community to favor stronger grazing by zooplankton is commonly called "top down" control, a product of biomanipulation in accordance with the trophic cascade. However, as with virtually all biological mechanisms, variability in response tends to be high, and we have much more to learn to increase the reliability of this approach.

Alternative Stable States

Some lakes suffer from both algal blooms and rooted plant infestations, but most shallow eutrophic lakes have mainly one problem or the other. Research led mainly by European limnologists has illustrated the stability of both plant and algal dominated states in lakes. When we manipulate these lakes to eliminate algal blooms or rooted plant nuisances, we risk tilting the balance toward the alternative state, resulting in either an alternative set of problems or a period of instability. The need to carefully assess management methods in light of stated goals and lake uses becomes very important in such cases, and we move from limnology to social science in may cases.

Limnology provides concepts and predictive power that can be used to develop sound management approaches, and supports management of specific lakes by providing the information necessary to make technically and economically justifiable decisions. Management without supporting limnology invites unexpected results and potentially negative consequences. Although limnological investigations carry a cost, money spent on studies can be more than offset by the long-term savings in the management implementation phase, and increases the overall knowledge base that supports advances in lake management.

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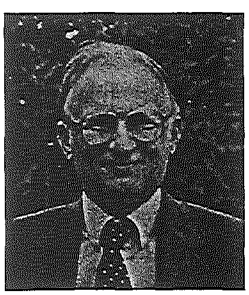
The Limiting Factor Concept

What Stops Growth?

Roger W. Bachmann

One of the earliest puzzles limnologists tried to solve was to explain why some lakes were more productive than others. Aside from academic curiosity, the answer to this question was of practical importance for fish production in lakes or ponds. In general, the more productive a lake is in terms of plant life, the higher the potential yields of fish, so there was interest in knowing how to increase the productivity of lakes in order to increase fish production. More recently, lake managers also have been interested in learning how to decrease the productivity of lakes in order to maintain or increase water clarity in lakes that have abundant growths of plankton algae.



The best explanation for productivity differences between lakes is found in the limiting factor concept first developed in the plant sciences and then applied to lakes and ponds. It says that the factor in the environment that is in shortest supply relative to the needs of the plants will determine the amount of plant material produced. For example, in order to grow, green plants need a supply of basic chemicals like carbon, hydrogen, oxygen, phosphorus, and nitrogen as well as smaller amounts of other elements such as metals like iron and magnesium. Also needed are stocks of living green plants, a source of light energy to combine the ingredients to form new organic matter, and time to accumulate the biomass. Thus, any one of these requirements—chemicals, light energy, or time—could be a limiting factor and control the amount of algae in a lake.

Nutrients as Limiting Factors

The concept of limiting factors has been applied with great success to lakes. Several lines of evidence have been used to show that the elements most often present in the smallest amounts relative to the needs of plants were either phosphorus or nitrogen. Hydrogen and oxygen are present in great abundance in water molecules and carbon dioxide is usually present in non-limiting amounts, however, every 100 grams of carbon used by plants in growth requires about 7 grams of nitrogen and 1 gram of phosphorus. Chemical analyses of lake water show that phosphorus and nitrogen are often present in smaller amounts relative to plant composition than other elements needed for plant growth.

Further proof of nutrients as limiting factors can be inferred from surveys of lakes around the world that indicate that the amount of plankton algae as measured by the amount of plankton chlorophyll is directly related to the amounts of either total phosphorus or total nitrogen. For example, in Florida lakes (Figure 1) there is a very strong correlation between the average amount of algal chlorophyll in a lake and the average amount of total phosphorus in the lake water. We also find that in these same lakes (Figure 2) there is a strong correlation between the amount of algal chlorophyll and the amount of total nitrogen in the lake water. This comes about because generally the concentrations of these two elements are related to each other (Figure 3). Lakes with high concentrations of phosphorus tend to have high concentrations of nitrogen and vice versa, so the statistical correlations in themselves do not provide proof of a cause-and-effect relationship.

Empirical evidence for the role of phosphorus and nitrogen as limiting factors is found in the response of lakes and ponds to the artificial addition of these elements. We could cite as examples the responses of fertilized fishponds, lakes receiving sewage effluents, and controlled experiments where these elements have been added to whole lakes. In general, the addition of phosphorus and nitrogen to a water body will increase the rate of production of plant materials (with a few exceptions that will be noted later). Likewise, there are examples of lakes that have shown decreases in algal populations when a nutrient source like a sewage effluent has been diverted. These are examples of nutrients as limiting factors.

In deep lakes the nutrient concentrations and, thus, the algal populations, are usually directly related to nutrient inputs to the lake. Accordingly, an increase in algal populations ordinarily indicates an increase in nutrient input (or loading). Shallow lakes, however, are a little more complicated (see article on pp. 42-46 for more information. If macrophytes (large aquatic plants) are abundant over most of the lake area, the lake waters will tend to have lower amounts of plankton algae and have a better water transparency than would be the case if the macrophytes were not present. This happens because the macrophytes and their attached periphyton remove nutrients from the water leaving less for the plankton. They also reduce the turbulent water movements that keep plankton algae in suspension. Consequently, the removal of a significant amount of macrophytes from a shallow lake (through say chemical or biological control or a water level change) often results in a significant increase in the abundance of plankton algae even though there is no change in nutrient loading.

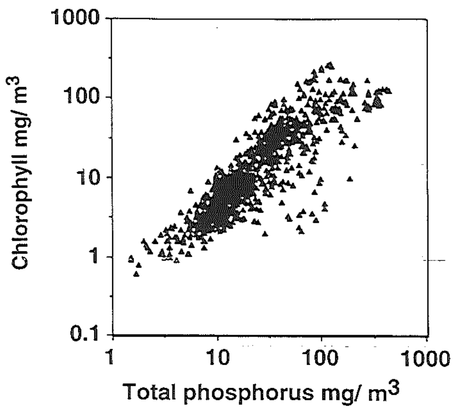


Figure 1. Annual average chlorophyll concentrations and annual average total phosphorus concentrations in several Florida lakes.

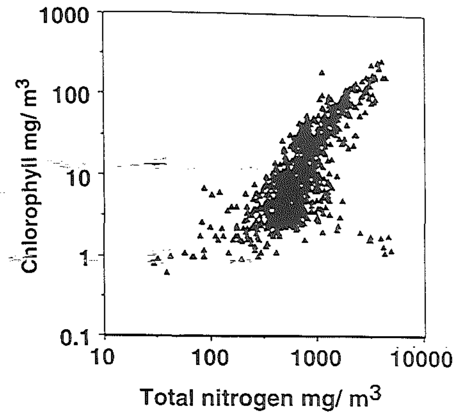


Figure 2. Annual average chlorophyll concentrations and annual average total nitrogen concentrations in several Florida lakes.

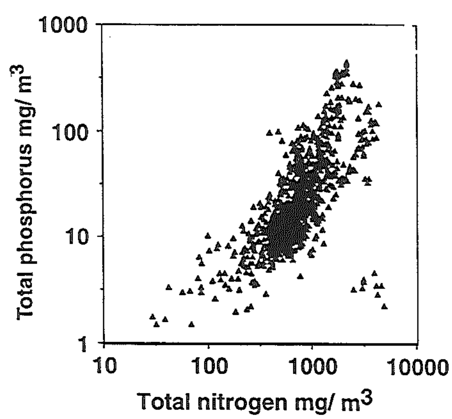


Figure 3. Annual average total nitrogen concentrations and annual average total phosphorus concentrations in several Florida lakes.

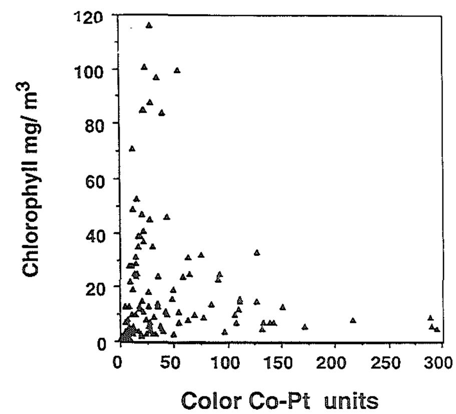


Figure 4. Chlorophyll concentrations in several Florida lakes with varying amounts of water color. The cobalt-platinum scale (Co-Pt units) indicates the amount of yellow-colored organic material (humic acid) that is dissolved in the lake water. Lakes with high values for color may appear tea-colored to dark brown.

Other Limiting Factors

Because of the known importance of nutrients as limiting factors, there has been a strong focus on nutrient control in modern lake management, and we sometimes forget that there are other kinds of limiting factors. For example, the availability of light energy can be a limiting factor. In the state of Kansas the artificial reservoirs tend to have high turbidities due to high concentrations of suspended clay particles that originate in the sedimentary rocks of the watersheds. The result is that light ➠

becomes the limiting factor and the algal populations do not grow to the levels that we might expect on the basis of the nutrient concentrations in the water. In Lake Okeechobee, Florida, wind-driven waves regularly resuspend muddy sediments in this large, shallow lake and make the water turbid. Here, also, light rather than nutrients limit algal populations.

The concept of limiting factors has been applied with great success to lakes.

In some parts of the country, swampy watersheds can generate humic acids that stain lake waters a yellowish to brownish color and reduce light penetration. For example, in Figure 4 the chlorophyll concentrations in several Florida lakes are shown in relation to the color of the waters. When the color is less than about 75 Co-Pt units (the Co-Pt units indicate how much yellow color is in the water) the chlorophylls range from next to nothing up to about120 milligrams per cubic meter. Lakes with color values above 75 do not develop the same high chlorophyll concentrations. Since the data also show that nutrient concentrations do not decrease with increasing water color, this is another indication of light as a limiting factor.

Last, there are three other factors worth mentioning that limit the rate of growth of algal populations: water temperature, time, and grazing by invertebrates. First, let's consider water temperature. At very low temperatures the growth rates of algae are reduced even though nutrients and light may be abundant. In general this means that it takes longer for a population to build up in a cool lake than it would under warmer conditions, however, in the end the maximum population is usually determined by the nutrient concentrations just as in a warmer lake.

Time becomes a limiting factor in a flowing water system like a rapidly flushed reservoir when there is not sufficient time for algal populations to reach their maximum levels before the water leaves the reservoir. A good example of this would be Silver Springs, Florida, where a huge spring emerges from a deep cavern and forms a large river. The water is exceptionally clear in the spring boil and for several miles downstream, yet if one collects a jar of this water and allows it to sit for a few days in the light, it will turn green as the algae grow and utilize the nutrients present in the spring water. In this case, time—and not nutrients—is the factor limiting the amounts of algae found in the spring and upper river.

Third, sometimes grazing by small invertebrate animals (zooplankton) on plankton algae may be sufficient to remove the algal cells from the water faster than new cells are produced. The end result is to have less plankton algae present than would be indicated by the amounts of nutrients present in the water. This phenomenon has been noted in lakes where fish that control the zooplankton populations by feeding on them are significantly reduced through winterkills or artificial removal.

The use of the concept of limiting factors is a valuable tool for lake and reservoir management. It provides a logical and scientific basis for determining what regulates the algal populations in a water body and leads to management options for their control.

Dr. Bachmann received his limnological training at the University of Michigan and since 1963 has been a professor of limnology, first at Iowa State University and more recently at the University of Florida. His current research is aimed at understanding the limnology of shallow lakes. He can be reached by e-mail at: <Mdbach@aol.com>.