

THE ROLE OF THERMOCLINE MIGRATION IN REGULATING ALGAL BLOOMS ¹

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Introduction

Previous hydrological studies of eutrophic Lake Mendota, Wisconsin, have shown that the allochthonous phosphorus loading is small during June 1 to October 1, when massive, recurrent blooms of bluegreen algae cause serious deterioration of water quality. Consequently, it was hypothesized that the surges of algae biomass were dependent on refluxing of nutrients (N and P) by periodic depression of the thermocline by meteorologic inputs. Mortimer (1969) suggested that such a mechanism might be significant. This study reports the results of a field investigation of the possible significance of this mechanism as a factor controlling bluegreen algal blooms in Lake Mendota, Wisconsin. The approach used was to determine metalimnetic and epilimnetic ammonia, phosphorus and chlorophyll *a* concentrations, and monitor the lake's thermal structure in order to provide estimates of the vertical flux of N and P caused by thermocline depression. Particular attention was given to examining the correlation between depression and subsequent increases in chlorophyll for Lake Mendota in 1971.

Experimental Approach

Figure 1 is a schematic of Lake Mendota illustrating some of the details of its environment that are pertinent to this hypothesis. The prevailing wind directions in summer are shown by arrows. The hypsometry of the lake is known, which was requisite for this study. The maximum fetch is approximately 9 kilometers and occurs when the wind is out of the southwest. Meteorologic data were provided by the U.S. Weather Bureau Station at Truax Field, about 7 kilometers ENE of the lake's center. Sampling was accomplished by vertical profiling at stations approximately evenly spaced along the transects. The primary transect was parallel to the wind vector at

the time of sampling. The secondary transect was orthogonal to the first. Occasionally, it happened that the lake was becalmed, in which case stations were chosen which were widely spaced in the lake. Sampling was performed in the afternoon. Normally the afternoons are characterized by moderate southwest breezes which generate whitecaps except during cold front passage from the northwest.

Parameter estimation

Chlorophyll was sampled every meter down past the thermocline at each of 5 to 8 stations selected on any given day. Sampling took place on 24 days between mid-June and mid-October. Chlorophyll *a* concentrations were determined by fluorometry, using the filter combination reported in Strickland and Parsons (1968) on a Turner fluorometer. Water samples were filtered through Reeve Angel 934AH glass fiber filters and the glass fiber filters were extracted using a methanol solution. The solution consisted of 98 percent methanol and 2 percent bicarbonate buffer solution, by volume. The bicarbonate buffer was prepared by adding 16.8 grams of NaHCO₃ and 0.80 grams of NaOH per liter of water. The fluorescence units were related to 665 nm absorbances. Absorbances in 98 percent MeOH at 665 nm were related to absorbances of identical quantities of chlorophyll in 90 percent acetone. The concentrations of chlorophyll *a* were calculated following Strickland and Parsons (1968).

Several statistics connected with the temperature profiles and later used in the vertical transport model are explained in Figure 2. The *Boundary* between the epilimnion and metalimnion is taken to be that depth at which the second derivative of the $T = f(z)$ function is a minimum. This statistic will be called D_e for depth of the epilimnion. Similarly, the boundary between the metalimnion and hypolimnion is taken to be that point where the second derivative of f is maximum. The *Thermocline* is then specified to be that point in depth below the surface where the temperature is midway between the two temperatures associated with the maximum and minimum in the second derivative. These random variables become statistics after observations of them are made on the lake. The thermocline depth is usually defined as the z value of maximum absolute value of the first derivative of the function f (Hutchinson, 1957). This is at the inflection point (where the second derivative equals zero) when the

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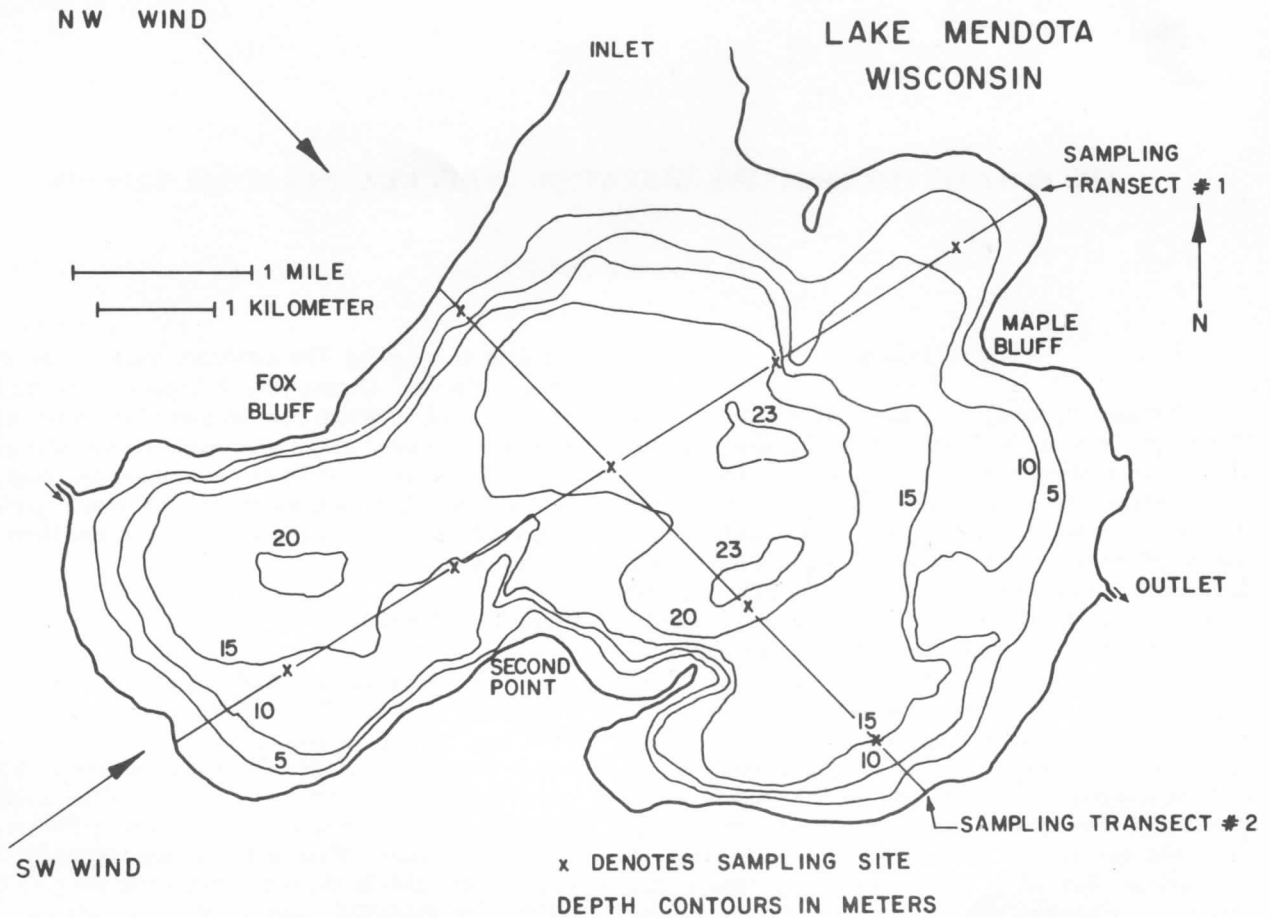


Figure 1. Lake Mendota, Wisconsin, showing bathymetry and sampling transects.

graph of f is sigmoidal. In this case, the operational definition of the thermocline explained above coincides with the classical one. Using the classical definition of the thermocline, the epilimnion boundary and thermocline are often at identical z . However, because of the steepness of the temperature curve in the upper metalimnion, a change of a couple of degrees in the temperature associated with the thermocline changes the thermocline depth by a very small amount.

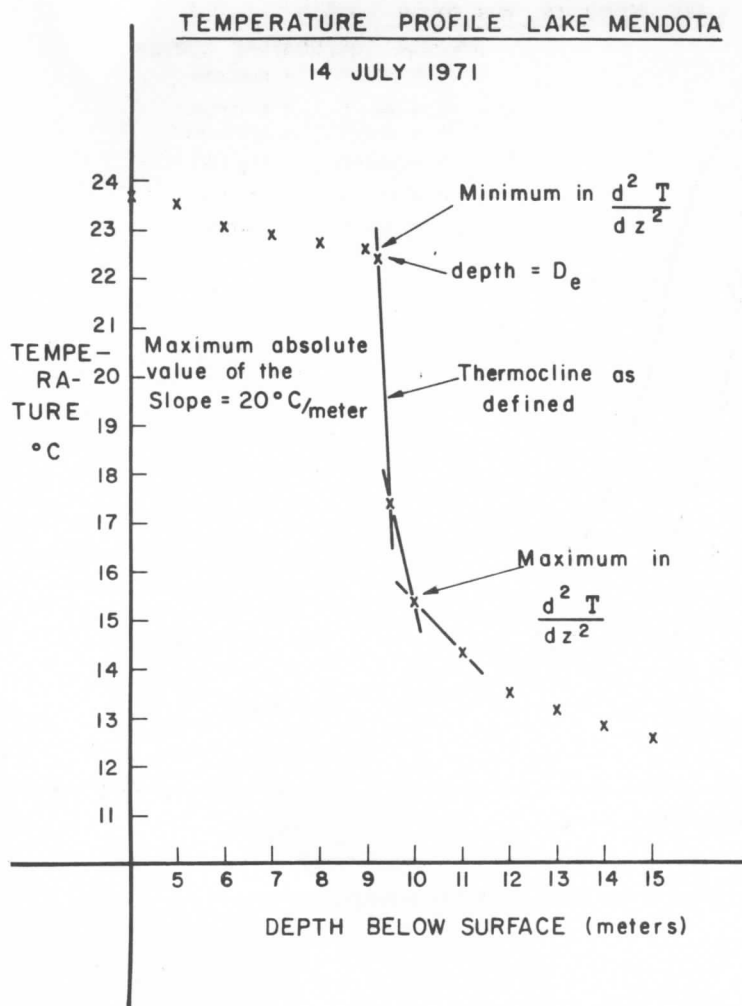
Since the temperature observed at depth z at time t is a random variable which sometimes takes values in a large range over a few minutes because of progressive internal waves, and over a longer time span because of standing internal waves or active wind stress, it is not worthwhile to attach too much importance to an individual thermocline or boundary statistic. However, it is useful to graphically determine the epilimnion boundary and thermocline statistics for the various profiles on each sampling day in order to compare their values with the statistics for the average temperature curve. The average temperature curve is just the graph of the average temperature for each depth plotted against depth. This is a mean temperature profile for that day. Since the design

was to sample upwind and downwind stations with equal frequency when the lake was actively windstressed, the statistics connected with the average temperature curve are approximately unbiased.

Total phosphate followed the persulfate procedure of Menzel and Corwin (1965), using the molybdate-blue, ascorbic acid procedure in the colorimetric step. Phosphorus fractions were defined in accordance with Strickland and Parsons (1968). Ammonia-N was analyzed using an alkaline-phenol-hypochlorite AutoAnalyzer procedure as modified by Kluesener (1972). Nitrate-N analysis followed Kahn and Brezenski (1967) and also involved use of a Technicon AutoAnalyzer.

Vertical transport model

Figure 3 shows several of the mean temperature curves for the period June 16 to July 21. Tremendous heat inputs into the metalimnion and hypolimnion occurred during the period July 8-14. Note that the heat gains between 6 and 8 July and 14 and 21 July are negligible by comparison. The displacement of the



LAKE CROSS SECTION
Illustrating Epilimnion Expansion
and the change in the Average
Epilimnion Boundary Statistic
(\bar{D}_e)

E = Epilimnion
M = Metalimnion

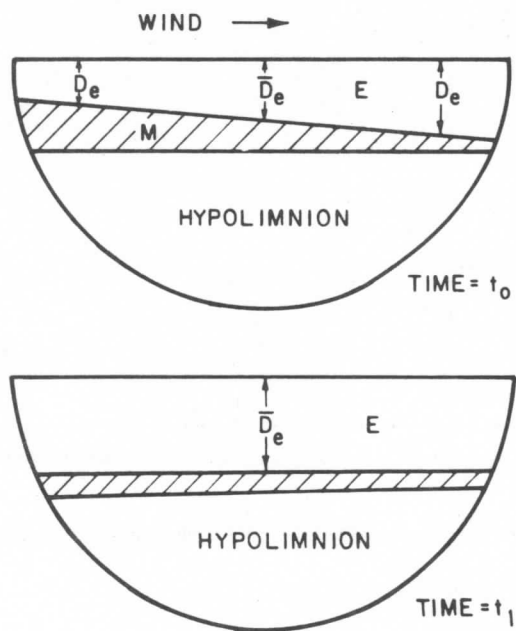


Figure 2. Illustration of boundary statistics.

thermocline associated with this heat transport occurring during a major cold front is typical. No significant amount of this heat gain can be accounted for by the process of oscillation of standing internal waves (Dutton and Bryson, 1962). This is so since the time interval for the heat gain is too short. On the contrary, the explanation lies in the turbulent exchange of epilimnetic water with metalimnetic water during the cold front passage. This process extends the boundary of the epilimnion with the result that nutrients in this added volume element are directly annexed by the epilimnion. In addition, it causes some warming of the water remaining in the metalimnion and hypolimnion.

If it is assumed that solutes have turbulent exchange coefficients the same as heat, then knowledge of the concentrations of ammonia and phosphorus in the metalimnion and hypolimnion prior to the wind disturbance enables the calculation of the vertical transport of

nutrients using changes in average temperature profile. Approximate mixing ratios R_z between epilimnion water and the metalimnion water in each volume element at depth z in the metalimnion and hypolimnion are calculated by Equation 1. The total mass transport of solute s is the sum of the component transports from each depth element (Equation 2). Each of the component transports during the period t_1-t_0 is equal to the average excess concentration of the solute (as compared to the epilimnion) in the volume element at depth z multiplied by the volume of the element multiplied by its mixing ratio (Equation 3). The mixing ratio defined is based on conservation of heat and the constancy of the specific heat of water over the temperature range of interest. It is assumed that the epilimnion reaches a uniform temperature before epilimnion boundary migration begins. Based on the comparative coefficients of turbulence in the epilimnion and the metalimnion, and on actual field observations this is not unreasonable.

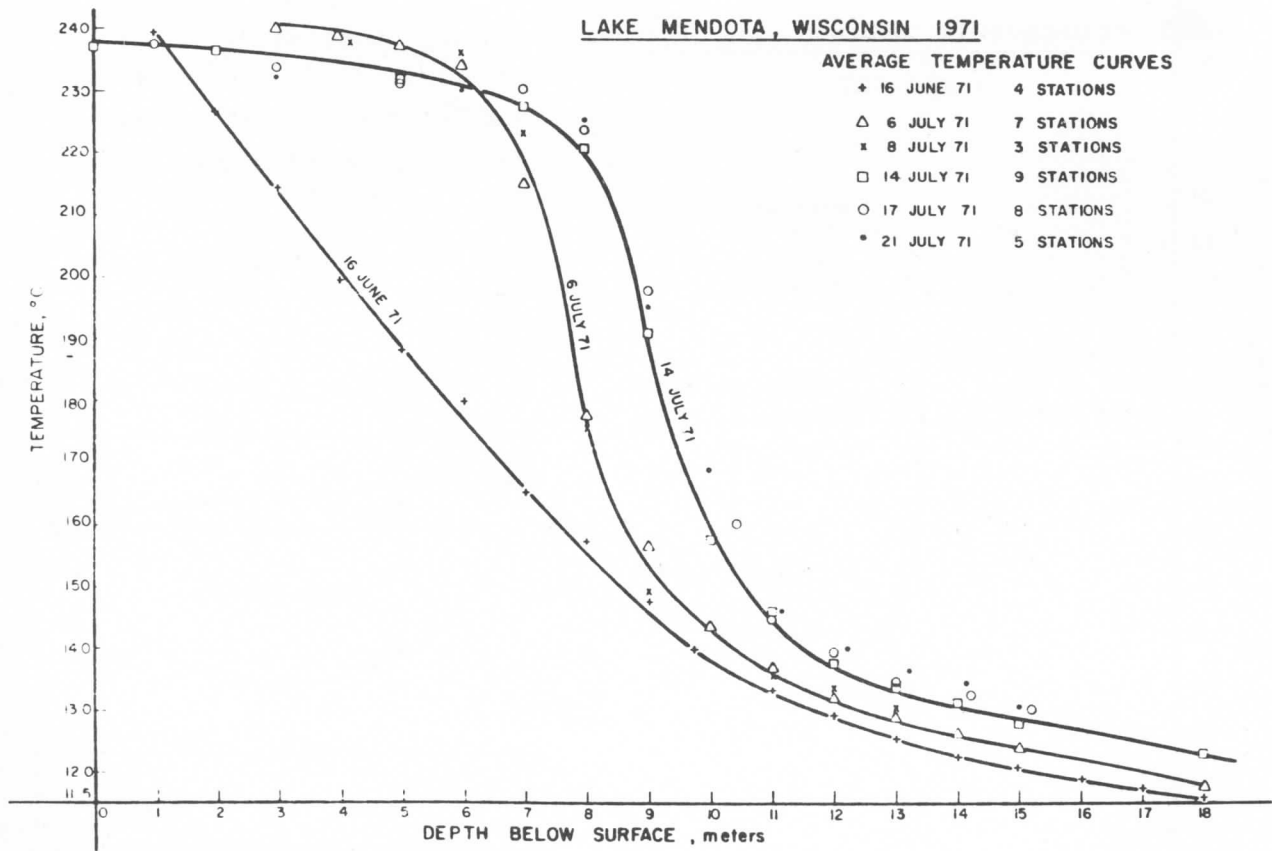


Figure 3. Lake Mendota, 1971, showing stochastic seasonal progression of average temperature curve.

VERTICAL TRANSPORT MODEL

Let:

- V_j = volume of the j th depth element
- $[s]_j$ = average concentration of solute s in depth interval j
- $[s]_{e,t_0}$ = average concentration of solute s in the epilimnion at time t_0
- F_j = solute transport component from the j th depth interval
- F_e = solute transport component due to epilimnion expansion
- t_0 = initial time
- t_1 = later time
- R_z = mixing ratio at depth z . Here Z is the average depth of the depth interval j
- \bar{T}_{e,t_0} = average epilimnion temperature at time t_0
- T_{z,t_1} = temperature of water at depth z at time t_1
- F = total transport of solute s over time interval $(t_0 - t_1)$

Mass transport equations

$$R_z = \frac{T_{z,t_1} - T_{z,t_0}}{\bar{T}_{e,t_0} - T_{z,t_0}} \dots \dots (1)$$

$$F = F_e + \sum_j F_j \dots \dots \dots (2)$$

$$F_j = V_j \{ [\bar{s}]_j - [\bar{s}]_e \} R_z \dots (3)$$

Let R_z be the approximate mixing ratio at depth z below the surface. R_z is approximate since it is derived considering water exchange between two water reservoirs at different temperatures, with the heat source reservoir (the epilimnion) considered to be very large relative to the metalimnion water reservoir. This assumption implies that the epilimnion temperature remains stationary in spite of the heat exchange that has taken place. In fact, the epilimnion temperature drops during a period of thermocline depression because of accelerated sensible and latent heat transfer to the atmosphere and because of water exchange with the metalimnion and expansion of the epilimnion. The cooling of the epilimnion that results from sensible and latent heat transfer to the atmosphere introduces a negative bias to R_z . Calculations indicate that this is the overwhelmingly dominant factor causing the temperature drop in the epilimnion during a cold front passage. One trouble with the mixing ratio R_z is that the average epilimnion temperature at the critical time of mixing may be imperfectly known unless temperature monitoring is possible using remote sensing. The result is that when the denominator of the R_z expression is small, the uncertainty in the ratio is large. If the epilimnion is cooled during the time interval (which is the case when deepening occurs because of cold front passages), then it is possible to define another mixing ratio statistic based on the final average temperature of the epilimnion. It is not hard to see that this new statistic R_z^* is greater than R_z for all z . In fact, R_z^* is an upper bound for the true mixing ratio. A recommended course is to use the average of R_z and R_z^* in computing transport. The uncertainty in the average epilimnion temperature at the critical time of mixing can be reduced by temperature profiling at more frequent intervals. Naturally, if the epilimnion temperature has been reduced by extensive mixing and by sensible and evaporative heat loss, it tends to rebound rapidly with the onset of still, hot weather. This happened after August 5, 1971.

The model as described predicts the transport of N and P based on measurements of the initial and final states of the density partitioned water column. There is no attempt to dynamically describe the water movements which are attendant in the meteorologic "event" which causes the mass transport. In this sense, the approach is a statistical estimation one, with the focus on determining the pertinent system parameters (such as subsystem boundaries, concentrations of solutes and heat contents), and the changes in these parameters over the time interval, as accurately and precisely as possible. No attempt has been made to separate the vertical transport into specific components such as transport resulting from upwelling or mass transport involving entrainment of colder water at the epilimnion boundary because of changes in the Richardson number accompanying the currents set up by Langmuir circulation helices. As interesting as these individual hydraulic problems are, their exact resolution is not prerequisite to describing the net changes in the partitioning of the lake's nutrient pool over the entire time frame.

Sweers (1970) considered the thermocline as a dynamic boundary. The vertical eddy diffusivities at the bottom of the epilimnion vary over time in response to the variable inputs of momentum from windstress. The partition state of the lake is not deterministic with respect to time since the partitioning agent is the time sequence of meteorologic inputs to the lake. An effect of this is that the boundaries of the subsystems (epilimnion, metalimnion, hypolimnion) are not constant with time, even over an interval of a few days or weeks in the summer, for the subsystem boundaries respond to the continuing sequence of meteorologic inputs, the early part of which was critical in their development. Both the timing and the magnitude of the vertical nutrient transport events are random variables.

Figure 4 illustrates the chlorophyll regime before and after one of the major wind events of the summer, namely, a cold front passage accompanied by strong, enduring winds that occurred on July 12-13. The statistics plotted are the average concentrations of chlorophyll at each depth below the surface on the two successive days. One unit on the ordinate is equivalent to 0.288 mg/m^3 chlorophyll a . The bars denote the total range of the 5 order statistics for each depth on each of the two days. Using the averages and the hypsometric table, the total chlorophyll a in the lake on July 8 was 2000 kilograms and on July 14, 4300 kilograms. Nonparametric statistics can be used to test the differences between the *medians* at each depth on the two successive days. The sampling design tends to bring out the possible range of each chlorophyll statistic because upwind and downwind stations are always included. It is clear that the true power of the statistical tests comparing the median concentrations at each depth on the successive days is actually greater than can be calculated using the data presented. Nevertheless, the sample ranges at most depths do not come close to overlapping. This implies that the change in total epilimnion chlorophyll was highly significant during the period 8-14 July. Furthermore, Figure 4 indicates that only an insignificant amount of the total lake chlorophyll lies below the thermocline in Lake Mendota. This percentage decreased as the summer progressed.

As was expected from hydrodynamic considerations, the thermocline and epilimnion boundary statistics associated with the individual temperature profiles vary with distance downwind. Most importantly, it was found that for each of the two random variables (thermocline depth and epilimnion boundary), the mean of the individual statistics, the median, the average of the maximum and the minimum of the statistics, and the statistics derived from the average temperature curve usually agreed within ± 0.2 meters. The range for all stations was sometimes as great as 2 meters. The statistical estimation problem of interest is to detect *significant* displacements of the epilimnion boundary and the thermocline over time. This will be treated in detail in another paper.

CHLOROPHYLL IN LAKE MENDOTA,
WISCONSIN

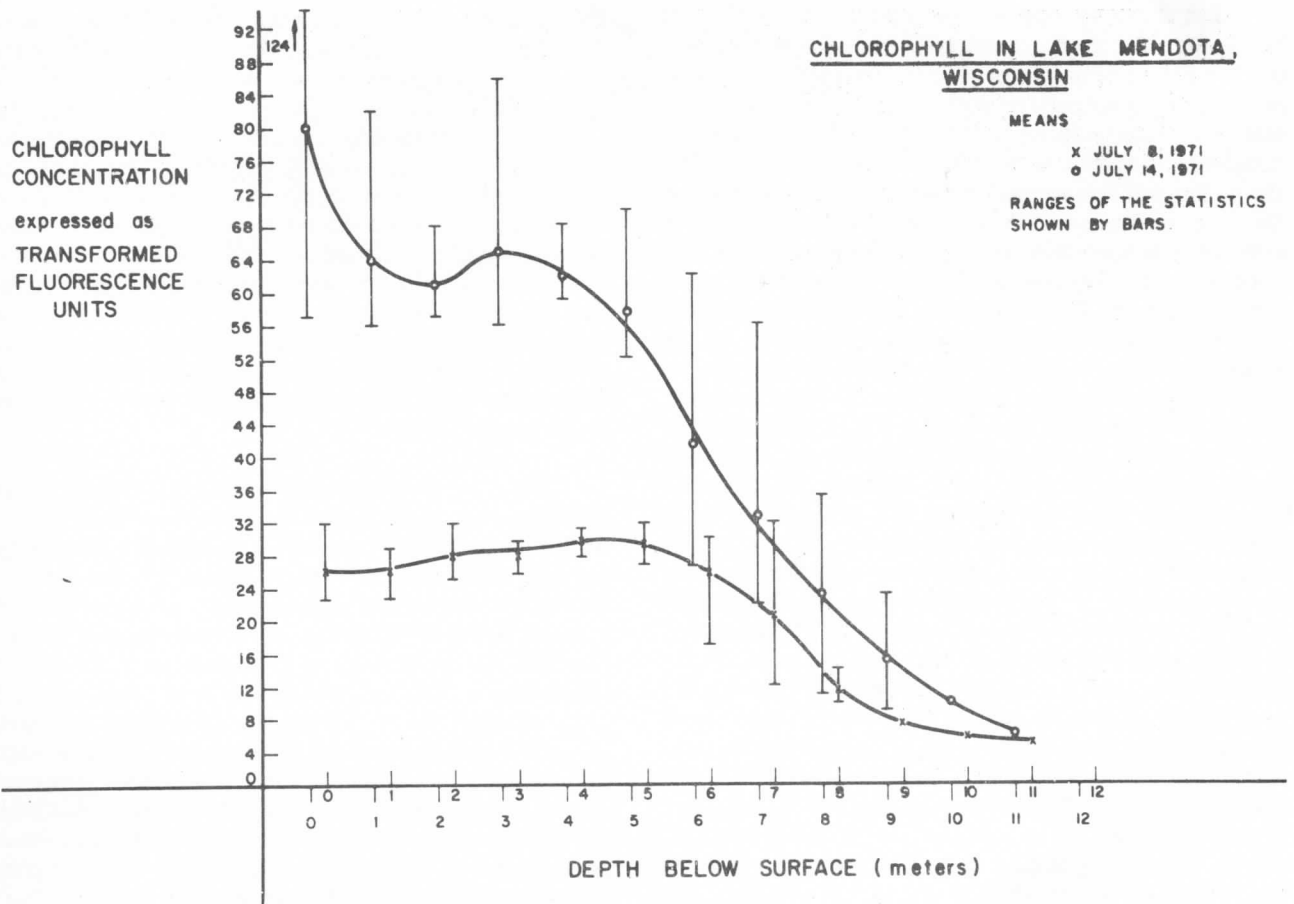


Figure 4. Chlorophyll in Lake Mendota, 8, 14 July 1971. One unit on the ordinate is equivalent to 0.288 mg/m³ chlorophyll *a*.

It was found that the epilimnion boundary statistic is the most useful because it is usually sharply defined. It indicates expansion of the epilimnion at the expense of the metalimnion and hypolimnion, and is necessary for computing the total phosphorus in the epilimnion at any time *t*.

Results and Discussion

Figure 5 summarizes the observations on Lake Mendota during the stratified period, 1971. Total chlorophyll per square meter in the lake's pelagic zone (water depth > *D_e*), cumulative hours of sunshine, cumulative rainfall and the depth of the thermocline are shown.

The thermocline migrated downward 1.2 meters on July 12-13 and a total of 3.7 meters between July 12 and August 5. The thermocline migrated downward approximately a meter in the following month, i.e., between August 5 and September 9. Cumulative hours of sunshine does not present a very convincing parameter to account for the dramatic changes in chlorophyll during the summer investigated. The rainfall during the summer was seriously below normal except for the period from August 10-14, when approximately 2.5 inches of rain fell in three

thunderstorms. Consequently nutrient inputs from rain and rural runoff were probably lower than normal. The magnitude of the (chlorophyll per square meter) values attained suggests that the algae were driven into light limitation (Hepher, 1962, Steemann-Nielsen, 1962). At all times during the summer after mid-June, bluegreens were overwhelmingly dominant with *Microcystis*, *Aphanizomenon*, *Gleotrichia*, and *Anabaena* species in various combinations making up the population. *Anabaena* formed the first bluegreen algal bloom in early-mid July.

Epilimnion total phosphorus and total lake chlorophyll mass are shown in Figure 6, with the calculated vertical transport and measured changes in the total epilimnion phosphorus (mass) indicated by bars. Total chlorophyll reached very high values following those periods of active vertical transport. There are three significant maxima in the total chlorophyll curve. The first is in June when the algae were responding to inorganic nutrients in the epilimnion. This pulse came with the rapid warming of the water and development of the thermocline. Secchi disk readings throughout May and June indicate that the curve for chlorophyll was rising from late May until chlorophyll observations began on

LAKE MENDOTA, 1971

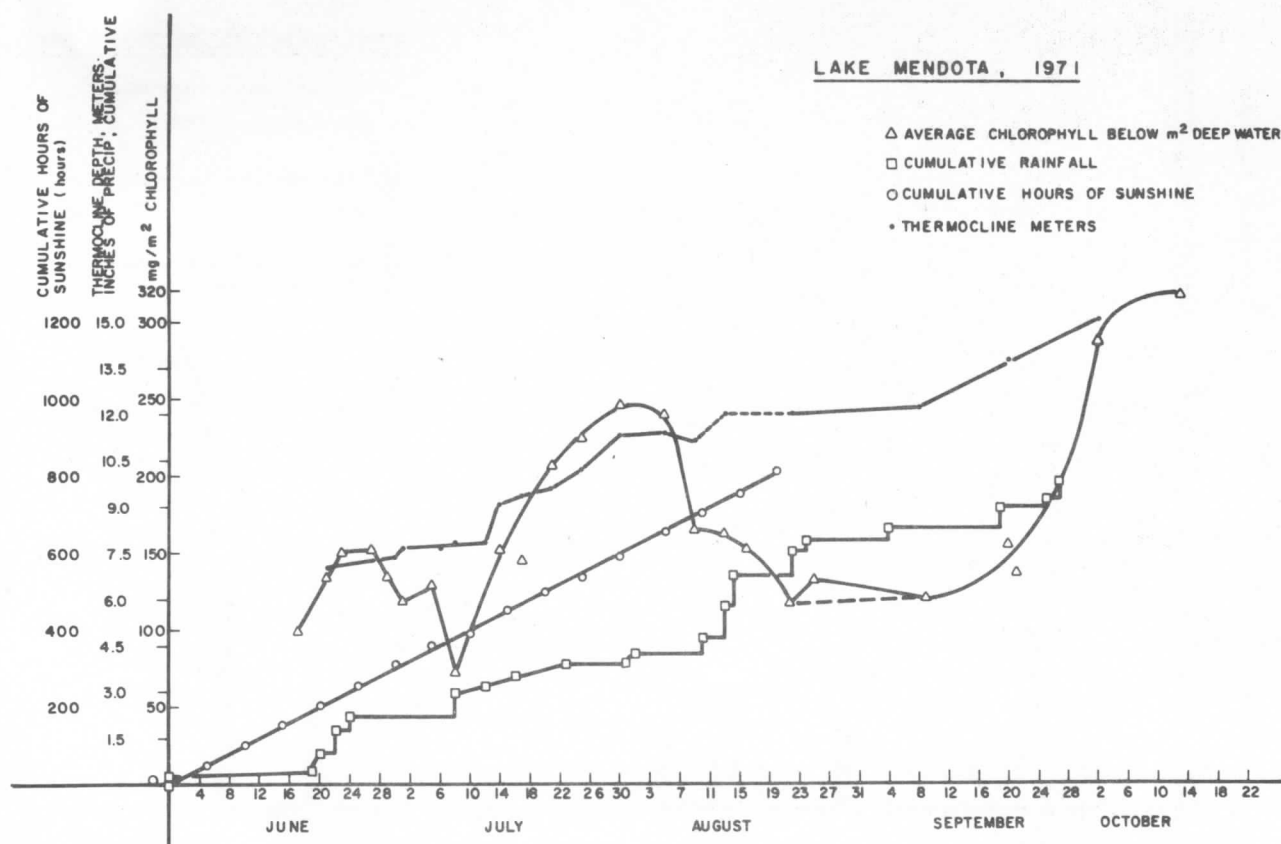


Figure 5. Summary graph for Lake Mendota, 1971, showing chlorophyll, cumulative rainfall, cumulative hours of sunshine, and thermocline depth as a function of time.

June 17. Exhaustion of nutrients occurred by late June in the epilimnion.

The two large chlorophyll peaks coincide with the two periods when significant thermocline migration occurred. The July period was characterized by frequent cold fronts and the September-October peak was associated with the rapid deepening that occurred with the onset of fall weather after what was initially an unseasonably warm and dry September. There was no significant amount of chlorophyll below the thermocline after the onset of sharp thermal stratification in mid-June. The minimum total chlorophyll in the lake occurred at the same time as the minimum total epilimnion phosphorus. Conversely, the corresponding maxima also agree in time. The total phosphorus content of the epilimnion increased from 5900 kilograms to 10,000 kilograms during the cold front of July 12-13. This is an increase of 70 percent. The chlorophyll more than doubled. The measured epilimnion phosphorus pool increased by 12,400 kilograms or 78 percent, between September 20 and October 2. The calculated vertical mass transport of P over the same period was 14,100 kilograms. Chlorophyll again made impressive gains. The sharp drop in chlorophyll between August 5 and August 9 was associated with an equally impressive drop in total epilimnion phosphorus and occurred during a period of hot, calm weather on the

lake. These drops can probably be attributed to settling of algae out of the epilimnion, although such a process is difficult to quantify directly.

The rapid loss of phosphorus and algae from the epilimnion during this hot, calm period in August suggests that sedimentation of a bloom can occur quite rapidly. The small increases in total lake chlorophyll around July 2 and August 25 may have their explanation in moderately strong winds that occurred on June 30-July 1 and again on August 22. The wind of June 30 thickened the epilimnion slightly but in a way that is not comparable to the big wind event of July 13. It is risky to attach too much significance to *small* changes in the total chlorophyll because chance alone may explain this variation in the statistic. This is being investigated. It must be emphasized that turbulence alone may favor development of higher total lake chlorophyll based on what is known of the physiology of photosynthesis. However, this factor does not appear to be controlling.

Nutrient transport accompanying thermocline depression can be expected to increase total lake chlorophyll only when the algae crop is limited by the nutrients being provided by this mechanism. For this reason, one would not expect vertical nutrient transport resulting from cold front passages to increase chlorophyll levels in mid-June

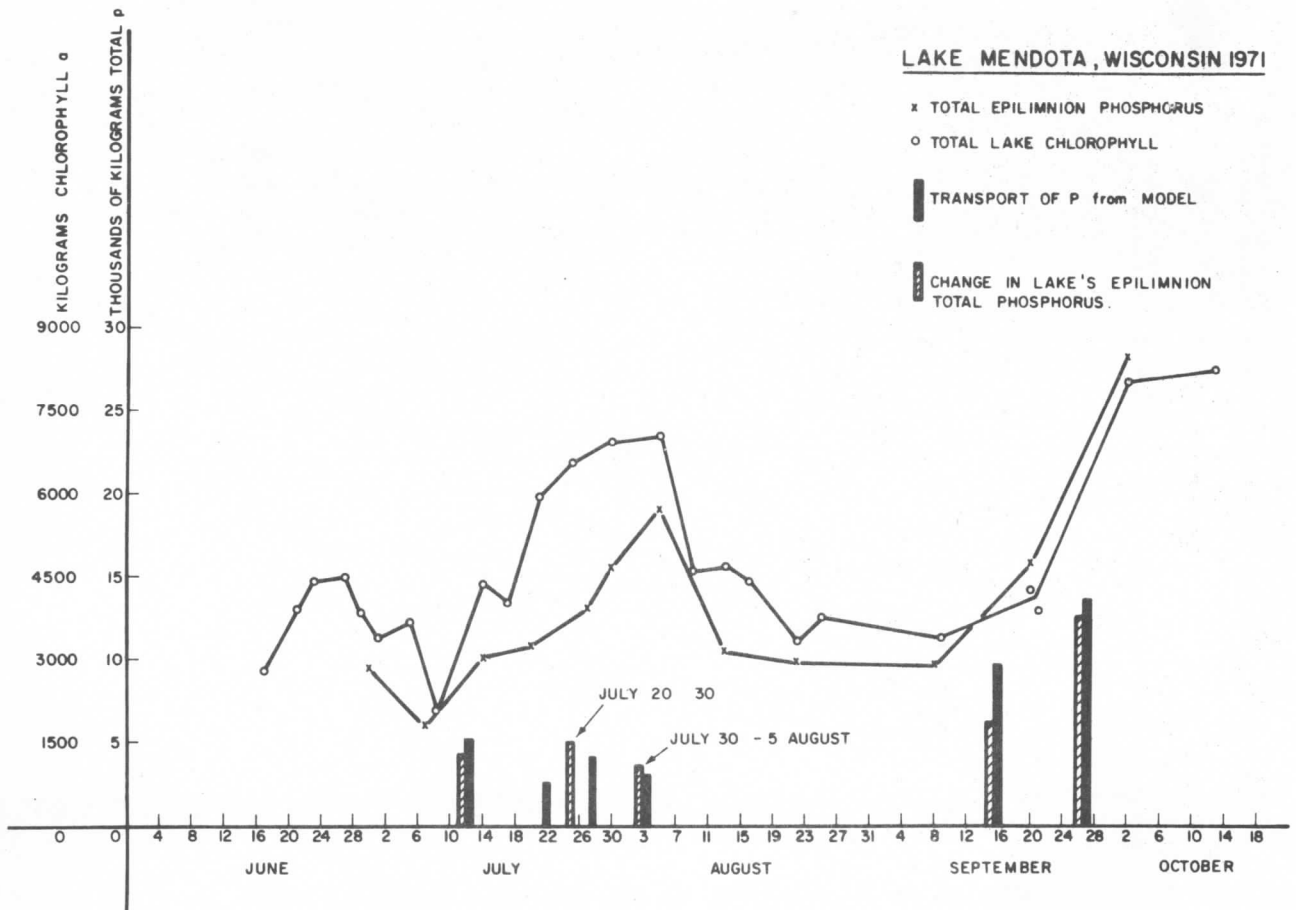


Figure 6. Lake Mendota, 1971, showing relationship between total epilimnion phosphorus and total lake chlorophyll (equivalent to total epilimnion chlorophyll for Mendota during the summer).

and mid-October when nutrient supplies in the epilimnion of Lake Mendota are ample.

It is difficult to establish cause and effect between vertical phosphorus and nitrogen transport and subsequent increases in chlorophyll. However, the following argument suggests that cause and effect can exist when the epilimnion is initially nutrient impoverished. First consider the total P content of the epilimnion on 8 July (estimated as 5900 kilos). The total is of course strictly greater than the mass of P associated with living algae biomass. In fact, data collected as part of this investigation indicates that probably less than 4000 kilos could have been part of a biomass at this time. The remaining P is in the other phosphorus fractions defined by Strickland and Parsons (1968). Furthermore, it has been estimated that live algae (marine) is approximately 0.9 percent phosphorus by weight (dry weight basis) (Redfield et al., 1963), and that algae other than the *Chlorophyta* are 0.2-1.0 percent chlorophyll *a* by weight (Strickland, 1965). Figure 6 shows that the total lake chlorophyll for Mendota reaches about 9000 kilos at times when nutrients cannot possibly be limiting. Based on the prevailing stoichiometry of algae, it seems unlikely that a 9,000-10,000 kilogram chlorophyll bloom will result

based on available phosphorus resources of about 4,000 kilograms. It must be emphasized, however, that if vertical mass transport of nutrients is *necessary* for the maintenance of large standing crops (as measured by chlorophyll) during the summer stratification period, it need not be *sufficient*.

Considering the large number of random variables involved and the blow-up in relative error that accompanies taking the difference of random variables, the agreement between changes in total P in the epilimnion as measured and the computed input because of turbulent exchange is surprisingly good. The computed transport exceeds the measured change in epilimnion P. However, the positive vertical transport component should always be greater over a time period than the net change since phosphorus loss due to sinking of algae is not considered. Sample calculations show that the P input due to the rainfalls plotted on Figure 6 is trivial in comparison to the vertical transport of P. Moreover, Rohlich (1966) reported in his review of the nutrient sources for Lake Mendota that the total P transport from streams tributary to Lake Mendota in the five-month period between May 1 and October 1, 1949, was 5900 kilograms. Forty-three percent of this figure was reactive phosphate. The total is

approximately equal to the total P transport estimated to have resulted from the single cold front passage of July 12-13, 1971. In the fall, such massive amounts of P are moved up that a large reserve of reactive P accumulates in the mixed layer. This does not occur during the summer. When considering algal nutritional requirements the metalimnion of Lake Mendota is relatively rich in P as compared with N. Nitrate is unimportant in the reduced metalimnion in late summer. Ammonia reaches concentrations above 2 mg/l-N by late summer in the lower metalimnion. The mass ratio of ammonia-N/total-P calculated to have been transported vertically into the epilimnion by the mechanism outlined during the periods

indicated by the bars is approximately 3.5/l. The metalimnion and hypolimnion P is almost entirely reactive phosphorus.

Table 1 is a summary of the phosphorus and ammonia-N transport calculated using the model during 1971. Some of the figures deserve special emphasis. During the period July 12-August 5 inclusive, the vertical transport of total-P was 15,170 kilograms. For the same period the ammonia-N transport was 53,800 kilograms. For the period July 12-September 20, the figures are 25,720 and 95,390 kilos, respectively. The time period is the last two months of the summer. The total-P content

Table 1. Vertical transport of phosphorus and ammonia-N in Lake Mendota, 1971.

Date Period and Element	F-Transport	F* Transport	Average
<u>8-14 July</u>			
1) Total-P	5,135	5,246	5,190
2) Ammonia-N	12,753	13,029	12,891
Ratio: $\frac{\text{Ammonia-N}}{\text{Total-P}} = 2.48$			
<u>21-25 July</u>			
1) Total-P	2,463	2,463	2,463
2) Ammonia-N	7,581	7,581	7,581
Ratio: N/P = 3.08			
<u>25-30 July</u>			
1) Total-P	4,670	5,670	5,170
2) Ammonia-N	20,800	25,400	23,100
Ratio: N/P = 4.46			
<u>30 July-5 August</u>			
1) Total-P	2,347	2,347	2,347
2) Ammonia-N	10,260	10,260	10,260
Ratio: N/P = 4.37			
<u>8-20 September</u>			
1) Total-P	9,100	12,000	10,550
2) Ammonia-N	35,870	47,320	41,600
Ratio: N/P = 3.94			
<u>20 September-2 October</u>			
1) Total-P	13,600	14,600	14,100
2) Ammonia-N	51,570	55,360	53,470
Ratio: N/P = 3.79			
<u>2-13 October</u>			
1) Total-P	25,950	28,070	27,010
2) Ammonia-N	98,990	108,100	103,550
Ratio: N/P = 3.83			

Note: Transport figures are in kilograms as P and N. F and F* figures refer to the computed transport using the R and R* ratios, respectively. Linear interpolation used in estimating nutrient concentrations below the boundary D_e of the epilimnion as a function of time.

of the epilimnion in late August was approximately 10,000 kilos. Lake Mendota's surface area is 39.1 km². Hence, the transport of P/m² surface area between 12 July and 20 September was 658 mg P/m². In analyzing nutrient transport as it affects lake eutrophication, it is the "loading" or input/m² which is most useful in making lake comparisons.

It is important to emphasize two distinctions between phosphorus transport from external sources and phosphorus transport resulting from the turbulent entrainment of metalimnion water. First, mass transport of phosphorus calculated using the summation involving R_z is entirely reactive phosphorus, since the concentration of reactive-P in the epilimnion is normally negligible. Hence, this P input is more readily available to algae than the particulate P resulting from land runoff, although this is not necessarily true for sewage-P. Secondly, the vertical mechanism described transports reactive-P directly into the non-littoral euphotic layer. Phosphorus inputs from external sources may be subjected to uptake by macrophytes or vegetation at the lake margins and therefore not become available to the phytoplankton.

It is difficult to detect small changes of temperature over time in the metalimnion and hold statistical significance. Because the means of temperatures measured at any depth *j* are random variables, this makes the transport model insensitive to slight perturbations of the metalimnion temperature regime. In addition, over longer time frames, downward heat flux via the mechanism of oscillating standing internal waves may play a role as suggested by Dutton and Bryson (1962). Heavy precipitation with the resulting runoff and turbidity currents can completely vitiate the model over the appropriate time frame. Bryson and Suomi (1951) discuss a dramatic case of this. Furthermore, the model is inappropriate for lakes where light penetration through the epilimnion to the metalimnion is sufficient to cause substantial warming over time (Bachmann and Goldman, 1965). This is not the situation in Mendota because of the low Secchi transparencies and the moderately thick epilimnion in summer. In spite of these sometimes important errors in the model the calculated transports over periods where these errors are negligible is impressive. Nevertheless, the mechanism outlined appears to be one control over the biomass (as measured by chlorophyll) because of its regulation of the epilimnion nutrient regime.

Conclusion

In conclusion, Lake Mendota provides an interesting example of a lake which is definitely not in a steady state with respect to nutrient transport from external sources during the stratified period. Instead, it depends on a stochastic process for the recycling of its own nutrient pool in order to maintain high chlorophyll levels during the summer. This type of periodic nutrient enrichment is

likely to be important in temperature lakes where metalimnetic reserves of N and P accumulate during the stratified period and where the thermocline deepens because of storms and seasonal progression. This mechanism for recycling of nutrients must be considered in estimating intra-lake nutrient transfers and in analysis of the interactions among morphometric characteristics of lakes and the time sequence of nutrient additions from external sources as they relate to biological productivity.

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