm just after homothermy to a maximum of about 6.4 ppm. The progression of thermal profiles appears in Fig. 4.

Deep mixing was interrupted for about a week in middle February by an unseasonal peak in radiation (Fig. 3) combined with calm weather. For this short period mixing was much more superficial, permitting a *Synedra* bloom to charge the top 20 m with oxygen. Deep mixing resumed with the decline in radiation, and the water column remained near minimum temperature until the end of March. A radiation peak in early March did not have the same effect as the one in February because of the heavier wind that accompanied it; this not only prevented temporary stratification, but probably offset heat gain as well by increasing heat loss from the surface. The water column reached a minimum temperature of 24.4°C on 20 March. Homothermal heat accumulation was very brief and raised the water temperature only 0.1°C before the deepest water stopped circulating. May marks the beginning of stratification and rapid heat accumulation.

Air temperature data for other years reveal that the cool period of 1970-1971 is part of a truly seasonal weather pattern. The lake seems to have circulated the year it was visited by the Wallacea Expedition (Woltereck 1941) and unquestionably circulated during the 1967-1968 cool period (Frey 1969). There is little reason to doubt that circulation

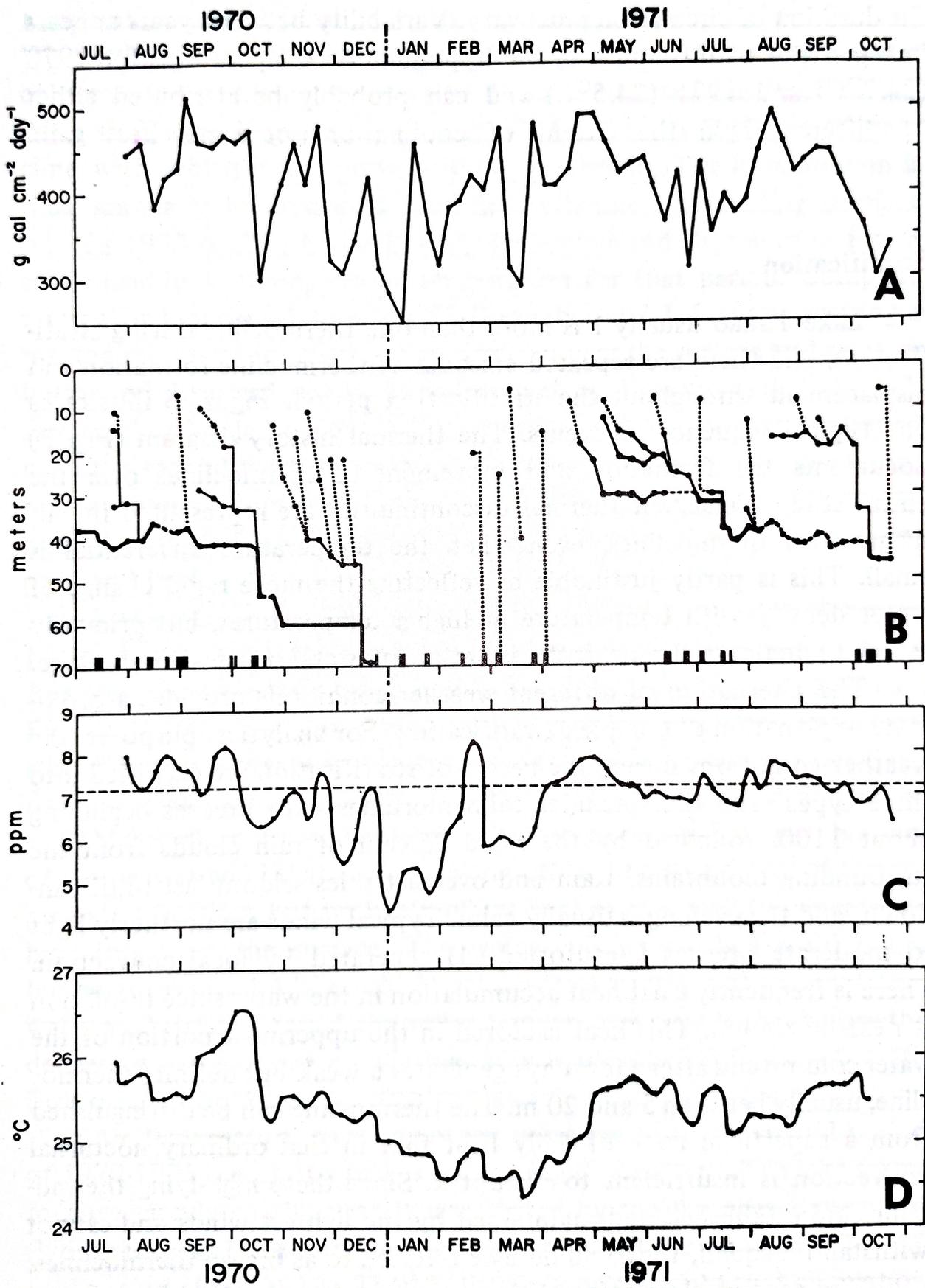
occurs yearly, but the deepest water may not always be fully mixed and the duration of circulation must vary. Variability between years appears in my data as a difference in the hypolimnetic temperatures for 1970 (24.7°C) and 1971 (24.5°C) and can probably be attributed either to differences in the extent of cooling or isothermal heat gain.

Stratification

Lake Lanao usually has more than one thermocline during stratification, and there are repeated episodes of thermocline formation and displacement throughout the stratification period. Figure 5 illustrates one typical sequence of events. The thermal history diagram (Fig. 3) documents the formation and movement of thermoclines over the entire study. Persistent thermal discontinuities are represented in this diagram as thermoclines, even when the temperature differential is small. This is partly justifiable as reflecting the more rapid change of water density with temperature at higher temperatures, but primarily serves to indicate the de facto isolation of water masses in the lake.

The alternation of different weather conditions provides a proximate explanation of complex stratification. For analytical purposes, the weather conditions during the period of stratification are classified into three types. The first includes calm mornings with breezes beginning about 1100, followed by the rapid descent of rain clouds from the surrounding mountains. Rain and overcast skies seldom last until sundown, and the evening is usually calm. Typical winds are northerly light to moderate breezes (Beaufort 1–4) generated by local convection. There is frequently a net heat accumulation in the water since insolation is near maximum. This heat is stored in the uppermost portion of the water column and after a few days generates a weak but definite thermocline, usually between 5 and 20 m. The thermocline can be distinguished from a superficial zone of daily heat flux in that ordinary nocturnal convection is insufficient to disrupt it. Since these high-lying thermoclines are established and maintained by the lightest winds and cannot withstand a squall, they will here be referred to as **breeze thermoclines**.

The second class of conditions accompanies the frequent squalls.



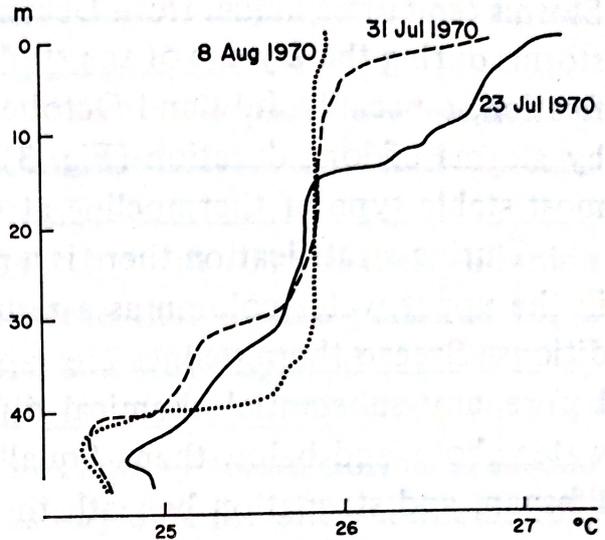
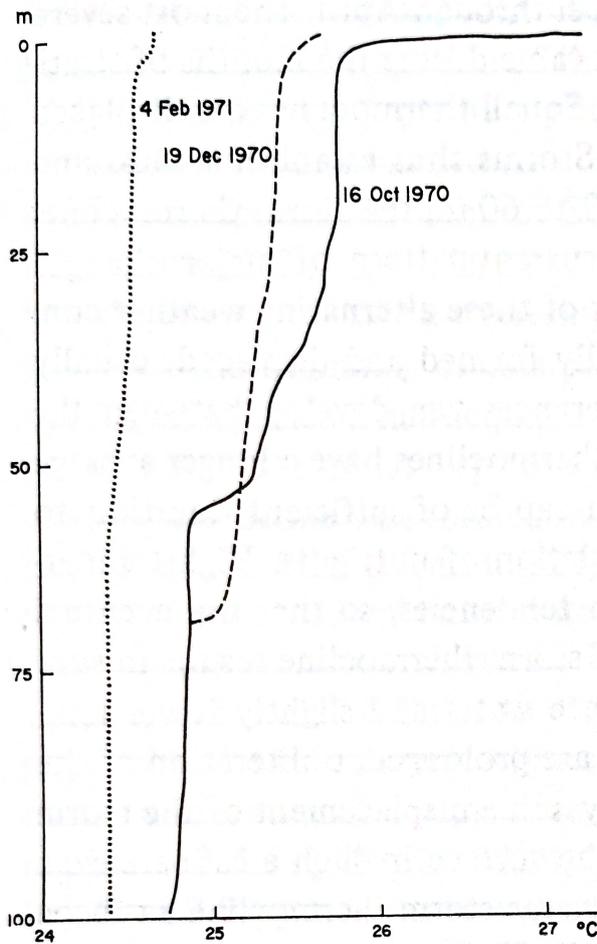


Fig. 5. Multiple thermoclines and thermocline displacement. Storms on 24 July and 6 August displaced the higher thermocline and finally fused it with the lower one.

Fig. 4. Thermal profiles for October, December, and February showing heat loss with seasonal cooling and the eventual temperature minimum at the end of circulation.

Typically there is a formation of heavy nimbus clouds over the mountains, followed in the early afternoon by rain and sufficient wind to cause whitecapping (Beaufort 5–6). Such conditions homogenize the water column to a depth of 20–30 m, thus displacing or obliterating the breeze thermocline but often establishing or reinforcing what will be called here a squall thermocline at a deeper level.

A third and most severe kind of weather occurs in connection with longer storms, some of which may be classified as tropical disturbances or typhoons. These storms are marked on the thermal history diagram (Fig. 3). Their full force is much less likely to strike the Lanao area than the northern Philippines, but high southerly winds (Beaufort 7–10) and prolonged reduction of insolation accompanying the worst of them.

Fig. 3. Thermal history diagram and variation in insolation, water temperature, and oxygen for the study period. A. Sunlight; each point gives the mean for the preceding 7 days. B. Thermocline history; dotted lines—breeze thermoclines; line—squall thermocline, heavy solid line—storm thermocline. Dashed segments of storm and squall thermoclines indicate smearing. Darkened segments of the abscissa are storm periods. C. Mean oxygen for the top 20 m; dashed line is saturation at 26°C, 700 m. D. Mean temperature between 2 and 45 m, station 1.

Storms tend to be milder from December through April. The most severe storms during the 2 years of the study came during the months of stratification, especially July and October. Squall thermoclines are displaced by storms of long duration (Fig. 3). Storms thus establish a third and most stable type of thermocline at 40 to 60 m, the **storm thermocline**.

During stratification there is a recurrent pattern of major changes in the upper water column as a result of these alternating weather conditions. Breeze thermoclines are rapidly formed and displaced, usually before any substantial chemical differences can develop between the water above and below them. Squall thermoclines have a longer average lifespan, and stagnation beneath them can be of sufficient duration to permit oxygen depletion and accumulation of nutrients. High temperatures in deep water accelerate these tendencies, so that the eventual homogenization of water down to the storm thermocline results in substantial chemical changes of the surface water and slightly lower temperatures at the surface. When storms are prolonged, obliteration of the squall thermocline can be followed by some displacement of the storm thermocline as well. The changes at the surface in such a case are even more pronounced, since water beneath the storm thermocline has been stagnant longer than any water above it. The upper water column is in this way subject to a series of stagnation – mixing cycles resulting from the formation of thermoclines that are later displaced.

Since the hypolimnion (the water column below the storm thermocline) retains its integrity throughout stratification, the pattern of thermocline formation and displacement in the epilimnion can be viewed as superimposed on a classical warm monomictic regime. When the upper thermoclines are displaced or the storm thermocline is slightly deepened, the effects are comparable on a restricted scale to circulation of the entire lake.

Brief separations of parts of the epilimnion must occur in all lakes when the weather is very calm. It would therefore be desirable to distinguish formally those cases in which chemically divergent layers are mixed, which even in productive lakes implies an isolation of layers for more than 1 or 2 days. Using a Greek prefix meaning incomplete. (F. Householder, personal communication), I propose the term **atelomixis** to describe any instance of vertical mixing of stratified lakes in which

water masses of substantially different chemical properties are homogenized without obliteration of the hypolimnion.

The events of September and October 1970 provide a case history of atelomixis in Lake Lanao (Fig. 3). Intense heating and relatively calm weather in the second week of September established a squall thermocline at about 30 m, which isolated the bottom 10 m of the epilimnion for about 5 weeks. An overlying breeze thermocline persisted for 2 weeks at the beginning of this period and was displaced some 8 m by squalls, after which it had acquired sufficient depth and health difference to resist any substantial displacement except by severe storms. A second squall thermocline was formed in this way over the original one but did not resist two brief storms in early October, which fused the two squall thermoclines at 33 m but did not mix the stagnant layer beneath the original one. A severe storm on 12 October caused atelomixis, homogenizing the water column to the level of the storm thermocline and depressing the storm thermocline some 10 m. During the 5-week history of the deeper squall thermocline the oxygen content of the 30–40 m stratum of the epilimnion changed from near saturation (7.5 ppm) to less than 3.0 ppm. The marked effect of atelomixis on the chemistry of the euphotic zone is indicated by the change in mean oxygen concentration of the upper 20 m from 7.5 to 6.2 ppm just after the storm (Fig. 3).

The exact effects of atelomixis and the circumstances under which it occurs in Lake Lanao are variable. The mixing of a stagnant layer below a squall thermocline in early August 1970 is an instance of atelomixis, but the resulting chemical changes at the surface were less pronounced than in other cases because the thermocline was less than 2 weeks old when mixing occurred. Atelomixis on 15 December 1970 was undoubtedly more pronounced because of seasonal cooling than it would otherwise have been. It occurred under still different circumstances in the middle of July 1971: Only the storm thermocline was involved, since the repeated storms of the previous month had prevented the formation of a squall thermocline. Beginning in middle August 1971, the epilimnion below 20 m was isolated for about 6 weeks by the formation of a squall thermocline which persisted for a long period of calm weather. Atelomixis in two episodes during early and middle October ultimately

depressed the squall thermocline to the level of the storm thermocline. The initial depression of the squall thermocline to 35 m was accompanied by an increase in free nitrate in the top 15 m from 0 to 8 g liter¹; atelomixis in this instance was only weakly reflected by a decline in oxygen concentration in the top 20 m. Several days of stormy weather separated atelomixis and sampling, so most of the oxygen debt probably had been offset by diffusion.

Atelomixis takes three forms in Lake Lanao: 1) A secondary, high-lying (squall) thermocline persists for a time sufficient to allow the accumulation of decomposition products and depletion of oxygen below it. Displacement of this thermocline to the bottom of the epilimnion results in substantial changes of surface water chemistry (6 August 1970); 2) Under the same initial circumstances as for the first case, part of the hypolimnion is also mixed (15 October 1970); 3) In the absence of a layered epilimnion, the (storm) thermocline is depressed so that part of the hypolimnion is brought into the epilimnion (15 July 1971). In any of these instances the degree of chemical change in the euphotic zone accompanying atelomixis depends principally on the duration of isolation of the mixed layers and on their relative volumes.

The effect of windy weather in producing atelomixis is as much influenced by events before a storm as by the events that accompany it. This is well illustrated by two profiles taken a day apart during some of the most violent weather encountered (Fig. 6). The stability of the storm thermocline was sufficient to resist displacement entirely so that no atelomixis occurred. The storm thermocline is in approximate equilibrium with the strongest winds at about 40 m. The exception in October 1970, when the storm thermocline was depressed below 50 m, may well be explained by the pronounced decline in isolation that accompanied this prolonged storm.

The cooling effect of storms is illustrated by a set of profiles for June 1971 (Fig. 7). Just before the first profile the lake had accumulated a great amount of heat over a period of calm sunny weather. Low isolation and high rates of heat loss due to storm winds greatly reduced the stability of stratification. Rapid heat recovery can of course follow such a loss whenever calm weather resumes.

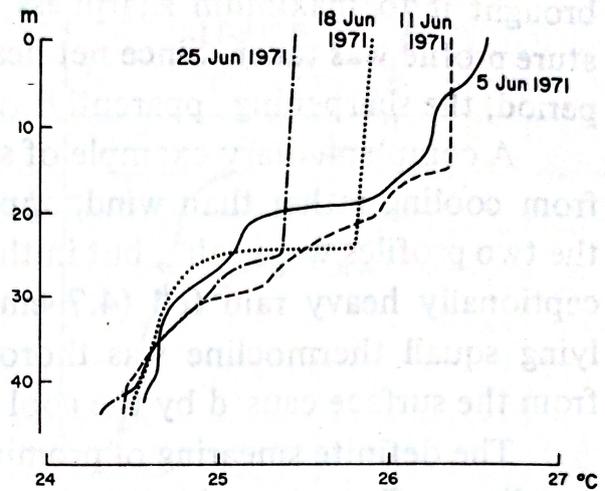
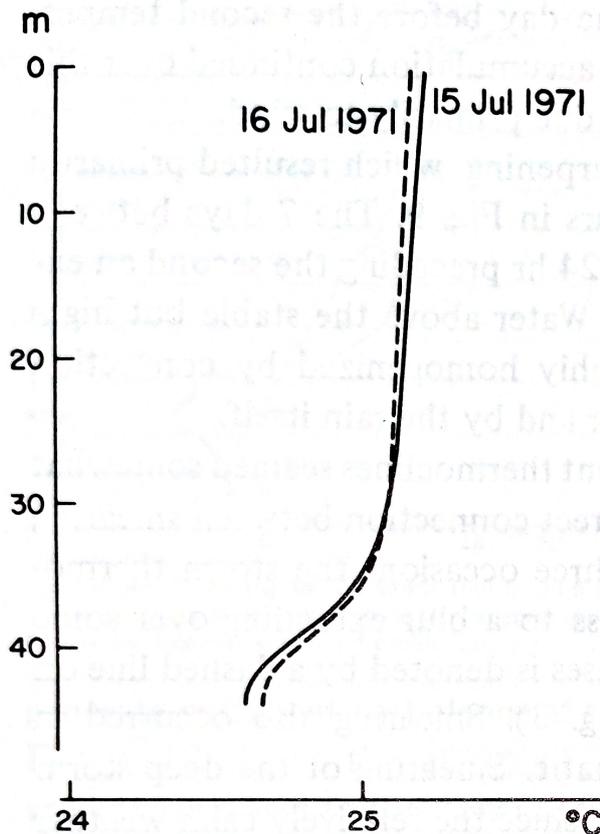


Fig. 7. Nonseasonal heat loss due to storms. Storms occurred between each of the profiles.

Fig. 6. The effect of typhoon winds on a deep storm thermocline. There is no change in the thermocline owing to the stability derived from its great depth.

Curve shape

The precise distribution of temperature with depth in the lake is regulated for not only by those factors causing the formation and displacement of thermoclines but also by factors that affect their sharpness and by certain immediate influences of mud and air on the water in contact with them. Phenomena of this type in the Lanao data are of four kinds: thermocline sharpening, thermocline smearing, unstable temperature inversions, and stable temperature inversions.

The minimum instantaneous slope of temperature curves decreases to nearly zero in response to climatic changes that promote mixing in the upper parts of the water column. Heat accumulation leads to the development of a substantial density profile near the surface, which sharpens markedly as a result of moderate cooling or wind.

Figure 8 illustrates the sharpening effect of a squall on an exceptionally stable breeze thermocline. Before the squall, breezes and nocturnal convection did not transfer heat beyond 15 m — the level of the breeze thermocline. Winds associated with the squall on the afternoon of 24 September displaced the thermocline by some 5 m and

brought it to maximum sharpness the day before the second temperature profile was taken. Since net heat accumulation continued over this period, the sharpening apparently was due primarily to wind.

A complementary example of sharpening, which resulted primarily from cooling rather than wind, appears in Fig. 9. The 7 days between the two profiles were calm, but in the 24 hr preceding the second an exceptionally heavy rain fell (4.7 cm). Water above the stable but high-lying squall thermocline was thoroughly homogenized by convection from the surface caused by the cool air and by the rain itself.

The definite smearing of prominent thermoclines seemed somewhat puzzling at first, since there was no direct connection between smearing and any obvious climatic event. On three occasions the storm thermocline passed from maximum sharpness to a blur extending over some 10 m; its reduced integrity in these cases is denoted by a dashed line on the thermocline history diagram (Fig. 3). Smearing also occurred in squall thermoclines but was less dramatic. Smearing of the deep storm thermocline is particularly significant, since the relatively calm weather that coincided with smearing in two of the three cases suggests that turbulence originating at the surface was not directly involved. Smearing in each case did follow stormy weather, but with considerable delay. While the direct effect of storms is to sharpen thermoclines and deepen them, internal waves of oscillation, and perhaps internal travelling waves of oscillation, and perhaps internal travelling waves as well, probably

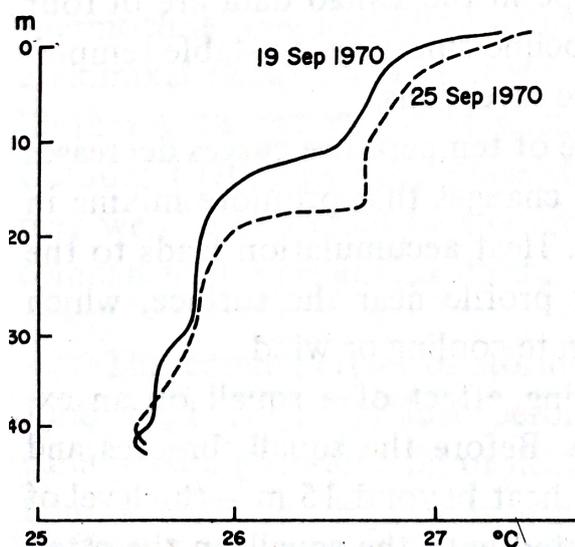


Fig. 8. Sharpening of a thermocline by wind.

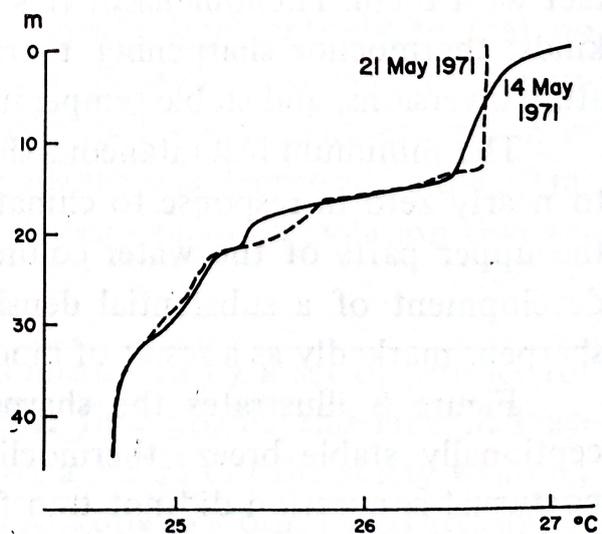


Fig. 9. Sharpening of a thermocline by a rain of 4.7 cm just before the second profile.

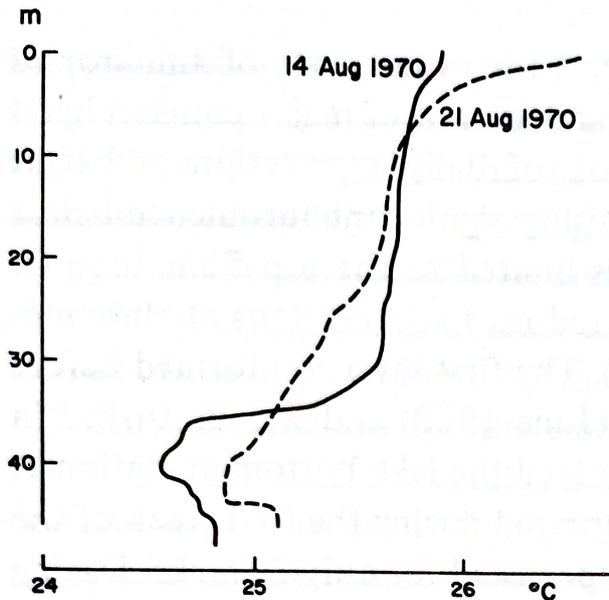


Fig. 10. Smearing of the storm thermocline in calm weather, probably due to turbulence generated by internal waves of oscillation.

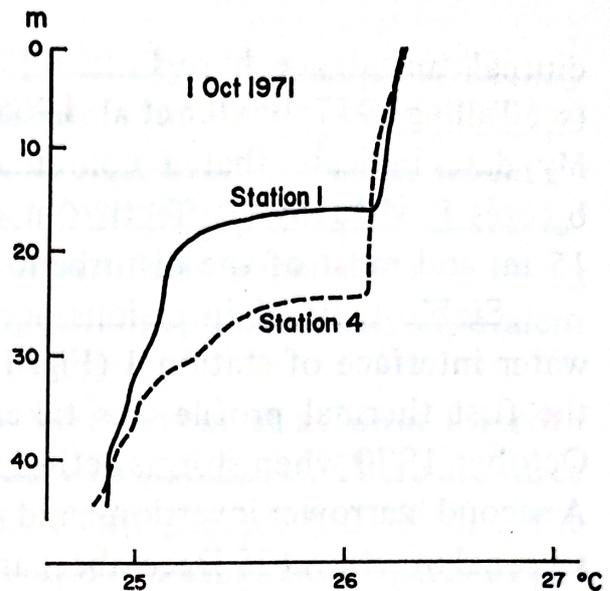


Fig. 11. A seiche affecting the squall thermocline. Stations are 8 km apart.

generate sufficient turbulence at the thermocline to cause the smearing. Figure 10 shows the effect of a typhoon, which homogenized the epilimnion down to the storm thermocline, and the smearing that occurred during the succeeding week of calm weather.

Because I made no extensive study of internal seiche movements there is only circumstantial evidence connecting internal oscillations and thermocline smearing. Tests at multiple stations on 10 of the sampling dates turned up only two clear seiches, neither of which had any obvious effect on thermocline structure. Figure 11 provides one diagrammatically simple example of a tilted squall thermocline. Some minor seiche effects are also visible in Fig. 3. All cases of marked thermocline smearing followed heavy storms, which presumably supplied the energy for a high-amplitude oscillation. On many occasions, however, typhoons were not followed by noticeable changes in the form of the thermocline.

Temperature inversions occasionally appear at the top of the water column and indicate active convection from the surface. Figure 12 illustrates unstable thermal inversions of two types: The April profile is an example of heat loss to the air on a cool clear night, the inversion of the March profile is due primarily to a heavy evening rain. Heat loss to the air is undoubtedly a nightly occurrence of considerable importance, but produces a detectable inversion only in the calmest weather. The frequent afternoon rains must have a similar effect. Similar patterns of

diurnal turbulence have been reported for other parts of the tropics (see Talling 1957; Baxter et al. 1965) and are not of major concern here. My data indicate that a combination of daily convection and light breezes is virtually ineffective in causing significant turbulence below 15 m, and most of the disturbance is limited to the top 5 m.

Stable thermal inversions occurred on two occasions at the mud-water interface of station 1 (Fig. 13). The first inversion formed before the first thermal profile was taken (June 1970) and was destroyed in October 1970 when storms actively mixed the lake bottom at station 1. A second, narrower inversion band appeared during the first week of the seasonal overturn (25 December) and persisted for only 3 weeks. During the entire stagnation of 1971 there was no inversion layer at station 1.

At its maximum extent in August 1970, the first inverted layer could be detected about 4 m from the bottom of the inversion to a maximum of 0.22°C higher than the overlying water. Integration of the August temperature curve gives 44 cal of excess heat beneath the inversion for every square centimeter of lake surface. This heat is presuma-

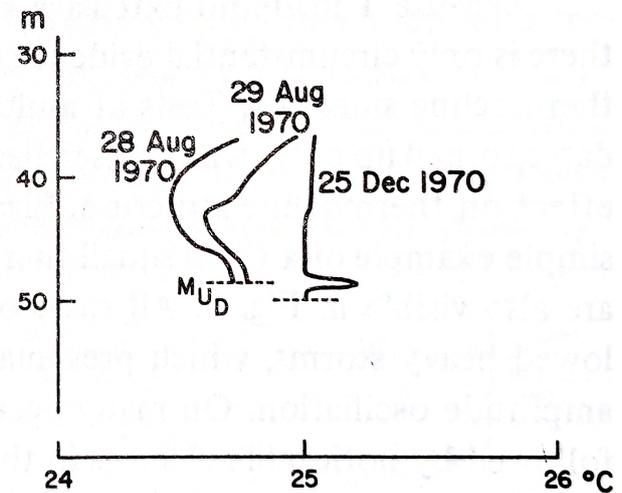
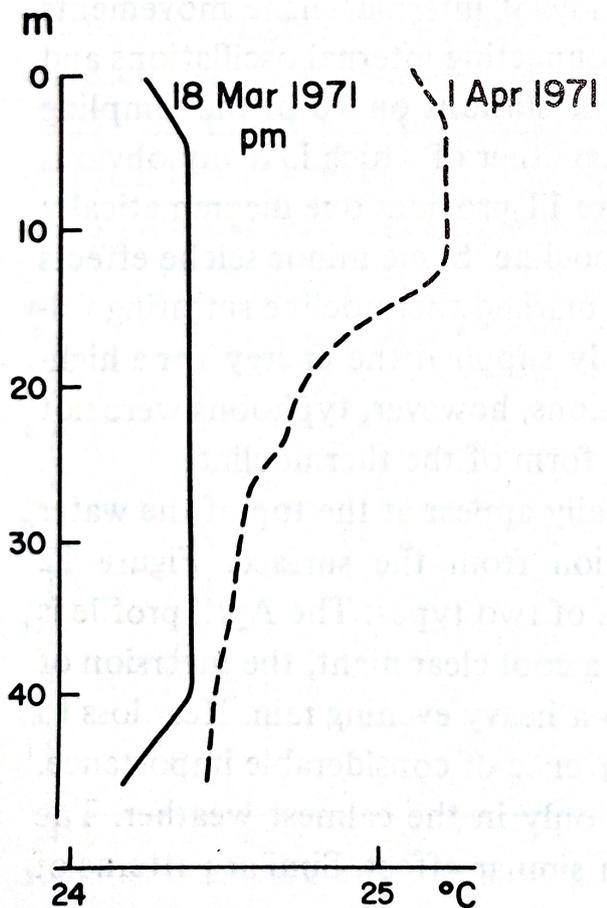


Fig. 13. Stable temperature inversions at station 1.

Fig. 12. Unstable temperature inversions caused by nighttime cooling (April profile) and a cool evening rain (March profile).

bly stabilized by solutes that increase the density of the layer sufficiently to prevent upward convection. To create a uniform density in the inverted layer just equal to that of the coolest overlying water would require an excess salt profile passing from 0 at the top of the inversion to 70 ppm at the bottom. On an areal basis this amounts to some 14 mg cm² of solutes, assuming an ionic composition approximately equivalent to that of the upper water column.

Any explanation for the stable inversions must account for both the excess heat and the solutes necessary to stabilize it. There are three possible explanations: heat retention from a preceding date when the water was warmer, underflow density currents from other parts of the lake, and metabolic heat stabilized by mineralization products. Heat retention seems the best explanation for the short-lived, narrow inversion band over the bottom at the start of circulation in December (Fig. 13). According to this theory, the inversion was absent just before stratification broke down. When homothermal cooling occurred, however, a narrow band of water just above the mud resisted mixing, presumably because of its higher solute content, and therefore remained warm. Continued mixing also accounts for the gradual dissipation of this heat and the consequent disappearance of the inversion.

It is hard to account for the persistence of the broad inversion band earlier in 1970 without postulating a small continuous supply of heat, since some dissipation of heat seems inevitable. The absence of the inversion on the bottom in deeper water (100 m, station 4) nevertheless tends to support the heat-retention theory here too. An alternative or supplementary explanation is that intense mineralization in littoral areas during the hot season creates density flows that reach deeper water. The underflow requirements would seem to be prohibitively large to provide the sole explanation for this inversion, even without losses to dissipation in transit, a full 8 cm of depth would have to be added at station 1, given a density-stabilized underflow at 30°C from the shore. Moreover, the inversion did not appear the following year. No hot springs are known or suspected, and the rivers are almost as dilute as the lake. The decomposition of organic compounds could also continuously supply heat from the bottom, but once again the demands on the source seem unreasonable.

The most tenable explanation for the June-October inversion is that heat was transferred from above to the bottom by the usual mixing processes, and the lowermost portion of the water column was at this time stabilized by the passage of solutes from the mud. Cooling at a later date resulted in the addition of a slightly cooler but more dilute layer above. After its inception by heat retention, the inversion may have been maintained by density underflows from the littoral zone. The remaining question is why this process was not repeated during the 1971 stratification. The hypothesis requires a marked cooling episode that would affect water at the 45 m level after the lake had already warmed considerably. There is evidence that a stable thermocline formed especially early in 1971, which may have prevented the necessary temperature change in deeper water. There was also much more turbulence around the storm thermocline during 1971, as shown by smearing of the thermal profile and higher oxygen readings just over the bottom. Greater turbulence on the bottom at station 1 probably had the dual effect of dissipating any local solute accumulation and reducing the escape rate of solutes from the sediments by maintaining higher oxygen levels at the mud-water interface.

Heat Budget

The annual heat budget (M_{ba} , Hutchinson 1957, p. 493) for Lake Lanao in 1970, as calculated by the method of Birge (1915), is $7,250 \text{ cal cm}^{-2}$. The figure for 1971 is $4,500 \text{ cal cm}^{-2}$. As the temperature data suggest, heat accumulation is greatly affected by variations in weather during the period of stratification. Although the minimum yearly heat content of the water column probably varies little between years ($\text{M}_{bw} = 121,300 \text{ cal cm}^{-2}$). The peak heat content is greatly influenced by the distribution of windy periods and brief reductions in insolation during stratification. This explains the great difference in the annual heat budget for the 2 years as well as frequent reversals in weekly mean heat flux. The peak heat content of the water column does not represent the culmination of a relatively smooth seasonal increase in insolation. In fact the weak seasonal weather changes between April and November are almost entirely blotted out by aperiodic weather events, so that the

lake could reach peak heat content on almost any day between 1 May and 30 November. Under such circumstances the annual heat budget has the disadvantage of hiding the truly impressive amounts of heat flux that occur in both directions. Comparative figures for the heat budget of Lake Victoria are higher ($\Theta_{ba} = 9,000-11,000 \text{ cal cm}^{-2}$; Newell 1960; Talling 1966) and heat accumulation is probably more regular. Neither Victoria nor Lanao approaches the value given by Deevey (1957) for Atitlan ($\Theta_{ba} = 22,000 \text{ cal cm}^{-2}$), which must be atypically large for tropical lakes.

Maximum heat gain for a 1-week period in 1970 was $250 \text{ cal cm}^{-2} \text{ day}^{-1}$, 54% of the total insolation for that week. Comparable figures for the peak week of 1971 are $290 \text{ cal cm}^{-2} \text{ day}^{-1}$ and 59%. Heat gain was high whenever low water temperatures were combined with high insolation. Rates of heat loss were maximal during the brief cooling episodes of stratification rather than during the period of steady heat loss that accompanied the yearly temperature minimum. For example, an average of $290 \text{ cal cm}^{-2} \text{ day}^{-1}$ left the lake during the week 8-15 July 1971. The lake thus lost over 40% of its annual heat budget in connection with a single long storm, although most of the heat was quickly regained in subsequent calm weather. Since the bulk of $398 \text{ cal cm}^{-2} \text{ day}^{-1}$ insolation was also absorbed during this period, total losses were near $650 \text{ cal cm}^{-2} \text{ day}^{-1}$ and must have been even higher for certain days of the week. Losses of only slightly lower magnitude accompanied the tandem typhoons in middle October 1970. Maximum heat loss during the predominantly calm seasonal cooling period was only $170 \text{ cal cm}^{-2} \text{ day}^{-1}$, or about $450 \text{ cal cm}^{-2} \text{ day}^{-1}$ including the incoming radiation.

Discussion

One principal difference between Lake Lanao and its middle-latitude counterpart is the markedly greater responsiveness — the low ceiling on density difference across the thermocline, and the virtual absence of geostrophic influences on mixing.

Despite Juday's (1915) obviously true assertion that a high rate of density change at high temperatures makes tropical thermoclines possible, the upper limit of density difference across the thermocline is

substantially lower in the tropics than in lakes of the temperate zone. Talling (1966) has illustrated this for Lake Victoria. The peak temperature difference between layers for Lanao (24.5-26.2°C) corresponds to a density difference of 0.43 mg liter⁻¹. For a curve of the same shape in a temperate lake having a hypolimnion of 4°C, an equal density profile would be established with an epilimnion of only 12°C. Raising the hypothetical epilimnetic temperature from 12°C to the more familiar 20°C range gives density differences more than three times as great as any that occur in Lake Lanao. Since for a given density gradient, the stability of a thermocline increases with its distance from the surface, the smaller density differences across thermoclines in the tropics will be compensated by a thicker epilimnion than would develop under identical wind stress at middle latitudes. However, when the epilimnion is thicker, the work of the wind required to distribute a fixed amount of incoming heat is greater. Consequently, the tropical lake should also have a more uneven distribution of heat within the epilimnion for the same wind stress. The tendency toward uneven heat distribution is intensified by the temperature-density factor if epilimnetic temperatures are high, as they are likely to be in tropical lakes of low to moderate altitude. On Lake Lanao, resistance to mixing within the epilimnion is manifested by the formation of multiple thermoclines.

A second important latitudinal contrast in water movements derives from the Coriolis force. Although it is not worthwhile to consider differences in geostrophic acceleration at slightly different latitudes, a comparison of temperate and tropical lakes must include this factor. Currents in the northern hemisphere are deflected to the right by the Coriolis force, which acts at right angles to a current and increases in strength with its velocity. The force varies with the sine of the latitude from zero at the equator to a maximum at the poles. Theoretical treatments are complex and are more realistic for oceans than for lakes, especially near the equator, but quantitative considerations clearly illustrate the potential influence of latitude on thermocline depth (Munk and Anderson 1948). At high to middle latitudes, a significant proportion of the strength of any horizontal current in the epilimnion is dissipated by the Coriolis force. According to Ekman's (1905) empirical treatment (see also Hutchinson 1957), depth of frictional resistance to mixing (D) can

be calculated as a function of wind strength and latitude for a column of water with uniform density. The approximation predicts that the 6 m sec^{-1} of wind necessary to mix Lake Lanao (120 m) when it is homothermal would only mix the top 50 m if the lake were located at 45° N latitude. For the tropical lake, the mixing potential of a given wind strength is thus about double that for the temperate counterpart. All layers that form from the surface under the influence of wind will consequently be thicker in the tropics than under identical conditions at higher latitudes. In this way the Coriolis force augments the influence of wind on heat distribution in tropical lakes.

The preceding arguments suggest that multiple layering is likely to be more common in tropical than in temperate lakes, hence the same may be said of atelomixis, which frequently follows the breakdown of such complex stratification. Mixing of isolated layers is of course in itself not a sufficient condition for atelomixis, since the layers will not differ significantly in their chemistry if the isolation has been of short duration. In general, however, the minimum time for significant chemical divergence of isolated layers will be shorter in the tropics due to the effect of higher water temperatures on chemical and biological processes. Two important conditions that lead to atelomixis — complex, semistable stratification in the upper water column and rapid metabolism at all depths — are thus likely to occur in tropical lakes.

Some examples of multiple thermocline formation and atelomixis appear to support the hypothesis that these phenomena are generally important in tropical lakes. Ruttner's (1931a, b) survey of lakes on Java and Sumatra contains examples of multiple thermoclines (Lake Pakis, Lake Toba) and a case of atelomixis involving the depression of the thermocline in a simply stratified lake (Lake Pasir). His extensive data are handicapped by the brief observation period for each lake and by the gaps between measurements in the profiles. Woltereck (1933) reports for Lake Taal, Luzon, what must have been atelomixis resulting from typhoon winds. In his work on Lake Victoria, Talling (1966) distinguishes between a yearly phase of circulation, a phase of weak stratification. During the second phase, formation of two thermoclines is the rule and the upper thermocline is subject to displacement, although it is frequently difficult to distinguish displacement from tilting. Beauchamp's

(1939) data for Lake Tanganyika provide some instances of complex layering in the upper water column.

The details of stratification are certain to be greatly affected by such factors as morphometry and local climate. On the large East African lakes, for example, a combination of maximum fetch, significant winds generated by the lakes themselves, and the steady nature of the seasonal southeast trade winds probably makes the weather windier and not so much inclined to the short-term variation in wind strength and insolation that is characteristic of Lake Lanao. Multiple thermocline formation and thermocline displacement are therefore not like to be so exaggerated as in Lanao, even though these may be regular features of the stratification period. A similar situation may exist in Lake Atitlan at some times of the year if the frequent heavy winds reported by Deevey (1957) prevent the accumulation of heat near the surface. Very small lakes or heavily sheltered ones may be superficially similar to their temperate counterparts in developing a single high-lying thermocline. In such lakes the epilimnion would be thinner due to the reduced effectiveness of wind, and vertical zonation of the epilimnion would therefore be less likely to survive ordinary diurnal convective mixing. Atelomixis should occur in these lakes when the thermocline is depressed during storms, but is not so likely to involve multiple layering.

The discussion has thus far emphasized events in deep water are somewhat different. Homothermal periods in tropical lakes are similar to those of temperate lakes in that they are accompanied by deep mixing and redistribution of nutrients and oxygen. Several lines of reasoning suggest, however, that mixing of a nearly homothermal water body will generally be less effective in the warm tropics than in the temperate zone. The geostrophic factor will of course promote deeper mixing in the tropics, but this effect is countered by three other conditions that typify tropical circulation periods. Perhaps most important of these is the much greater energy that is needed to mix the deep portions of a warm lake if there is even a slight thermal gradient. Birge (1910) calculated the minimum amount of energy required to mix a 1-m column of water 1 cm^2 with a uniform gradient of 1°C as 0.0067 ergs between 4 and 5°C , and 0.2174 ergs between 25 and 26°C . Obviously a tiny thermal gradient in the deep water of a temperate lake

would be ineffective in resisting mixing, but the same gradient in the tropics could prevent complete homogenization of the water column. Secondly, a seasonal trend toward homothermy can be interrupted in the tropics, as it was on Lanao. Finally, the overall influence of convective mixing may be greater in temperate lakes just before circulation due to their vastly greater heat loss.

Evaluation of the extent of deep mixing from oxygen data alone is deceptive in tropical lakes because the water temperature remains high during circulation. In Lanao, for example, deep mixing reduces the primary productivity to minimum levels because the euphotic zone is continually diluted from below, whereas oxygen consumption continues at maximum rates due to the high temperatures. Rapid oxygen consumption during circulation thus accounted for at least part of the oxygen deficit (about 1 ppm) in 1971 at the beginning of stratification. The same factors must be important in the evaluation of oxygen depletion in such deep lakes as Toba, Indonesia (Ruttner 1931a), and Mainit, Philippines (Lewis, in prep.). Although the great oxygen deficit in the depths of these lakes obviously could not have resulted from the decomposition of one year's phytoplankton crop, the profiles of other substances suggest some degree of recent mixing. Circulation in these lakes is evidently sufficient to prevent meromixis, but not vigorous enough to offset oxygen consumption or completely homogenize the water column.

Lake classification

Tropical lakes of low to moderate altitude are divided according to frequency of deep circulation into polymictic, warm monomictic, and oligomictic types (Hutchinson and Löffler 1956; Hutchinson 1957). The geographic localization of these lake types has become increasingly difficult and ambiguous as tropical limnology has broadened its base.

The nomenclatural confusion signifies a conceptual weakness in the zone scheme of classification, well illustrated by Lake Lanao. Lake Lanao is warm monomictic, but a lake of the same size 40 m deep at the same location would unquestionably be polymictic, while a lake 200 m deep would probably not homogenize fully during circulation

and could thus be called oligomictic. Clearly morphometry is as significant as geography in distinguishing tropical lake types. It therefore seems advisable to retain the same nomenclature, but replace the current geographic zone concept with a geographic gradient concept.

A lake will be polymictic if it is sufficiently deep to stratify but not sufficiently deep to support a thermocline that is in equilibrium with the strongest winds of the stratification period. For purposes of discussion, the geographic factor, including both latitude and altitude, can be distinguished from the morphometric factor, including both depth and vulnerability to wind stress, if we consider theoretical variation in the maximum possible depth of the polymictic type for lakes of comparable size and exposure.

The stability of a thermocline increases as a function of its distance from the surface. To achieve a fixed stability, thermoclines having different density gradients must therefore exist at different depths. The density gradient across a thermocline is in turn related in a predictable way to latitude and altitude. The geographic trend in density gradients thus implies a geographic trend in the depth of thermoclines having a given stability, hence in the maximum possible depth of polymictic lakes.

The geographic trend in density difference across a thermocline reflects the simultaneous variation of two density factors that have already been discussed with specific reference to Lake Lanao. First, an increase in temperature difference between water layers is accompanied by an increase in density difference between the layers. Second, for a given temperature difference between layers, an increase in temperature is accompanied by an increase in density difference. From these trends and the geographic distribution of air temperature minima, it follows that the maximum possible depth of a polymictic lake is least at sea level in middle latitudes and increases toward the poles, toward the equator, and with increasing altitude. Polymixis is by this line of reasoning not restricted to the tropics, except in the sense that the theoretical maximum depth of such lakes is greatest in the tropics at high altitudes, so that the category is more likely to include a randomly selected lake in this region. The applicability of polymixis to many small lakes of the far north has been noted by Schindler (1971). The geographic gradient associated with polymixis of course terminates at the

highest altitudes and latitudes, where cold monomixis predominates because there is insufficient heat uptake to permit any significant stratification. At any latitude or altitude, the maximum depth of the polymictic type can be expected to increase with size and exposure to wind stress, but this need not obscure the geographic trend.

Many lowland tropical lakes that are too deep to be polymictic are warm monomictic, since they circulate yearly in response to a seasonal weather pattern. This category probably includes Lakes Atitlan, Amatitlan, Ilopango, and Cotapeque in Central America (Juday 1915; Deevey 1955), Titicaca in Peru (Gilson 1964), the low mountain lakes Bulera and Luhondo in equatorial Africa (Damas 1955), Lanao and probably Taal (Woltereck 1941) in the Philippines, at least some of the lakes of moderate depth in Indonesia (e. g. Lake Lamongan) surveyed by Ruttner (1931a), and numerous others.

Still other lakes do not circulate fully on a yearly basis. Following the original definition of oligomixis, some of these lakes may mix irregularly at long intervals. Such lakes must be confined to the truly equatorial regions and would probably have to be small or heavily sheltered. No well-documented example seems to exist, but possibilities include some of Ruttner's lakes, especially in middle Sumatra, and some lakes that have recently been investigated in Ethiopia (Baxter et al. 1965).

More important than the strictly oligomictic lakes are those that become nearly isothermal and mix deeply on a yearly cycle but do not homogenize completely. These lakes are not truly meromictic since they lack a pycnocline during the cool season, hence it seems most reasonable to expand the oligomictic designation to include them. Ruttner's data for Lake Ranau, Sumatra, were evidently taken just after a deep circulation and probably exemplify a lake that is transitional between the warm monomictic type and the oligomictic type with monomictic tendencies. The lake apparently was isothermal without quite becoming chemically homogeneous in January just before Ruttner's visit. Other examples of this kind of oligomixis probably include the five deepest of Ruttner's lakes, Lake Mainit in the Philippines, and those of the deep East African lakes that lack a salt-stabilized monimolimnion.

The deep oligomictic lakes must mix sufficiently to prevent true meromixis. There are two mechanisms by which this mixing could occur. First, exceptionally cool years may result in density inversion and active mixing of the entire lake. This is unlikely for several reasons. Cooling undoubtedly varies from year to year, but it is difficult to imagine any probable amount of departure from mean minimum temperature sufficient to cause gross convective interchanges between top and bottom. Descending convection cells should quickly lose their force due to initially small density gradients. Moreover, many of the lakes are considerably deeper than any probable maximum value for depth of frictional resistance to mixing. Finally, there is almost no evidence to support the notion of occasional turnover in this kind of lake. Anecdotal evidence that Lake Nyasa produced an exceptional algal bloom in 1946 (Beauchamp 1953) implies a greater degree of vertical exchange than has ever been observed, but unfortunately does not establish the nature of this exchange.

The alternative to an occasional full overturn is a substantial interchange each year at the time of temperature minimum that would continually return dissolved substances to the epilimnion and dilute the deeper water. Although this interchange might vary in degree, it need never constitute a turnover. It is difficult to guess whether such circumstances would necessarily lead to the accretion of deep-water heat. If so, one possibility for maintaining heat balance could be elaborated from Talling's (1963) hypothesis on cool underflow currents in Lake Albert. Heat gain at the surface of a deep layer could be offset by cool, dense water moving downslope during rains, at night, or during the coolest part of the year. Several of the profiles from Lake Lanao are interesting in this connection. Figure 12 shows a profile taken in calm weather during the coolest part of the year after a heavy rain. The lower portion, just above the lake bottom at station 1, is considerably cooler than any temperature ever recorded for the deepest portions of the lake and probably represents an underflow of some kind. However, it is impossible to determine as yet whether comparable underflows help stabilize the deepest layers of tropical lakes.

The deep-water temperatures of tropical lakes probably provide the best empirical means currently available for placing specific lakes on

a geographic gradient. Ruttner (1931a) and Löffler (1966) have already shown the effect of altitude on deep-water temperatures. In recognition of the similar effects of latitude, it seems desirable to establish some criterion of conversion between these two geographic factors and thereby consider their joint effect. For this purpose it is convenient to compute a composite altitude factor by adding the true altitude of a lake to an approximation of the additional altitude required to equal the latitudinal effect on the annual air temperature minimum. This can be justified a priori only if there is a significant relationship within the tropics between latitude and yearly air temperature minima and a posteriori only if it accounts for more variation between lakes than could be accounted for by altitude alone. The procedure meets both of these criteria.

The mean temperature of the coolest month at 12 sea level stations between the Tropics of Cancer and Capricorn (Rumney 1968) was used in a test for correlation of mean minimum air temperature and latitude. The correlation proved to be highly significant and rather marked ($r = -0.84$) and was assumed to provide sufficient justification for an assessment of mean minimum air temperature on the basis of latitude. Altitude can likewise be converted to a mean temperature effect by recourse to the mean normal lapse rate ($0.67^{\circ}\text{C } 100 \text{ m}^{-1}$). Latitude and altitude are thus interconvertible via air temperature at a rate of about 49 m altitude per degree latitude. The resulting altitude factor, obtained by summing the altitude of a lake with the altitude equivalent of its latitude, has been calculated for the eleven major tropical lakes of Fig. 14. The correlation of altitude factor and hypolimnetic temperature for these lakes is highly significant and accounts for most of the variation between lakes ($r = +0.97$).

Because the thermal regime of a lake influence its chemistry and biology, a predictable geographic thermal trend among lakes is potentially significant to the comparative limnology of the tropics. Such a trend not only gives perspective to the study of individual lakes, but also implies some parallel degree of predictability in such factors as decomposition rate, oxygen deficit, and efficiency of nutrient cycling.

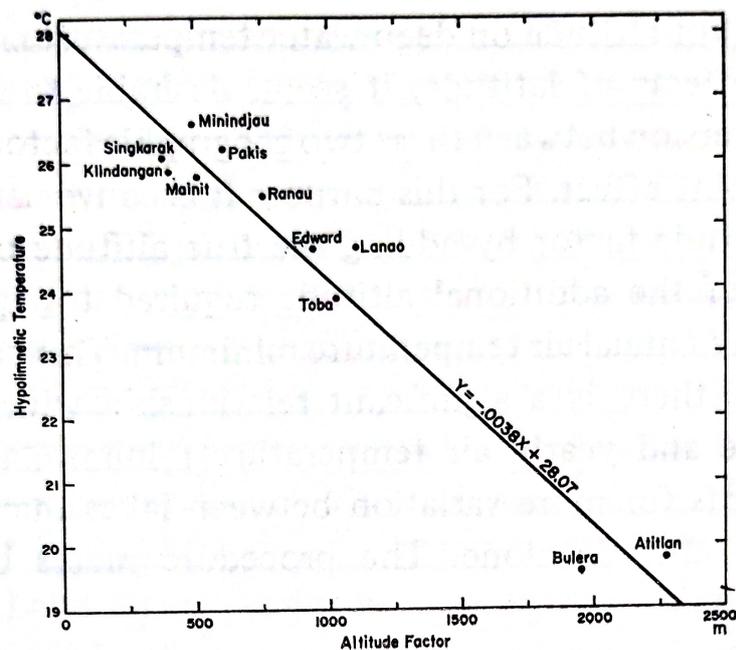


Fig. 14. Relationship between altitude of tropical lakes, corrected for latitude, and their hypolimnetic temperatures (*see text*). Sources for temperatures are cited in text. The product-moment correlation coefficient is 0.97 (highly significant).

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