

Iron, Organic Matter, and Other Factors Limiting Primary Productivity in a Marl Lake

Abstract. Primary productivity of phytoplankton, measured as rate of carbon-14 uptake, was increased by adding iron and other nutrients to lake water, but was not increased by adding nutrients in the absence of iron. Concentrations of chelated iron ranging from 0.010 to 5.0 parts of iron per million increased primary productivity. Iron as a nutrient limiting primary productivity is related to the morphometry, physicochemical characteristics, and low productivity of the lake.

In the trivalent or oxidized form, ionic iron is practically insoluble in alkaline, oxygenated lake waters (1). Iron is present in such waters in the colloidal, particulate, or complexed form. Iron and other metals complexed by chelating agents (organic molecules) are maintained in solution. Fertility of waters has often been considered only in terms of mineral content—mainly phosphorus and nitrogen. Considering only inorganic nutrients has neglected the possible importance of dissolved organic matter. Saunders (2) has stated that one of the functions of dissolved organic matter in lakes is the chelation of metals.

Marl lakes are so named because the sediments are composed chiefly of calcium carbonate. Characteristically, primary productivity (rate of photosynthetic fixation of carbon) is low. The water has a pH of 8.0 or above, is highly transparent, and contains small quantities of phosphorus and nitrogen.

Nutrients limiting the primary productivity of natural phytoplankton populations of a marl lake were investigated at Blind Lake in Washtenaw County, Michigan. Bottles containing lake water and added nutrients were suspended in the lake at a depth of 1.5 m for 5 to 9 days. On the final day of exposure, C^{14} in the form of sodium bicarbonate was added to each bottle, and samples from each bottle were filtered 4 to 5 hours later. The radioactivity of the filtered samples was measured to determine the effect of added nutrients on photosynthetic C^{14} uptake. Nutrients added were chelated iron (3) and Chu No. 10 (4) modified by omitting ferric chloride, soil extract, and minor elements.

The results indicate that nutrients did not increase primary productivity greatly unless chelated iron was also added (Table 1). Because tests were performed from July to November, variability in the results is due in part to

seasonal changes in phytoplankton and water chemistry. However, for experiments on any particular date, C^{14} uptake was greater for nutrient additions containing chelated iron than for those not containing chelated iron. Results similar to those shown in Table 1 were obtained by adding nutrients to water from two other marl lakes. Chu No. 10 nutrients and ferric citrate-citric acid or ferric chloride also increased C^{14} uptake.

Two parts of iron per million were added in most experiments. Chelated iron ranging in concentration from 0.010 or 0.020 to 5.0 ppm of iron and Chu No. 10 nutrients increased C^{14} uptake. Neither the quantity of this chelated iron nor the quantity of iron in natural waters available to phytoplankton is known, but more than 0.020 ppm of iron is often found in lakes.

The data in Table 1 might be questioned because the water was confined in bottles for as long as 9 days. However, similar results were obtained by adding nutrients directly to a marl lake (5). After chelated iron was added to this lake, primary productivity was 4 times greater than the primary productivity before treatment. Primary productivity was approximately 60 times greater after both chelated iron and commercial fertilizer were added, but in another marl lake to which only commercial fertilizer was added, primary productivity increased less than 4 times. These results indicate that iron limited primary productivity. Is iron a limiting nutrient owing to its absence or owing to its limited availability within the lake system?

A chelating agent, HEDTA (6), was added to jars containing mud and water from Blind Lake. Under aerobic conditions, iron in the water increased from 0.020 to 0.20 ppm in 2 days because ferric iron in the mud was chelated by HEDTA in the water. The iron complex formed is chemically equivalent to the complex (3) that stimulated C^{14} uptake. Iron is obviously present in the mud.

Under anaerobic conditions, iron in the sediments is reduced to the soluble bivalent form and is released into the bottom waters. If a lake is deep and productivity is low, iron is not released because normally the bottom waters contain oxygen throughout the year. In Blind Lake, iron is released only in years when the water mass is not completely aerated (7) during spring circulation. Incomplete aeration may

Table 1. Uptake of C^{14} by phytoplankton. The values are the ratio of uptake with added nutrients to uptake without added nutrients. Numbers in parentheses indicate the number of experiments with each nutrient addition.

Nutrients added	Range	Average
Chu No. 10 and chelated iron	3.83–116 (7)	28.9
Phosphorus, nitrogen, chelated iron	6.92–22.1 (3)	12.5
Chelated iron	2.64–4.08 (2)	3.86
Phosphorus and nitrogen	0.81–1.51 (4)	1.24
Chu No. 10	0.36–3.59 (5)	1.76

occur frequently—especially when the lake stratifies early in the spring owing to hot, calm weather—because Blind Lake is deep (80 feet), relatively small (68 acres), and sheltered from winds by hills and trees. These factors do not insure a regular regeneration of iron and may affect the availability of iron to phytoplankton.

Other nutrients, including phosphorus and nitrogen, are also released from the sediments under anaerobic conditions. Under aerobic conditions, iron and phosphorus in the water may be precipitated and sedimented as ferric phosphate. Thus the factors that control the supply of iron and other nutrients are related. The results (Table 1) indicate that iron was the primary limiting nutrient but that additional phosphorus and nitrogen were essential for large increases in primary productivity.

The relationship of factors limiting primary productivity in Blind Lake suggests a circular causal system (8) in which lake morphometry and low productivity limit nutrient regeneration from the sediments. This limits nutrient availability and productivity. Also, because productivity is low, it is postulated that the lake lacks sufficient dissolved organic matter to chelate iron and that iron thus limits primary productivity. Added dissolved organic matter (synthetic chelating agents) increased the availability of iron under experimental conditions, and chelated iron increased primary productivity. This does not imply that iron is supplied to phytoplankton by this means only, but is indirect evidence that naturally occurring chelating agents have ecological significance in determining the fertility or productivity of aquatic ecosystems (9).

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References and Notes

1. G. E. Hutchinson, *A Treatise on Limnology* (Wiley, New York, 1957), vol. 1.
2. G. W. Saunders, *Botan. Rev.* **23**, 389 (1957).
3. The chelated iron added was iron sodium N-hydroxyethylethylenediamine triacetic acid.
4. S. P. Chu, *J. Ecol.* **30**, 284 (1942).
5. C. L. Schelske, F. F. Hooper, E. J. Haertl, *Ecology*, in press.
6. HEDTA is trisodium N-hydroxyethylethylenediamine triacetic acid.
7. A temporary biogenic meromixis (see 1).
8. G. E. Hutchinson, *Ann. N.Y. Acad. Sci.* **50**, 221 (1948).
9. This preliminary report is a portion of a paper presented at the 22nd annual meeting of the American Society of Limnology and Oceanography at Pennsylvania State University, University Park (Sept. 1961) and represents a portion of a Ph.D. thesis (University of Michigan).
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Probability of Signal Detection in a Vigilance Task

Abstract. It is hypothesized that the probability of detecting a signal in a vigilance task depends upon its temporal location with respect to the preceding series of signals. Probability of detection should be at a maximum when the signal occurs after a temporal interval which is equivalent to the mean of the intervals between the preceding signals detected. The experimental results support this hypothesis.

In advancing an expectancy theory of vigilance I have hypothesized that "the probability of detection of a signal in a vigilance task is greatest when the signal occurs after an interval which is equivalent to the mean of the inter-signal intervals preceding the interval in question: detection probability is low immediately after a signal, increases as the mean inter-signal interval of the preceding series is approached, and if

not reinforced by the occurrence of a signal, again decreases" (1). In other words, a peaked symmetrical distribution of detection probabilities is hypothesized.

This report describes a study undertaken to verify the hypothesis. The general plan was to expose subjects to a series of eight signals over a period of 32 minutes. The signals were of sufficiently small magnitude to ensure that not all observers would detect all signals. Inter-signal intervals employed were 0.5, 1.5, 2.5, 3.5, 4.5, 5.5, 6.5, and 7.5 minutes. The mean of this series is 4 minutes, though an interval of 4 minutes was not included. Different groups of subjects (simultaneously tested in individual isolation booths) were presented with the intervals in different random orders.

The eight signals of the 32-minute program were followed without a break by a ninth "test" signal which was presented after an interval of 0.25, 1.5, 4.0, 6.5, or 10 minutes, and the percentage of observers detecting the "test" signal was computed.

The test employed was a clock-test. The clocks (one per booth) were electric, 8 inches in diameter, with a black face and a single black second hand having the tip painted white for 1 inch. The hand revolved continuously, once per minute, except when a signal occurred. Signals were defined as 0.30-second stoppages of the clock hand. The subjects' task was to depress a hand-held microswitch whenever a signal was detected.

To test the hypothesis, it was important that subjects not be misled concerning the lengths of the inter-signal intervals but at the same time it was necessary to employ programmed signals of small magnitude in order to encourage missed detections to the subsequent "test" signal. To surmount this problem a small bright light above the clock appeared for a period of 1.0 second immediately following any undetected signal.

Eighty-six subjects, paid housewives, were employed. Each undertook the task twice, each time with a differently randomized program, each program having the "test" signal after a different interval. The total of 172 possible "test" responses is far from ideal but nevertheless served the purpose. The plan called for simultaneous testing of groups of seven subjects but several appointment cancellations at the last moment resulted in an allocation

of the 172 possible responses to the "test" signal in the uneven numbers of 39, 28, 38, 26, and 41 to the five "test" signal intervals respectively.

The data in Fig. 1 show probability of signal detection (percentage of signals detected) as a function of the length of interval between the last programmed signal and the "test" signal. Curve A represents data from all 86 subjects and consequently includes those who missed none of the programmed signals, that is, those who found the task "easy," as well as those who missed a large number of the programmed signals, that is, found the task "difficult." The drop in detection probability from 6.5 to 10 minutes is significant at the .05 level of confidence, but as a number of subjects are represented at both points this is probably a conservative figure.

Curve B, on the other hand, represents data exclusive of those from subjects who missed 0, 1, or 2 programmed signals, and of those from subjects who missed 6 or 7 programmed signals. (No subject missed all 8 signals.) Curve B is representative, then, of subjects who missed 3, 4, or 5, or in the region of 50 percent of the programmed signals, and were consequently considered the most sensitive instruments for testing the hypothesis. In addition, any possible correlation effects consequent to plotting two data points for a single subject have been removed: no subject is represented in curve B more than once.

It is apparent that curve B is grossly representative of the distribution hypothesized. A statistical analysis was undertaken to determine whether the probability of detection at 0.25 and 10 minutes differed significantly from that at 4 minutes. Because of the small sample upon which these three points of curve B are based, a total of 36 subjects, the data for 0.25 and 10 minutes were collapsed and chi square computed for the resulting 2×2 contingency table, after applying Yates's correction for continuity (2). Chi square was computed to be 5.5307, which is significant beyond the .02 point.

While the middle plotted point of curve B cannot be considered peaked with respect to those adjacent, the general shape of the complete curve is considered to be in support of the hypothesis.

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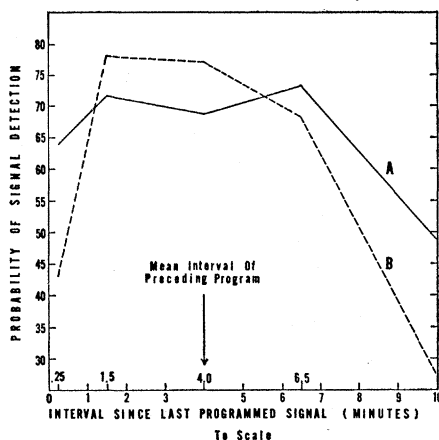


Fig. 1. Probability of signal detection and percentage of signals detected as a function of the length of the interval between the last programmed signal and the "test" signal.