

# Lake Ecosystem Energetics: The Missing Management Link

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## ABSTRACT

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Phosphorus plays a central role in the bioenergetics of organisms and ecosystems (recall Adenosine Triphosphate [ATP], substrate level phosphorylation, cyclic and noncyclic photophosphorylation). It is a role which no other atom can duplicate. Phosphorus is of paramount importance in lake management because it most often limits the degree of phytoplanktonic autotrophy (algae growth). However, many other aspects of lake ecosystem structure and function offer substantial promise for the future of lake management and restoration. One such aspect, ecosystem energetics, is too often neglected or misunderstood by the lake manager.

There are fundamental differences between autotrophication and allotrophication, trophic and detrital dynamic structures, eutrophication and lake succession, and how these ecosystem components and processes can be effectively managed. An understanding of the nitrogen, sulfur, iron, and phosphorus cycles of lakes yields insight into new restoration technologies (e.g., alum surrogates, anaerobic aeration, biomanipulation) and potential long-term impacts of existing methods (sulfate loading, copper sulfate, aluminum sulfate). Methods to control eutrophication, and its in-lake consequences, are directly related to the energetics of a lake ecosystem, as are treatments of symptoms. Lakes are complex ecosystems in which all living organisms interact collectively with physical and chemical processes of the environment. Understanding a lake ecosystem is understanding nature, and will lead to more effective stewardship of the ecosystem in which we play a major role. This introduction to lake ecosystem energetics is intended to illustrate some fundamental relationships among biology, ecology, physics, chemistry, and lake management.

**Key Words:** ecosystem, energetics, respiration, detritus, phosphorus, nitrogen, autotroph, heterotroph.

*"Kapieren und Kopieren ('First understand Nature, then copy it.'). Nature is our foremost teacher; the task of technology is not to correct Nature, but to imitate it."*

Viktor Schauberger  
(1885-1958)  
(Alexandersson 1990)

Lake managers eager to correct problems which plague our lakes (algae blooms, dense weed infestations, habitat loss, water quality degradation) may lose sight of fundamental ecosystem processes. Lake restoration efforts often are undertaken without a full understanding of potential effects and consequences. Management technologies tend to be focused exclusively on matter, particularly phosphorus, with little consideration of ecosystem energetics. In this paper we discuss the flow of energy through the lake ecosystem (ecosystem energetics), its relationships to the physical-chemical structure and function of a lake, and its implications to lake management.

We begin at the most fundamental level, describing the basic respiration and production processes performed by organisms. These basic biological processes are then assembled into an ecosystem context where organisms performing different energetic processes interact, with each other and with the environment. We distinguish among standing crop, biomass, and productivity; distinctions which are very important to effective lake management. Likewise, we distinguish among typically overlooked autotrophication (eutrophication), allotrophication (dystrophication), and lake succession.

We examine interactions between ecosystem energetic processes and material-cycling in lakes—particularly the respiratory role of the nitrogen cycle, sulfur-iron-phosphorus interactions, and their significance to lake management. We describe the food web of lakes, illustrating the trophic and detrital dynamic structure, and how they interact via non-predatory losses and bactivory. These trophic interactions are then related to the physical structure of a stratified eutrophic lake ecosystem, to illustrate effects of different compensation depths.

Finally, lake ecosystem energetics are discussed for three categories of lake management technologies: control of eutrophication, control of eutrophication consequences, and treatment of eutrophication symptoms.

"Kapieren und Kopieren." This discussion of ecosystem energetics is intended as a primer for those wishing to learn more about their lake, as a reminder to lake managers that "life is energy," and perhaps to spark an idea for an innovative lake restoration technology with a principle that mimics nature. This is not a new discovery of ecosystem energetics, but a reminder that lakes are living ecosystems. Nor is this a detailed exposition of energetics and management implications; it is an introduction which we hope will expand our perception of the "ecosystem organism," and our impact on it.

## Respiration

*"Life is energy."* A living organism is a highly ordered arrangement of matter that takes advantage of chemical energy released in the "combustion" of organic material. Fundamentally, life exists on earth because living organisms synthesize enzymes that catalyze chemical reactions. Enzymes lower the activation energy required to initiate chemical reactions, which subsequently yield far more energy (increased Gibbs free energy) than the original investment of energy in enzyme synthesis made by organisms. Simply put, all living organisms burn organic matter in a slow, controlled way: respiration. In this respect there are only two differences among all living organisms: 1) source of the fuel—whether it is made by the organism (autotrophic) or another organism (heterotrophic); and 2) the oxidant used to combust the fuel, and completeness of reactions.

The respiration process can be simply depicted by equation 1 (Fig. 1), where  $(CH_2O)_n$  represents fuel (organic matter) and "X" represents the substance used to combust it (oxidant). Respiration is an "oxidation-reduction" reaction where organic matter is "oxidized" to carbon dioxide and another substance (X) is "reduced." The process involves breaking and reformation of chemical bonds and transfer of energy. Separating oxidation from reduction, the respiration equation 1 becomes equations 2 and 3 (Fig. 1). All organisms do this. The only differentiating feature is the substance (X) used to

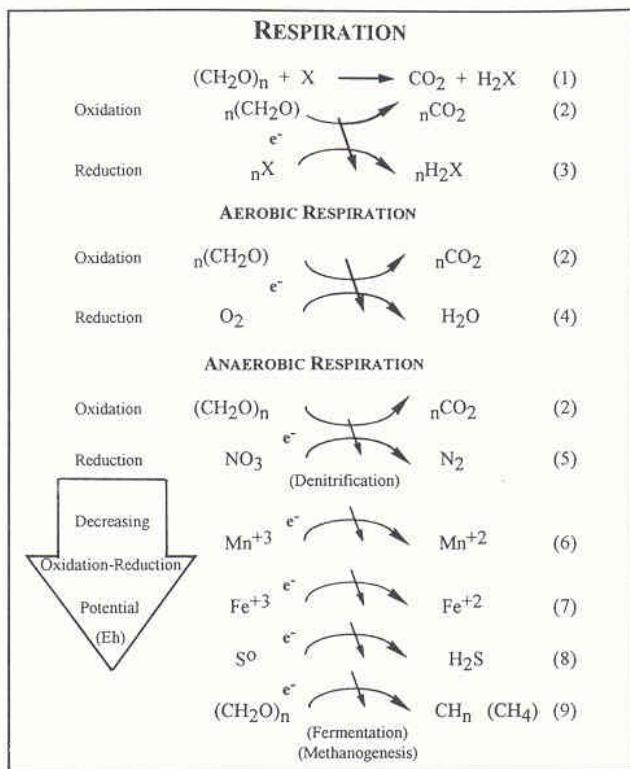


Figure 1.—Fundamental oxidation-reduction reactions of respiratory processes.

accept transferred energy ("terminal electron acceptor" [TEA]).

Organisms that require oxygen to combust organic matter (such as humans) perform aerobic respiration (Fig. 1; equations 2 and 4). In aerobic respiration, organic matter is oxidized to carbon dioxide and oxygen (TEA) is reduced to water. Oxygen is the X in equations 1 and 3 for aerobic respiration (Golterman 1975). Oxygen in the carbon dioxide product is from the organic reactant, not from the oxidizing agent (oxygen).

Many organisms do not require oxygen to combust organic matter. Indeed, humans perform intermediary steps before oxygen is used (e.g., lactic acid production). Anaerobic respiration is the process by which organic matter is combusted (oxidized) using an alternate TEA (to oxygen). The alternate can be a variety of substances (X) which become reduced. Some examples include dissimilatory nitrate reduction (equation 5), manganese reduction (equation 6), iron reduction (equation 7), sulfur reduction (equation 8), and fermentation (equation 9; Gottschalk 1979).

These alternates are shown in the sequence in which they are used after oxygen is depleted (first nitrate, then metals, and finally other organic compounds in fermentation; Fig. 1). In the absence of oxygen, less available energy can be recovered from organic matter by respiration. Hence, products of

anaerobic respiration (inorganic products) and fermentation (organic products) contain residual energy which is subject to subsequent reactions.

## Production

As discussed above, all living organisms obtain the energy of life by combustion of organic matter. Autotrophs capture solar energy radiating through air or water and store ("fix") captured energy in the products of photosynthesis: oxygen and organic matter. (More accurately, energy captured by photosynthesis is not stored *in* the products of photosynthesis, but rather as environmental redox potential ( $E_h$ ) *between* the photosynthetic products.) Autotrophs essentially "make their own fuel" in a process called synthesis or production (Fig. 2; equation 10), the reverse of respiration (equation 1).

The "photosynthetic process" (phototrophy) is also an oxidation-reduction reaction, but uses solar energy to reduce carbon dioxide to organic matter. The oxidation-reduction couple is illustrated in equations 11 and 12 (Fig. 2).

In photosynthesis, X is oxygen and water is oxidized to oxygen (this is how our oxygen-rich atmosphere evolved). Water is chemically reduced oxygen; aerobic respiration reduces oxygen to water. However, photosynthesis is *not* the only process that produces organic matter. X can also be the reduced products of anaerobic respiration. For example, where X is sulfur, hydrogen sulfide is oxidized while carbon dioxide is reduced to organic matter. This process is called chemolithotrophy, and synthesizes organic matter in the absence of light. Other, very similar processes, occur such as chemoorganotrophy where an organic X is used, and "photo-assisted" organo- and photolithotrophy where solar energy is

needed. Organisms which do not produce their own fuel are dependent on organic matter produced by autotrophs (heterotrophs).

## Fundamental Ecosystem Processes

Now that we have discussed the basic productive and respiratory processes of life, it is time to discuss relationships between energy and matter in the ecosystem.

*Ecosystem is the unit of natural organization in which all living organisms interact collectively with the physical chemical environment as one physical system.* Operation of an ecosystem depends upon available matter and energy. Plants have the ability to divert energy from solar radiation (a physical process) to photosynthesis (a biological process). Energy diverted to photosynthesis is stored as reducing power in the organic matter of plants and as oxidizing power in the environment as oxidized X. Organisms use enzymes to recombine organic reducing power and environmental oxidizing power. Energy obtained by this recombination is used to live, to grow, to pass on to predators, and to read scientific journals. Living organisms represent "negative entropy." Energy originally captured as sunlight by plants is returned to the physical world as very low temperature heat released by biochemical reactions in all living organisms. The amount of biological activity in a lake ecosystem depends ultimately upon the amount of a) energy available for photosynthesis and b) biochemical "machinery" (for both photosynthesis and respiration) which can be constructed from available matter (nutrients). When energy is abundant and nutrients are limited, biochemical machinery is inadequate to use the energy available.

All life is based on carbon (central in Fig. 3). Synthesis of organic matter is shown on the left half, respiration of organic matter is illustrated on the right. The upper half depicts aerobic processes, and the lower half anaerobic processes. In aerobic photosynthesis (upper left in Fig. 3), photosynthetically active radiation (PAR) is captured by photosystems I and II (cyclic and noncyclic photophosphorylation, respectively). PAR is used to create reducing power ( $NADPH_2$  and Adenosine Triphosphate [ATP]), which converts the oxidized reactant ( $CO_2$ ) to the reduced product (organic matter). The electron donor (reduced reactant) is water; oxygen is the oxidized product.

In aerobic respiration (upper right in Fig. 3), organic matter is oxidized; the TEA is oxygen. Reducing energy contained in organic matter is recombined with oxygen to produce energy-rich compounds (e.g., ATP) in the Krebs Cycle (Tricarboxylic Acid Cycle) and the Electron Transport System. These are biochemical, enzyme mediated systems contained in organisms which perform aerobic respiration.

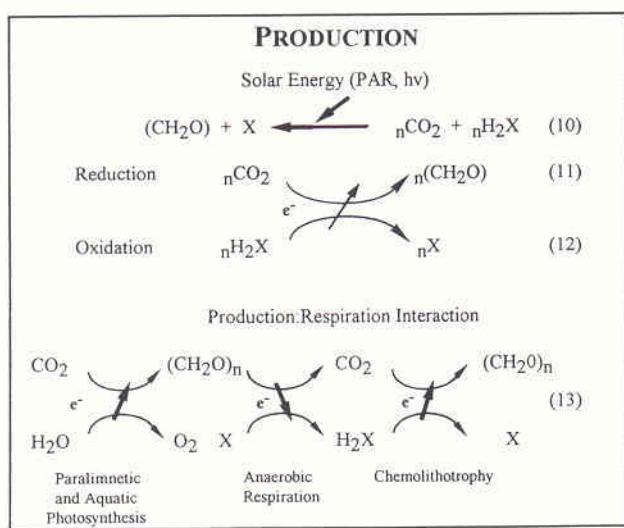


Figure 2.—Fundamental oxidation-reduction reactions of synthetic (productive) processes.

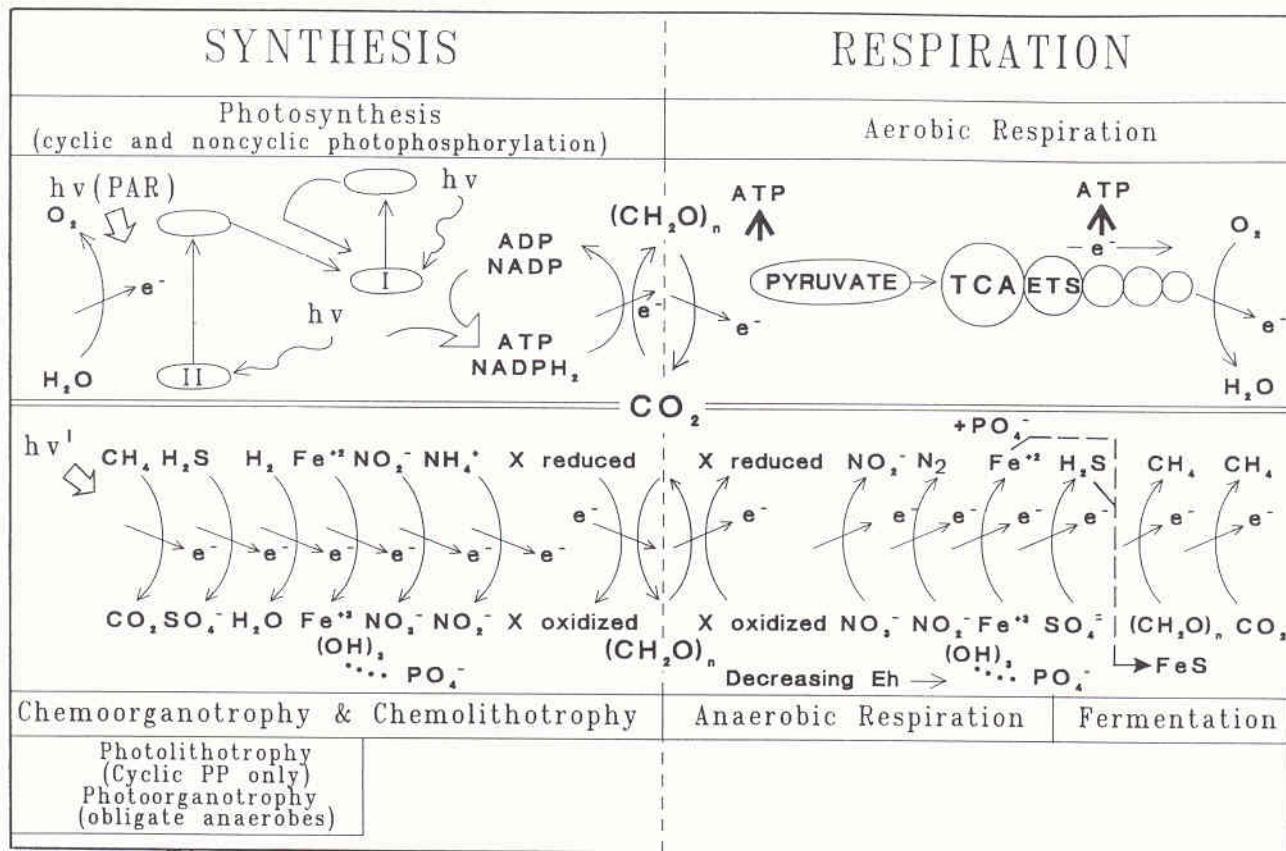


Figure 3.—Summary of major bioenergetic processes. Synthesis (left half) includes the photooxidation of water in photosynthesis (top left) and oxidation of reduced compounds in chemosynthesis (bottom left). All reactants in chemosynthesis are products of anaerobic respiration, with the exception of ammonia (the ammonia anomaly). Respiration (right half) includes aerobic (top right) and anaerobic (bottom right). Also shown is the coprecipitation of ferrous iron and sulfide (as ferrous sulfide) which reduces sediment P-binding capacity.

In anaerobic respiration and fermentation (lower right in Fig. 3), organic matter is oxidized without using oxygen as the TEA. The first alternate TEA used is nitrate, which is reduced to nitrite and nitrogen gas. Dissimilatory nitrate reduction (also called denitrification) is a particularly important process in anaerobic environments. Nitrate becomes an electron acceptor at an Eh of about 220 mv. The products of denitrification are all gaseous (N<sub>2</sub>O, N<sub>2</sub>, and CO<sub>2</sub>), hence are not retained by the aquatic ecosystem. Because of the importance to lake management, nitrogen transformations will be discussed in greater detail.

As all available oxygen and nitrate are depleted (by use as electron acceptors in respiration), ambient Eh decreases. At about 200 mv manganic manganese begins to be used as an alternate electron acceptor, being reduced to manganous compounds. As the Eh decreases further, insoluble ferric iron is used as an electron acceptor producing soluble ferrous iron. This reaction is reached at an Eh of approximately 120 mv. Ferric iron binds with orthophosphate (Einsle 1938, Hutchinson 1957). Bacterial reduction of ferric hydroxy-phosphate complexes results in large amounts of soluble inorganic phosphorus and ferrous iron diffusing across the sediment-water interface

(Kortmann 1980). The internal load of phosphorus which results is important to the trophic status of many lakes (Kortmann et al. 1982, Nürnberg 1984). If Eh continues to decrease (below -75 mv), sulfates are reduced to sulfides and organic compounds become electron acceptors (fermentation).

The oxidation-reduction system depicted in the lower right quadrant of Fig. 3 is an "ecosystem analog" to the electron transport system of an individual organism. The reduced products, however, enter and accumulate in the anaerobic environment. Several of the processes can be performed by the same organism. For example, some organisms have enzyme complexes capable of switching from oxygen to nitrate and, finally, to iron (facultative anaerobic bacteria; Golterman 1975, Gottschalk 1979). Organisms of this type are ubiquitous in the bottoms of lakes.

Reduced products of anaerobic respiration (and the reducing energy they contain) are not lost from the ecosystem. Upon diffusing to an oxidized environment, reduced products can be further oxidized, yielding energy for reduction of carbon dioxide and synthesis of organic matter. Chemolithotrophy and chemoorganotrophy are processes which synthesize

organic matter using only the reducing energy of the products of anaerobic respiration and fermentation, respectively (lower right in Fig. 3). When some light supplements the reduced chemical energy, the processes are called photolithotrophy and photoorganotrophy. Only photosystem I is involved (cyclic photophosphorylation); no oxygen is generated.

Anaerobic metabolism in lakes is an extension of the detrital side of the food web of trophic dynamics. Bacteria decomposing and respiring detrital organic matter, switch from aerobic to anaerobic respiration and fermentation when oxygen is exhausted. In the absence of oxygen, less energy is recovered from organic matter because respiration is incomplete. Thus, products of anaerobic respiration and fermentation (inorganic and organic, respectively) contain residual reducing energy, which drives chemolithotrophy. Bacteria which grow by chemolithotrophic metabolism enter the food web via filter-feeders, just like aerobic bacteria. Energy used in chemolithotrophy is residual energy from anaerobic respiration, energy originally fixed by either in-lake or terrestrial photosynthesis (Fig. 2, equation 13). Hence, *chemolithotrophy is a heterotrophic process*; energy was originally fixed by phototrophy (either allochthonous or autochthonous).

## Standing Crop, Biomass, and Productivity

Standing crop refers to the above-ground weight of organic matter which can be sampled or harvested at any one time from an area (Wetzel 1975). Biomass is the weight of all living material in a unit area at a given time. Hence, biomass is more comprehensive and should be used for ecosystem analyses. The biomass of a population, trophic level, or community does not reflect the rate of formation of new organic matter through time (production or productivity). Production refers to new organic matter formed over a period of time plus losses to respiration, excretion, secretion, mortality, grazing, and predation. Productivity is the rate of production per unit time. Biomass can be low, while productivity is high (e.g., when grazing and predation rates are high). Likewise, biomass can be large, while productivity is low (e.g., when grazing and predation rates are low). The distinction between biomass (at a given trophic level) and productivity (primary or secondary at a given trophic level) has important lake management implications.

## Autotrophy vs. Allotropy

"Trophy" refers to the rate of supply of organic matter. Lakes in which most of the organic matter is from autochthonous sources are referred to as autotrophic, whereas those dominated by the input of paralimnetic particulate organic matter (POM) and

dissolved organic matter (DOM) are termed allotrophic (Birge and Juday 1927). Rodhe (1969) presented a two-dimensional diagram which characterized major lake types according to dominance by allotropy or autotropy. His scheme included oligotrophic (low in both auto- and allotrophic organic sources), eutrophic (dominated by autotrophy), dystrophic (dominated by allotropy), and mixotrophy (high in both auto- and allotrophic organic sources). In allotrophic lakes (also called heterotrophic because they resemble a heterotrophic ecosystem organism), the ratio of primary net production ( $P$ ) to community respiration ( $R$ ) is less than unity ( $P/R < 1$ ) (Caspers and Karbe 1967). Likens (1972) modified the allochthonous:autochthonous diagram by Rodhe (1969), incorporating nutrient availability from internal and external sources. Wetzel (1975) presented a modification of the Rodhe (1969) diagram, while pointing out that the "low productivity of dystrophic lakes" refers to planktonic productivity, and that littoral plants completely dominate as sources of dissolved and particulate organic carbon. This raises important questions (with lake management implications) regarding littoral productivity as a component of the aquatic ecosystem.

Trophic classification is most commonly performed using parameters which reflect pelagic phytoplanktonic autotrophy (total phosphorus [TP], chlorophyll, Secchi). In small and/or shallow lakes, littoral production could constitute a large source of organic carbon that is external to the pelagic zone. Hence, littoral production would actually represent allotropy under the most commonly used trophic classification approaches. Littoral production resembles the paralimnetic POM and DOM source more than the phytoplanktonic source. Indeed, one could argue that the shallow littoral fringe surrounding the pelagic zone is an "emergent-submergent marsh," and is a paralimnetic component of the ecosystem. Its major contribution to the organic pool comes at the end of the growing season, as does that from the terrestrial paralimnion. Whether production by littoral plants is considered autotrophic or allotrophic depends on how boundary conditions between ecosystem components are defined.

Most trophic classification schemes (notably the trophic state index [TSI]; Carlson 1977) refer exclusively to phytoplanktonic and water column parameters. In lakes dominated by paralimnetic or littoral organic sources, the TSI will be low because autochthonous (pelagic, phytoplanktonic) production is low. As commonly used, TSIs refer to the level of planktonic autotrophy. Several trophic state classification schemes have used measures of lake community respiration. For example, Hutchinson (1957) presented a trophic classification scheme based on areal oxygen deficit rate. Kortmann et al. (1988) used the scheme by Hutchinson (1957), converting areal dissolved inorganic carbon (DIC) increment rate to oxygen deficit equivalents. Nürnberg (1984) presented an anoxic factor (AF). The AF is particularly interest-

ing, as it relates areal oxygen deficit to lake surface area (facilitating comparison to areal autochthonous productivity).

Use of these respiration-based approaches almost always indicates a higher degree of biological activity (trophy) than indices based on planktonic productivity parameters (TP, chlorophyll, Secchi). A high areal oxygen deficit rate, DIC increment, or AF in lakes of moderate to low TSI (which is not uncommon) indicates dominance by allotrophy and littoral autotrophy. As commonly used, TSI refers to phytoplanktonic autotrophy; production by littoral macrophytes would be considered allotrophic. Respiration-based trophic indices include littoral production as autotrophy.

We illustrate a three-dimensional trophic ontogeny of lakes (Fig. 4; extensively modified from Rodhe 1969, Likens 1972, and Wetzel 1975).

## Nitrogen Transformations

Although availability of phosphorus (P) is most often limiting to aquatic plants, quantities and forms of nitrogen can influence phosphorus availability and the type of biotic response to a given phosphorus level. Transformations between various nitrogen compounds in the nitrogen cycle of aquatic ecosystems offer significant management potential for lakes (Fig. 5). Most phytoplankton which create nuisance bloom conditions are capable of nitrogen fixation and are not dependent on dissolved combined forms of nitrogen. Nitrogen fixation occurs only in bacterial cells (bluegreen algae are prokaryotic, unlike other phytoplankton which are eukaryotic). Both the vegetative cells and heterocysts of bluegreen algae contain nitrogenase and can fix nitrogen. However, nitrogen fixation occurs only in heterocysts under aerobic conditions. A substantial amount of energy (from ATP) and a hydrogen source (from reduced ferridoxin) are required to reduce nitrogen gas to ammonia and, subsequently, to organic ammonia (e.g., amine groups of amino acids; Golterman 1975, Gottschalk 1979). Nitrogen fixation is inhibited by high cellular ammonia content (Gottschalk 1979).

Of the combined forms of nitrogen, the most important are ammonia and nitrate. Both can be assimilated to produce amino acids (amine groups). However, nitrate must first be reduced (assimilatory nitrate reduction), and this process is inhibited by ammonia. Decomposition of organic matter results in release and accumulation of ammonia (via deamination, ammonification). Under aerobic conditions, ammonia is oxidized in a two-step process called nitrification (Phase I to nitrite; Phase II to nitrate). This is one of the chemolithotrophic processes discussed previously. Bacteria which perform these processes are obligate chemolithotrophs. Under anaerobic conditions nitrification of ammonia to nitrate does not occur, and ammonia accumulates (often observed at the bottom of lakes).

Nitrate is the first alternate TEA used in anaerobic respiration when oxygen is exhausted. The energy yield using nitrate is very close to the yield for aerobic respiration (note the similar Gibbs free energy change,  $\Delta G$ ; Fig. 5). As long as nitrate remains available, the Eh remains above that required for iron reduction and subsequent sediment phosphorus release from ferric hydroxy-phosphate complexes in sediments. High concentrations of ammonia accumulate in anaerobic environments. Enhancing nitrification of ammonia to nitrate, and subsequent use of nitrate in denitrification, can stabilize Eh and reduce internal phosphorus loading.

## Sulfur-Iron-Phosphorus Interactions

The sulfur cycle and transformations also affect the iron-phosphorus dynamics of aquatic ecosystems (Fig. 6). The use of sulfate, or elemental sulfur, as a TEA occurs when oxygen is exhausted and Eh drops below about -75 mv. Reduction occurs in the water column and sediments. The end product of sulfate reduction is sulfide, which interacts readily with ferrous iron to produce ferrous sulfide ( $FeS$ ), and subsequently pyrite ( $FeS_2$ ; Doyle 1968). If ferrous sulfide precipitates from the water column and then forms pyrite, ferrous iron is no longer susceptible to oxidation to ferric iron with the return of aerobic conditions. Hence, phosphate binding capacity may be decreased.

The relationships among sulfur, iron, and phosphorus binding capacity raises questions about potential impacts from increased sulfate loading by algicide applications (copper sulfate), alum treatments (aluminum sulfate), and acid rain (sulfuric acid). The extent to which sulfide competes with orthophosphate for iron is a topic which warrants further research.

## Ecosystem Dynamics— Nutrients and Energy

When energetic processes are superimposed on a eutrophic lake ecosystem, one notes that the lake ecosystem consists of two major components: the "aquatic" component which is the waterbody itself, and the "paralimnetic" component which consists of the drainage basin or watershed (Fig. 7). The paralimnetic component could be divided into a variety of land-use fractions (urban, agricultural, and wooded/wetland used here), soil groupings, slope classes, or other categories. Likewise, the aquatic component could be divided into littoral zone; pelagic zone; benthic boundary layer; sediments; and during summer stratification into epilimnion, metalimnion, and hypolimnion. Dividing the ecosys-

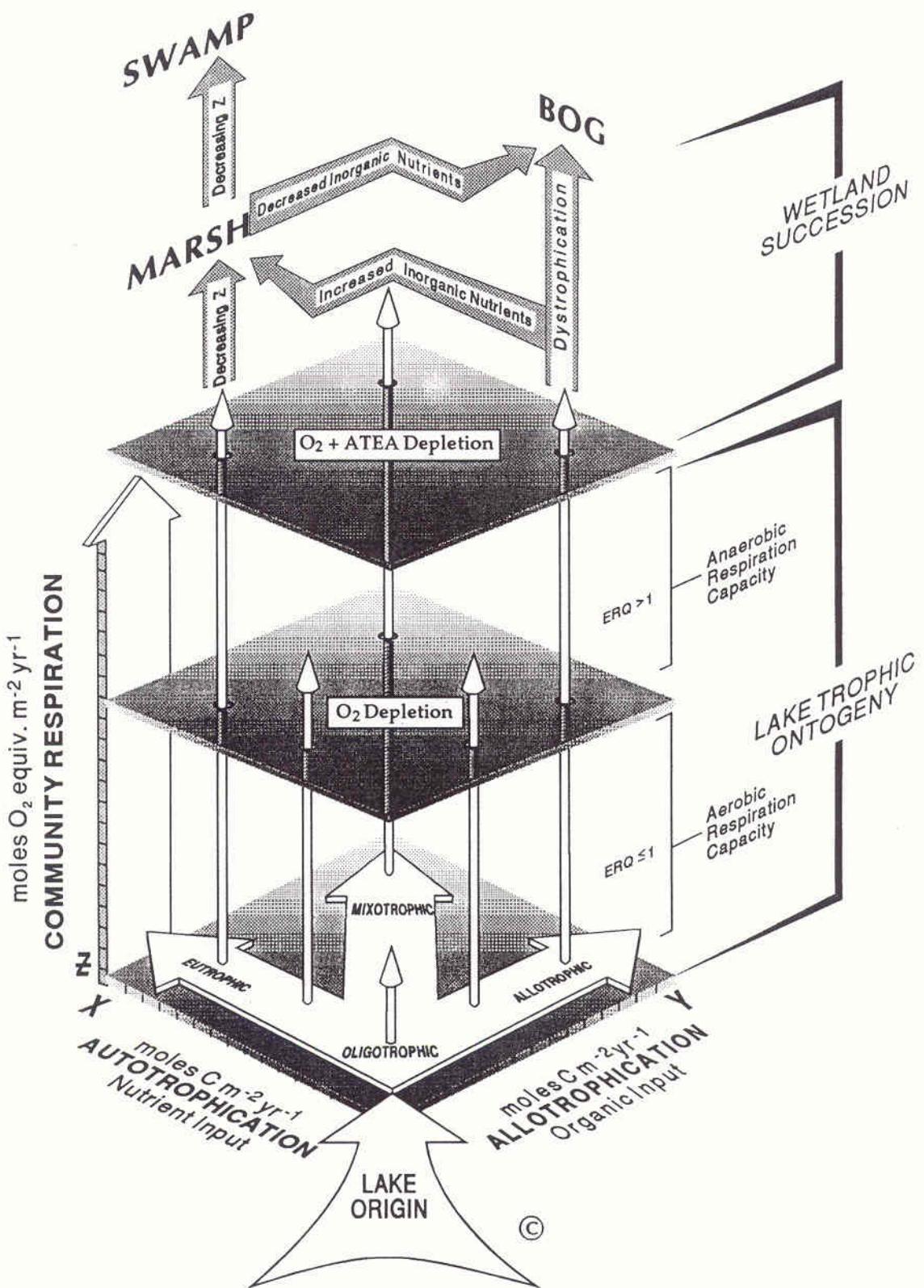


Figure 4.—Trophic ontogeny. Trophic state is a function of organic supply from autochthonous (X axis) and allochthonous (Y axis) sources. Community respiration (Z axis) is a function of total organic supply (autotrophy and allotrophy). When aerobic respiration capacity is exceeded, alternate terminal electron acceptors (TEAs) are used in respiration, chemical oxygen demand accumulates, and the ecosystem respiratory quotient (ERQ) exceeds unity. When total respiration capacity is exceeded ERQ stabilizes, organic accumulation accelerates, and succession is stimulated. Successional variants are illustrated as functions of depth, nutrient and TEA availability, and organic matter source.

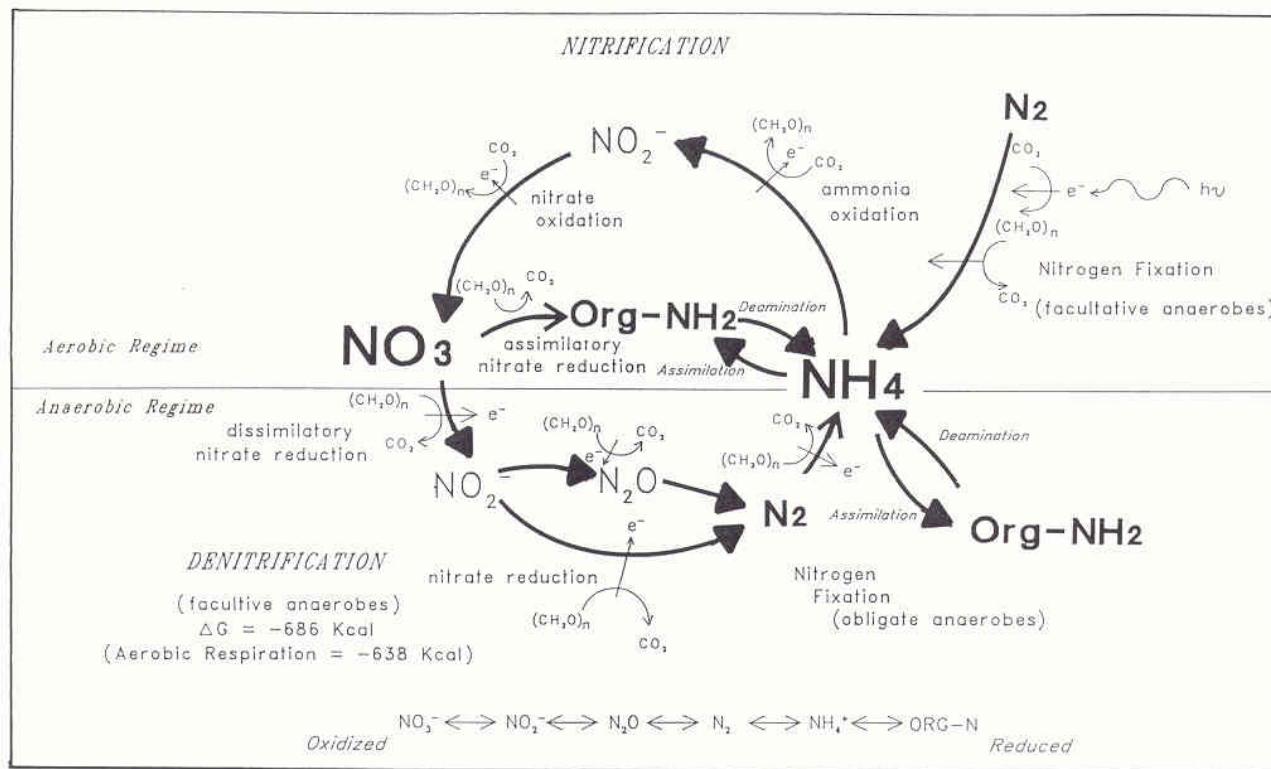


Figure 5.—The Nitrogen Cycle in lake ecosystems. Ammonia and nitrate are critical components of the cycle. Ammonia is generated by deamination of amino acid groups on either allochthonous or autochthonous matter. It is also the nitrogen compound formed by nitrogenase (nitrogen fixation). Ammonia is nitrified in aerobic environments to nitrate, which is subsequently either taken up (assimilatory reduction) or denitrified (dissimilatory reduction). Nitrate is the first alternate terminal electron acceptor (TEA) used in respiration following oxygen loss. While respiration operates in the nitrogen cycle, increased sediment P release does not occur.

tem into such categories enables the limnologist to apply compartment modeling techniques (donor control, recipient control) to evaluate structure and function (Kortmann 1980).

External nutrient loading is important because it generally controls production in the trophogenic zone of the aquatic component (autochthonous production). Terrestrial photosynthesis produces and releases organic matter which also enters the aquatic component as either POM or DOM. This allochthonous organic matter supports respiration in the aquatic component. The loading of allochthonous POM and DOM is as important to aquatic respiration, trophic dynamics, and ecosystem structure and function as nutrient loading which supports autochthonous production.

Compensation depth is the depth at which photosynthetic oxygen production by phytoplankton is balanced with respiratory demand for oxygen (the TEA in aerobic respiration). This depth is influenced by light penetration because PAR is required to drive Photosystem II (noncyclic photophosphorylation) which uses water as the reducing agent and generates oxygen (Fig. 3). The depth to which 1% incident PAR penetrates approximates the compensation

depth in a eutrophic lake, which is the boundary between the trophogenic (above) and tropholytic zones (below). Compensation depth can be estimated by multiplying Secchi disk depth by between 1.6 and 2.4, depending on light attenuation in lake water due to color, dissolved organic matter, etc.

Below compensation depth (in the tropholytic zone), net oxygen consumption occurs in a eutrophic lake. As alternate TEAs are consumed, Eh decreases. Eh tends to decrease with greater depth in the water column and in sediments (Fig. 7). Once the Eh of the ferric-ferrous iron couple is reached, both ferrous iron and phosphate accumulate. If Eh continues to decrease, sulfate is reduced to sulfide, which can remove iron and permanently reduce phosphate binding capacity.

Large quantities of dissolved phosphorus are released from sediments upon the reduction of iron, causing internal nutrient loading. Ferrous iron is reoxidized when it encounters oxygen (from the trophogenic zone), and tends to reprecipitate phosphorus. Accumulated hypolimnetic phosphorus can be transported to the trophogenic zone by eddy transport or wind mixing episodes, and can have dramatic effects on autochthonous production

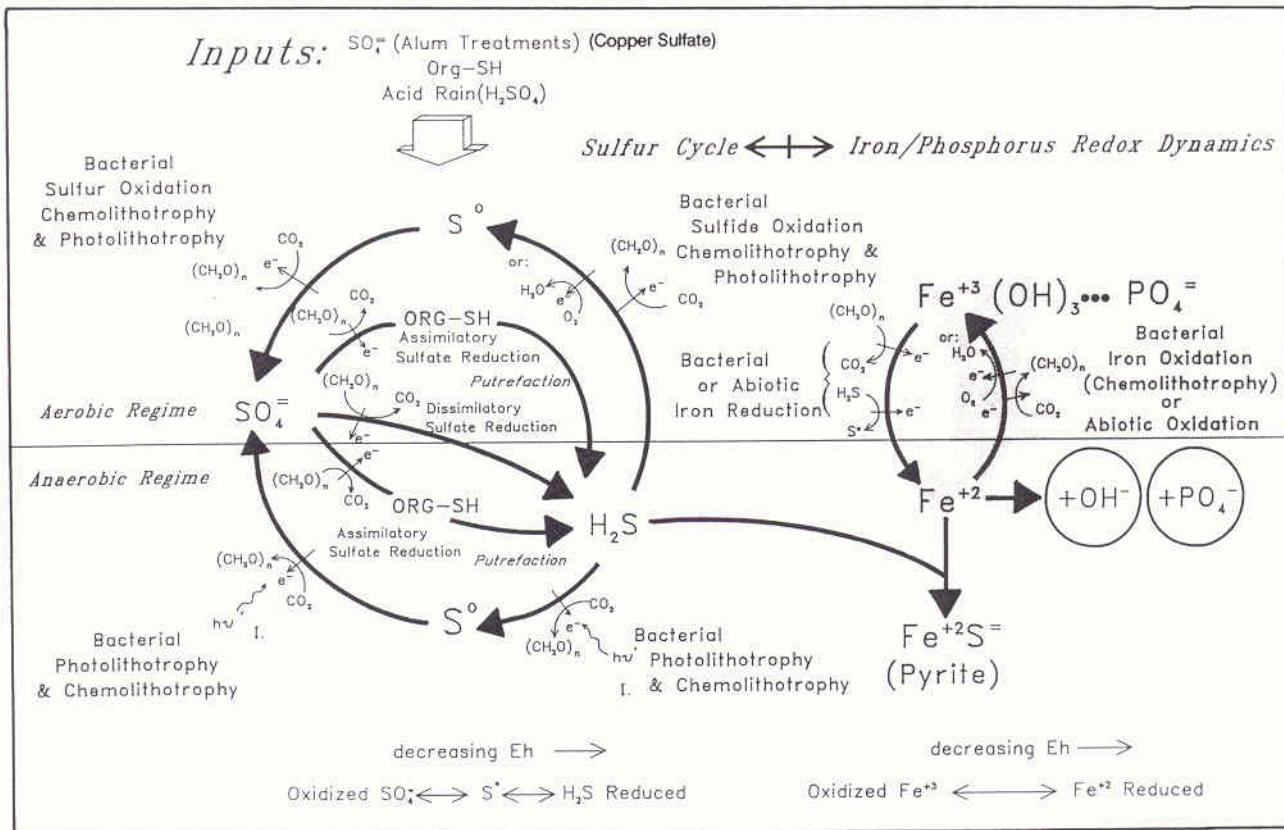


Figure 6.—The sulfur and iron cycles of aquatic ecosystems and interactions between anaerobic respiration products, ferrous iron and sulfide, which results in decreased sediment P-binding capacity.

(Kortmann et al. 1982). Note that carbon dioxide is a common product of all respiratory processes: aerobic, anaerobic, and fermentation. Measurement of DIC increment yields a more comprehensive estimate of total hypolimnetic respiration than oxygen consumption rate (Kortmann et al. 1988).

The specific location of the compensation depth relative to density and viscosity gradients in the metalimnion during thermal stratification is of particular interest in a eutrophic lake. Those three factors tend to dictate relative amounts of phosphorus transport to the trophogenic zone (increasing autochthonous production) compared to reprecipitation of phosphorus with reoxidized iron. When compensation depth occurs below the thermocline, a greater fraction of phosphorus will coprecipitate with iron, and less reaches epilimnetic waters. Phosphorus input is confined to metalimnetic waters, and can support metalimnetic layers of phytoplankton (especially bluegreen bacteria with low light requirements such as *Oscillatoria* sp.), chemolithotrophs, chemoorganotrophs, photolithotrophs, and photoorganotrophs (Golterman 1975). Production in the metalimnion is stimulated rather than epilimnetic autochthonous production. When water transparency declines, compensation depth ascends, and epilimnetic production is stimulated. It is important to remember that blue-

green algae (Cyanobacteria) are prokaryotic, unlike all other phytoplankton. Many species perform heterotrophic and chemosynthetic processes which can be beneficial (Golterman 1975, Gottschalk 1979).

The paralimnion is an integral part of the aquatic ecosystem. Terrestrial photosynthesis contributes to aquatic food webs, trophic dynamics, and internal nutrient cycling processes. The allochthonous input of DOM and POM represents a fraction, often a major fraction, of ecosystem production. Allochthonous DOM and POM support respiration in the lake just like autochthonous organic matter produced in the trophogenic zone of the lake. Nutrient loading from the paralimnion contributes to autochthonous production and subsequent respiration. Allochthonous DOM and POM contribute directly to respiration throughout the water column.

## Trophic Structure—Food Web

Lakes contain many life forms which work in concert to use material and energy in a highly ordered system. Energy enters the lake ecosystem by

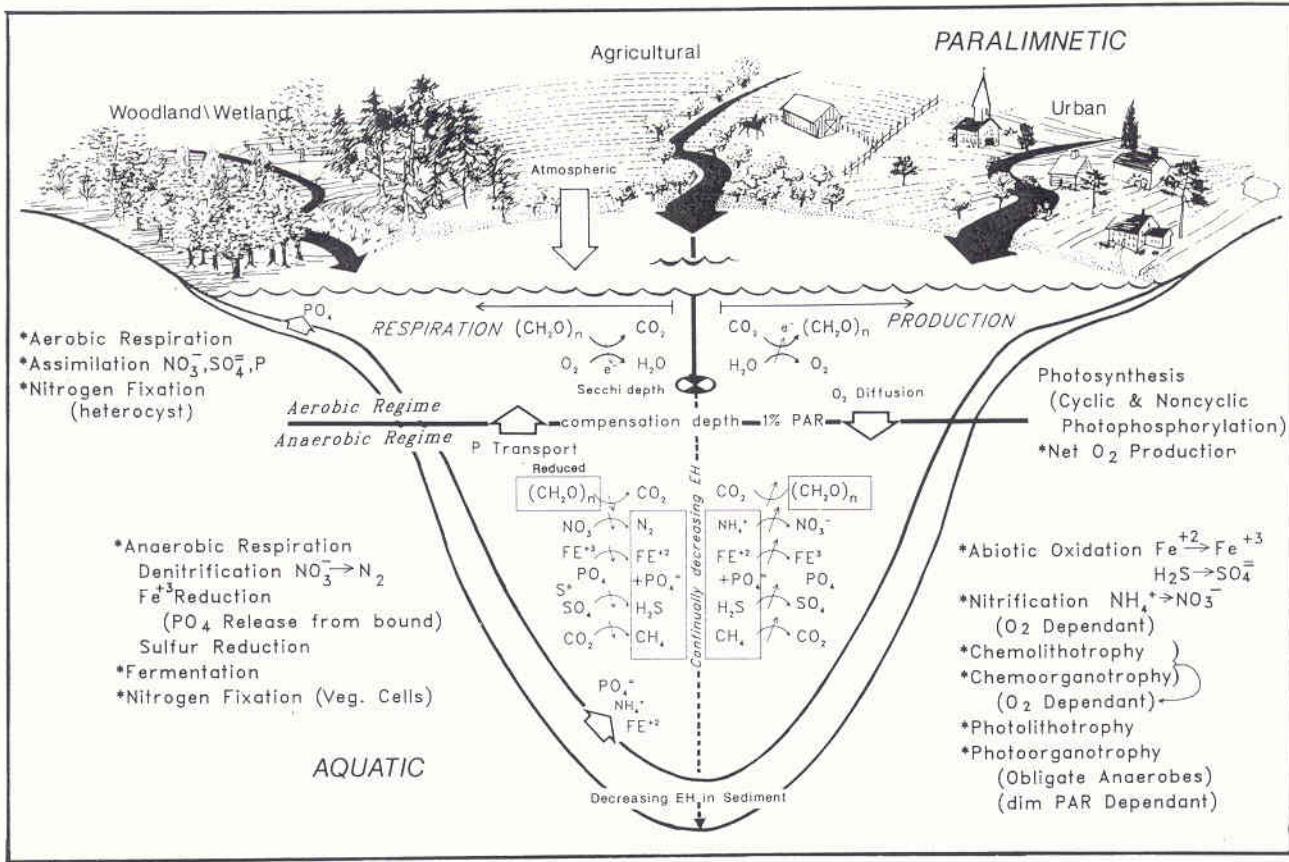


Figure 7.—Spacial relationships among productive and respiratory processes, oxidation-reduction potential (Eh) and light attenuation in a thermally stratified eutrophic lake ecosystem.

photosynthesis either in the lake or in the lake drainage basin (paralimnion). Autotrophs capture solar energy and store (fix) captured energy between the products of photosynthesis: oxygen and organic matter. Fixed energy is recovered when oxygen and organic matter are recombined in respiration. The products of respiration—water and carbon dioxide—are once again available for photosynthetic conversion to oxygen and organic matter.

Organic matter and energy fixed by autotrophs (primary producers), are passed on to the first tier of heterotrophs (herbivores or primary consumers; Fig. 8). Herbivory is a difficult biochemical step involving the conversion of plant (carbohydrate) material to animal (protein) material. In fact, herbivory is so inefficient that much plant matter goes uneaten, and is left to be decomposed by bacteria. In contrast to plants, bacteria are a good source of nutrition, and a large number of aquatic animals called filter feeders prey on bacteria as well as algae. The term "detritus" is used to distinguish organic matter decomposed by bacteria (which are subsequently the prey of filter-feeders) from organic matter preyed upon while alive ("grazed").

Omnivorous filter-feeders make the products of both aquatic and terrestrial photosynthesis (particu-

late and dissolved detritus) available to aquatic predators (secondary consumers) which eat primary consumers. Each step in the food chain from primary producers to the highest predators involves losses of organic matter and energy to respiration, incomplete digestion, etc. Thus, the collective mass (biomass) of autotrophs is larger than the biomass of primary consumers, and the biomass of primary consumers is larger than the biomass of secondary consumers, etc. The term "ecological pyramid" alludes to this phenomenon. Lakes which tap into the terrestrial food chain via the use of terrestrial detritus have anomalous consumer biomasses. Crossing-over between food sources by animals makes the term "food web" more accurate than "food chain," and reminds us that a lake is but part of a much larger ecosystem.

Lake ecosystems are complex, involving *both terrestrial and aquatic photosynthesis*, external and internal nutrients, grazer and detrital food webs, and aerobic and anaerobic metabolism.

Most energy enters a small lake through terrestrial photosynthesis in the watershed (paralimnion). Photosynthesis in the lake itself is limited by physical and chemical characteristics of the water. About one half of the incident PAR is reflected and refracted at the lake surface, and much of the rest may be

absorbed by lake water and organic matter dissolved in it (Wetzel 1975). Energy from terrestrial photosynthesis helps lakes by creating the terrestrial community which takes up nutrients and prevents erosion of drainage basin soil into the lake. However, large amounts of POM and DOM may be washed and blown into lakes from land. Terrestrial organic material affects physical/chemical properties and processes of lakes, combines with products of aquatic photosynthesis to support lake food webs, and accumulates in lake sediments.

The overall flow of energy between trophic levels is superimposed on a thermally stratified mesotrophic lake (Fig. 8). When compensation depth is within the metalimnion (which is often the case in deep, thermally stratified, mesotrophic lakes), the trophic dynamic structure is widely recognized. Autochthonous production by aquatic macrophytes (littoral zone photosynthesis) and phytoplankton (pelagic photosynthesis) is grazed by littoral invertebrates and pelagic zooplankton, then by forage fish preying on zooplankton, and finally by predatory fish (piscivores) on forage fish. This trophic dynamic structure prevails in the littoral zone and trophogenic pelagic zone of mesotrophic and eutrophic lakes.

The detrital dynamic structure of ecosystems is not as widely recognized or understood. It is often

considered to be the decomposition process but is rarely recognized for its role in ecosystem energetics. Most energy available in organic matter that is grazed, or preyed upon, is not assimilated by the consumer; it becomes nonpredatory losses and enters the detrital system (Wetzel 1975, Rich 1984b). Aerobic and anaerobic heterotrophic bacteria use nonpredatory losses to support their respiration. Heterotrophic bacteria are consumed (bactivory) by filter-feeders and detrital energy reenters the trophic dynamic structure.

Under anaerobic conditions, alternate TEAs are used, and reduced anaerobic respiration products are produced. Transport of the reduced products of anaerobic respiration from sediments to overlying water represents an abiotic energy flow called benthic detrital electron flux (BDEF). These reduced products contain residual energy which supports photolithotrophy, photoorganotrophy, chemoorganotrophy, and chemolithotrophy. This bacterial biomass is also available for bactivory by filter-feeders. Interaction from the detrital dynamic structure to the trophic dynamic structure occurs via bactivory and represents a major component of ecosystem energetics (Rich 1984a,b, Sanders et al. 1989). Terrestrial photosynthesis and subsequent POM and DOM allochthonous loading are important parts of

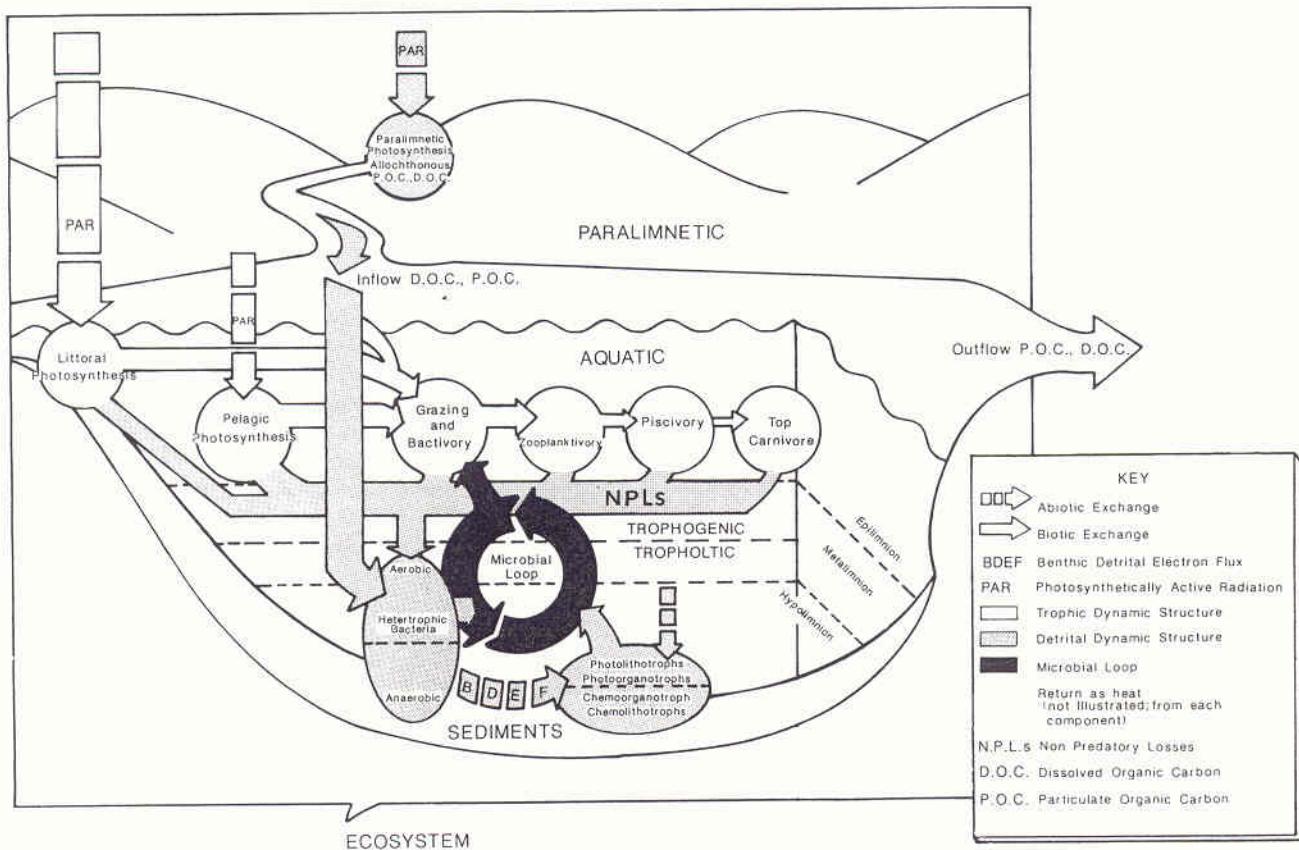


Figure 8.—Spacial relationships between compensation depth, trophic dynamic structure, detrital dynamic structure, paralimnetic and aquatic interactions, and thermal stratification structure in a eutrophic lake ecosystem.

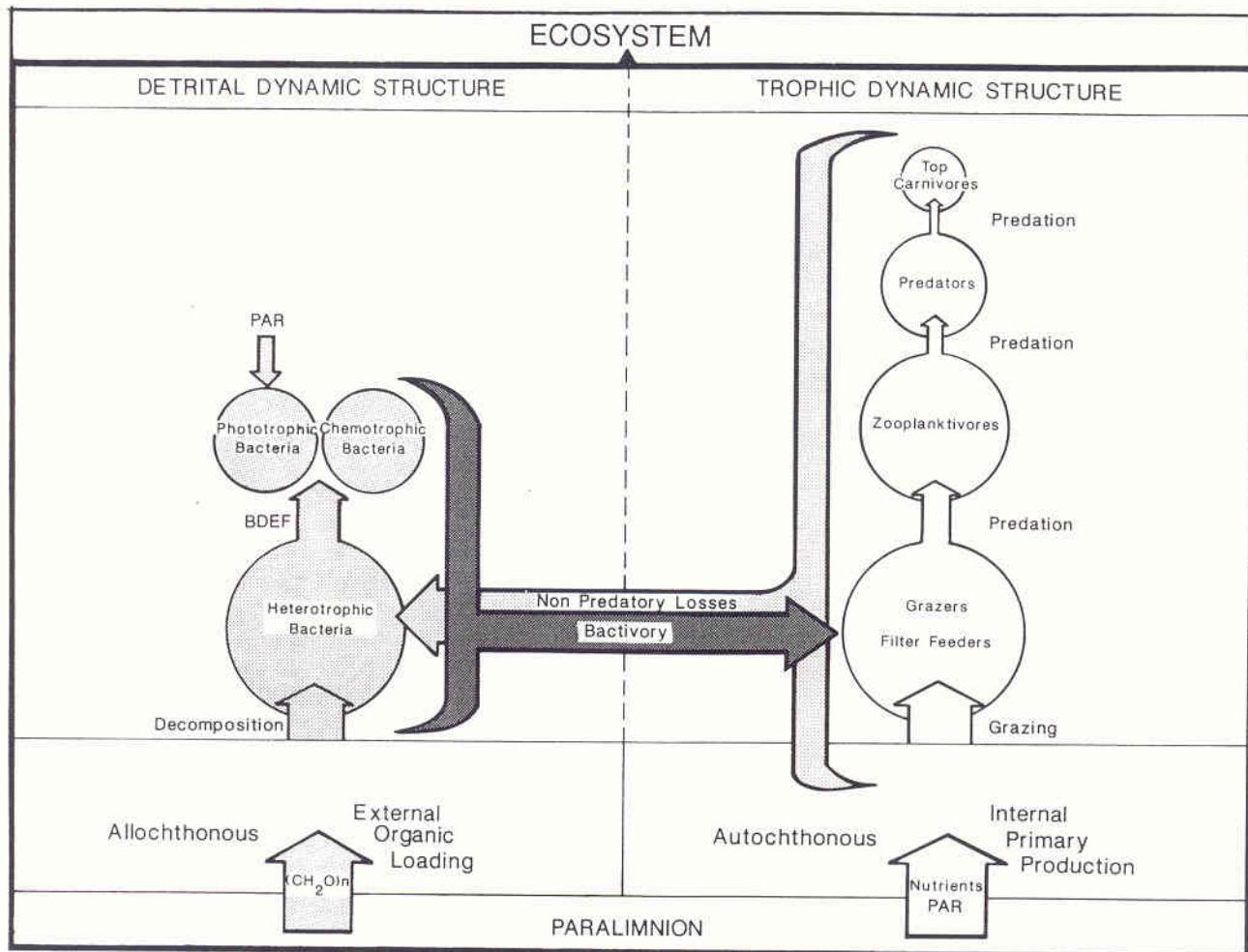


Figure 9.—Schematic summary of the interactive relationships between detrital dynamic structure and trophic dynamic structure of lake food webs.

the detrital dynamic structure, contributing to the detritus that supports heterotrophic bacteria, bacterial chemo- and phototrophies, and the higher food web system via a "microbial loop" and bactivory (Fig. 8).

Trophic and detrital dynamics are integrated in lake ecosystem energetics (Fig. 9). Input of nutrients (from the paralimnion) and PAR support internal primary production (autochthonous). Autochthonous production supports the food web of the trophic dynamic structure. Input of allochthonous organic matter enters the detrital system and supports heterotrophic bacteria which, in turn, contribute reducing power via BDEF to phototrophic and chemotrophic bacteria. The detrital dynamic structure is driven by nonpredatory losses from the trophic dynamic structure and by terrestrial detritus. The detrital system supports the trophic dynamic structure via bactivory at the primary consumer level, and by making nutrients available to support greater autochthonous production. Although schematically segregated in Figs. 8 and 9, in nature the detrital and trophic dynamic

structures are components of one integral structure (the ecosystem).

Eutrophication is an ecosystem response to increasing nutrient availability. The response involves increased autochthonous primary productivity. However, all other aspects of lake ecosystems are involved as well (biotic and abiotic, autotrophic and heterotrophic, autochthonous and allochthonous; Fig. 8). Trophic level energy exchange operates at a transfer efficiency (ecological efficiency) of approximately 10-15%. Ecological efficiencies are low because the denominator of the efficiency ratio (product/reactant = predator/prey) contains much organic matter (nonpredatory losses) not assimilated by predators. The low efficiency of trophic energy exchange does not reflect true *ecosystem* energetic efficiency (predator/prey-nonpredatory losses). Nonpredatory losses from all trophic levels enter the detrital system (Wetzel and Rich 1973), supporting a large biomass of heterotrophic microflora. The microbial loop is now recognized as a dynamic component of food

webs. Terrestrial photosynthesis provides a substantial supply of organic carbon to the aquatic detrital dynamic structure. Hence, both autochthonous and allochthonous carbon contribute to aquatic food web energetics, secondary productivity, and trophic state. Indeed, many lake ecosystems may be dominated by allochthonous inputs, detrital dynamic structure, and the microbial loop (Rich 1979; 1984a, b, Sanders et al. 1989, Vadstein et al. 1989). Anaerobic metabolism in lakes is an extension of the detrital side of the food web. Chemically reduced products of anaerobic respiration diffuse to the aerobic zone (BDEF; Rich 1979) and become reactants in chemolithotrophy. Chemosynthetic fixation of carbon is not truly autotrophic because reducing energy contained in reactants came from the incomplete (anaerobic) respiration of autochthonous or allochthonous organics. Food web dynamics become even more complex when one considers the phototrophic organisms which perform bactivory (Sanders et al. 1989), and raises the question of whether bactivory is performed to gain energy, nutrients, or both.

Nitrification can represent a substantial contribution to carbon fixation in eutrophic lakes. The reactant (ammonia) is not derived from a respiration process. It is produced primarily via deamination of amino acid amine groups. Nearly half of the dissolved organic nitrogen budgets of some lakes is in labile and refractory organic form (LDON and RDON; Kortmann 1980, 1981). Ultimate sources of ammonia include nitrogen fixation and assimilation in the aquatic and paralimnetic ecosystem components. We believe much of the historic difficulty with quantifying total oxygen demand (and sizing of aeration systems) can be attributed to this "ammonia anomaly." Total oxygen demand includes respiratory demand and nonrespiratory demand (e.g., chemosynthesis; Kortmann et al. 1993).

## The Ascent of Compensation Depth

In lakes where hypolimnetic oxygen demand exceeds dissolved oxygen supply, oxygen depletion occurs and anaerobic respiration products accumulate. Alternate TEAs are used in order of decreasing Eh (Fig. 7). The metalimnion performs a role as an oxidation zone in such lakes (Stauffer 1987). The vertical position of compensation depth (a function of transparency in productive lakes) relative to the density gradients of the metalimnion (a function of heat mixing dynamics) is critical to the expression of trophic state.

Light attenuation is a critical feature of lake ecosystems (Preisendorfer 1986). When 1% light penetrates the metalimnion, the stage is set for metalimnetic algal layers as well as an array of chemotrophs. The proportion of upward hypolimnion-epilimnion con-

stituent exchange is small relative to resedimentation (Kortmann 1981). As eutrophication advances, transparency declines, and compensation depth ascends, which leads to process changes (Fig. 10). When anoxia reaches the upper metalimnetic boundary, and the trophogenic zone becomes more shallow than the epilimnetic mixing depth, abrupt shifts in the phytoplankton community occur. Epilimnetic Cyanobacteria become dominant. Epilimnetic loading of bottom-generated constituents increases (Kortmann et al. 1982), and critical zooplankton refuge habitat is lost (Wright and Shapiro 1990). A shift from metalimnetic communities (e.g., *Oscillatoria* sp. which can perform phototrophy, chemotrophy, and heterotrophy) to epilimnetic Cyanobacteria blooms (e.g., *Anabaena* sp.) may occur as eutrophication advances. Biological activity in a lake ecosystem depends ultimately upon the amount of available (reducing) energy, and the amount of biochemical machinery (for both synthesis and respiration) which can be constructed from available nutrients.

P is typically the element in shortest supply relative to aquatic plant requirements; hence, it tends to limit autochthonous production (e.g., cyclic and noncyclic photophosphorylation). P is essential for heterotrophic processes (e.g., ATP, substrate level phosphorylation). Thus, autotrophs and heterotrophs compete for available P, as do abiotic chemical reactions (e.g., ferric hydroxyl phosphate complex formation). Of greatest concern in eutrophication abatement is availability of P in the trophogenic zone and its effect on internal primary production.

As nutrient availability increases, in-lake primary production increases. External nutrient loading from watershed (paralimnetic) sources initiates the increase in phytoplankton production. As a result of increased phytoplankton densities, transparency declines and autochthonous organic matter increases. Compensation depth becomes shallower. As compensation depth ascends, ultimately reaching the epilimnetic-metalimnetic boundary, a variety of changes occur. Eutrophication, initiated by increased external nutrient loading, perturbs the internal structure of the lake. Greater areal and temporal duration of anoxia (Nürnberg 1984) lead to increased anaerobic respiration and sediment nutrient release, and anaerobic synthetic and respiratory processes occur at shallower depths. Reprecipitation of sediment-released P decreases and transport to the trophogenic zone increases. As compensation depth ascends above the thermocline in a eutrophic lake, internal structure shifts from "control by diffusion" described by Mortimer (1969) to control by light penetration. Photosynthetic oxygen production occurs only in more shallow waters, and the trophogenic depth is less than the epilimnetic mixing depth. Nitrification and subsequent denitrification in deeper strata declines; ammonia accumulation intensifies.

As autochthonous production intensifies, Eh decreases further in deep strata, resulting in greater

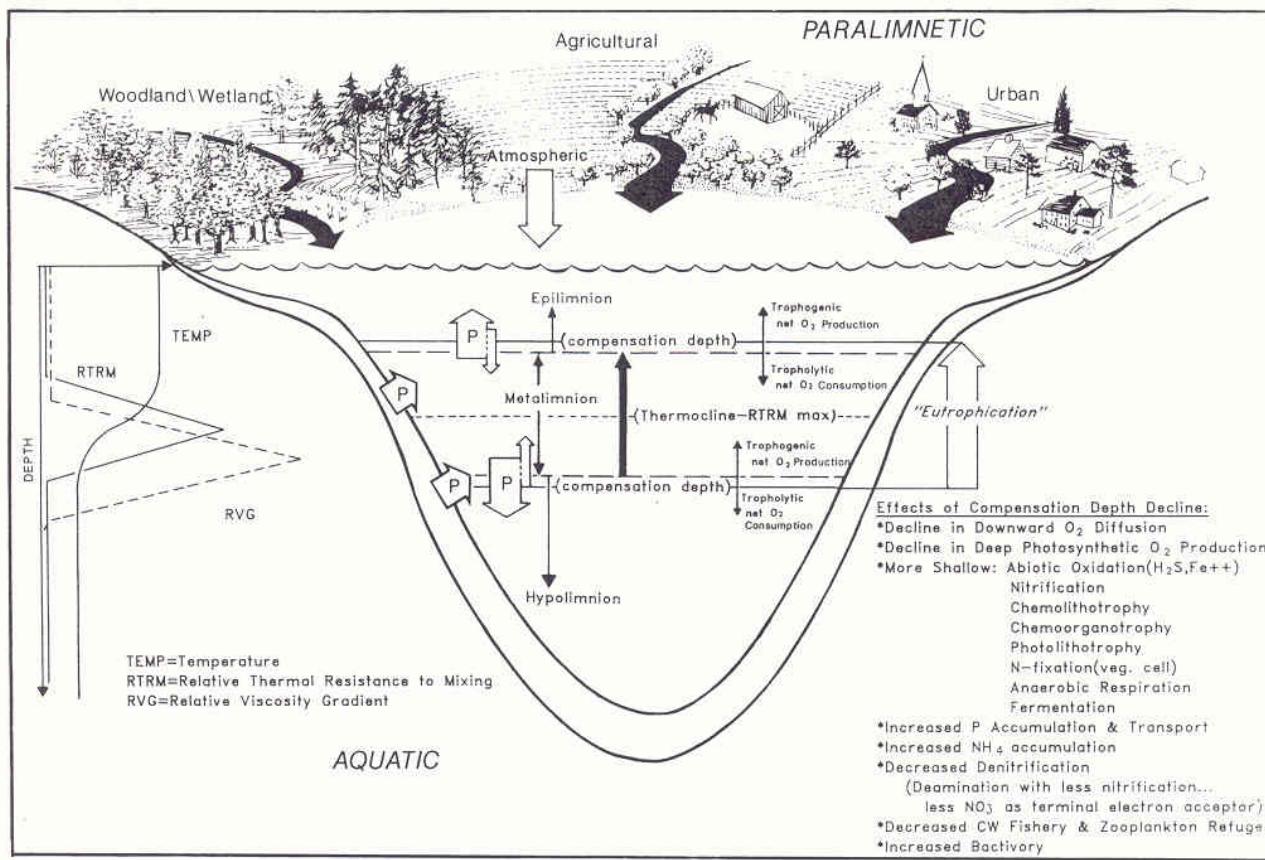


Figure 10.—Schematic illustration of ecological process responses during the ascent of the compensation depth as a result of eutrophication.

internal P loading, greater sulfide generation, iron removal as pyrite, and reduced P binding capacity. The organic load to the detrital dynamic structure increases, favoring bactivory (e.g., by *Bosmina* sp.) over phytoplankton grazing (e.g., by *Daphnia* sp.). The shift in dominance from trophic to detrital components may become more pronounced due to a decline in suitable habitat for piscivorous fish, an overabundance of zooplanktivorous fish, and decline in grazer refuge habitat. Watershed nutrient loading affects the entire structure and function of the lake ecosystem, not simply increased primary production. Therefore, reducing the external nutrient load should be an integral part of any program to remedy effects of cultural eutrophication.

When the external load cannot be reduced to adequately control autochthonous production (and its in-lake consequences), in-lake measures which manage the competition for P by autotrophs, heterotrophs, and abiotic reactions are useful for controlling trophic quality. Anaerobic aeration favors nitrification-denitrification, and uses iron generated by the lake's anaerobic respiration as a P precipitant (analogous to nutrient inactivation; Kortmann et al. 1991). Layer aeration (Kortmann et al. 1988, 1993) mechanically restores control by diffusion described

by Mortimer (1969) and enhances the oxidizing function of the metalimnion described by Stauffer (1987). Preventing spatial separation between the trophogenic boundary and epilimnetic-metalimnetic interface (mixing depth) is critical to managing trophic quality (especially buoyancy controlled Cyanobacteria), and can be achieved by reducing autochthonous production (by reducing nutrient influx) or by in-lake methods.

## Lake Restoration Technologies

Mortimer (1969) presented elements of the eutrophication process and its effects in the form of a simplified flux diagram (Fig. 11). His depiction of eutrophication and consequences of eutrophication is the basis for our categorization of lake management methods, with the addition of symptomatic approaches. Lake ecosystem energetics is involved with each technique within the three categories we describe: 1) control of eutrophication, 2) control of eutrophication consequences, and 3) treatment of eutrophication symptoms.

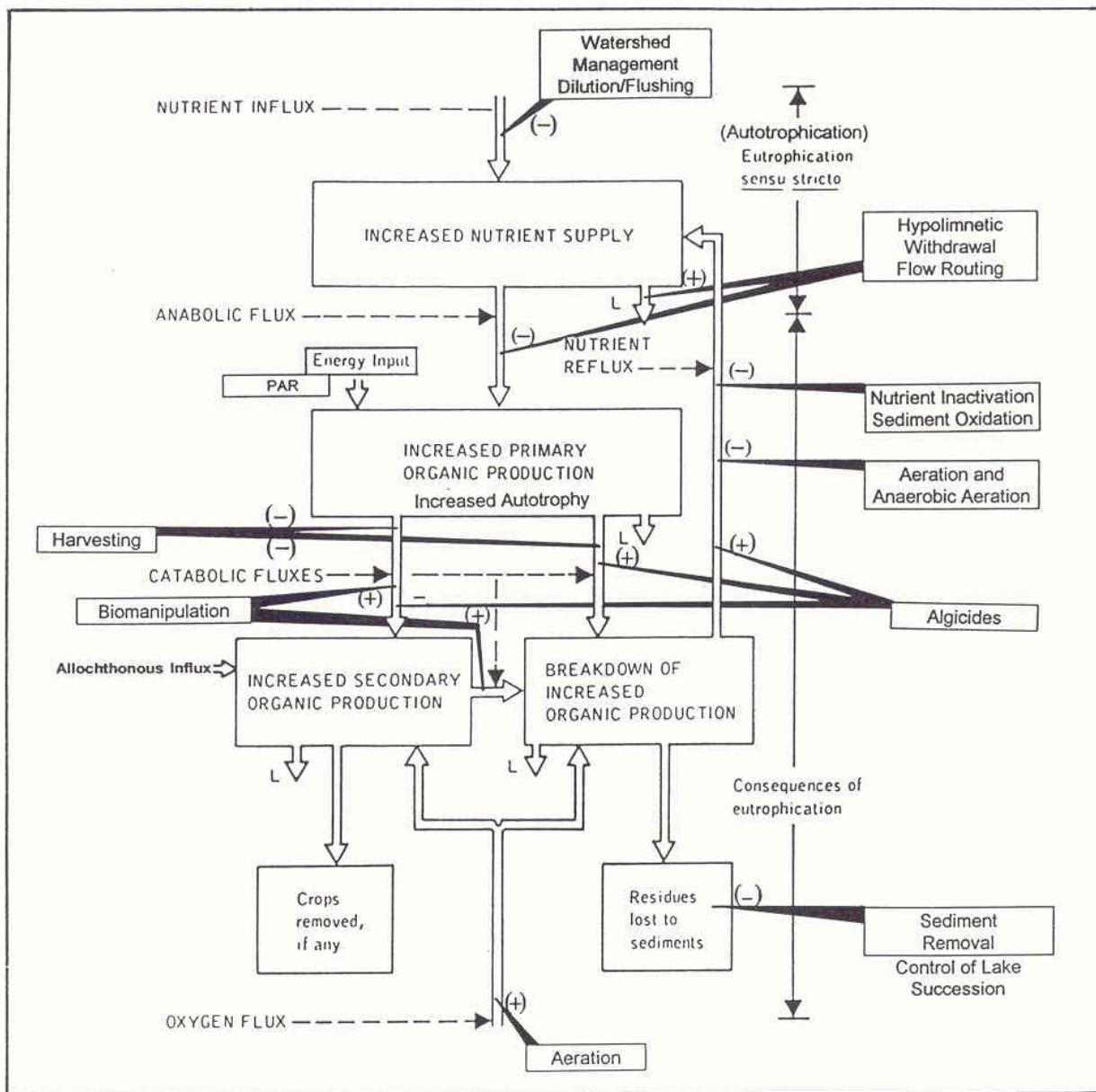


Figure 11.—Flux diagram of eutrophication and its consequences (after Mortimer 1969). L indicates a leak through the lake outflow. Superimposed are the principal effects of several lake management strategies; (+) indicating an increased flux, (-) indicating a decreased flux.

The best current textbook on lake management (Cooke et al. 1986) categorizes lake restoration methods into three basic groups: 1) techniques for nutrient control (diversion, wastewater and stormwater treatment, hypolimnetic withdrawal, dilution and flushing, nutrient inactivation, sediment oxidation, sediment removal, and hypolimnetic aeration); 2) methods to control plant biomass (e.g., artificial circulation, drawdown, harvesting, biological control, benthic covers); and 3) methods for liming of acidified lakes.

The use of herbicides and algicides was intentionally omitted from their treatment of lake manage-

ment methods because of potential adverse effects. We strongly agree that pesticide use should not be endorsed for broad-scale application to lake ecosystems. However, we include these methods in our discussion of energetic relationships to illustrate several potential adverse community effects, and because the use of aquatic pesticides for weed and algae control is more commonly practiced than all other lake restoration methods combined (Cooke and Carlson 1989). We have not included sediment removal, since it is our belief that this technology is for control of lake succession rather than eutrophication. Likewise, we do not include a discussion of

liming for the control of cultural acidification. Although sediment removal and liming are valid lake management methods, we limit our discussion to techniques for controlling eutrophication (and its consequences) in lake ecosystems.

## Control of Eutrophication

We define eutrophication as "autotrophication" (Fig. 4), a function of inorganic nutrient influx (depicted in Mortimer's flux diagram, 1969). Hence, methods to control eutrophication include those which reduce paralimnetic influx of nutrients which drive autotrophy. External loading of paralimnetic POM and DOM also contribute directly to community respiration, demand for TEAs, and food web dynamics. However, we distinguish this process by the source of organic matter. We define ecosystem response to increasing paralimnetic organic loading as "allotrophication," and as "dystrophication" where allochthonous organics overwhelm the system (Fig. 4). The external loading of mineral sediments decreases mean depth ( $\bar{Z}$ ) and accelerates ecosystem succession. Control of autotrophication, allotrophication, and succession involve reducing influx from the paralimnion (nutrients, organics, and mineral sediments, respectively).

Reducing nutrient, organic, and sediment influx is paramount to lake restoration. Total phosphorus and total nitrogen concentration of forested watershed runoff averages 0.015 and 0.51 mg/L, respectively (Omernik 1977). Agricultural and urban land uses dramatically increase nutrient loads, as well as organic and sediment loads. Stormwater runoff and wastewater inputs are among the largest sources of nutrients, and are also large sources of respiratory and nonrespiratory oxygen demand. Methods for controlling major sources include wastewater treatment (Rohlich 1969, Metcalf and Eddy Inc. 1972, Laak 1980), stormwater management (Weibel 1969, Schueler 1987, Stahre and Urbonas 1990), and agricultural best management practices (Biggar and Corey 1969). These should be rigorously pursued in all lake restoration projects, as they determine the innate nature of a lake ecosystem.

Diversion of a nutrient source (e.g., wastewater) is a control of eutrophication method as it reduces nutrient influx. Several management approaches which do not reduce nutrient influx may also be appropriately included in this category. Dilution/flushing decreases nutrient influx relative to system hydrology, flushing rate, and nutrient/organic export. Hypolimnetic or deep water outflow (aka flow routing) increases nutrient/organic export without reducing influx. These methods result in less nutrient availability to autotrophy via a reconfiguration of lake hydrology. These methods could be categorized as control of eutrophication consequences or as control of eutrophication.

## Control of Eutrophication Consequences

This category includes most lake management methods, techniques which manage the response to (or consequence of) nutrient influx. Those consequences include increased autochthonous productivity, changes in biomass (at various trophic levels), respiratory TEA demand, anoxia, sediment-P release, changes in habitat quality, and changes in the biological community. These methods modify the expression of trophic state (i.e., trophic quality) without necessarily altering productivity (i.e., trophic quantity). They change the character of a lake without reducing nutrient, organic, or sediment influx. A reduction in external nutrient, organic, and sediment loads sufficient to produce a recognizable reduction in algal or macrophyte production and biomass (eutrophication control), although desirable, is not always feasible or economically practical. Methods which control consequences of eutrophication are useful in such cases.

### Nutrient Inactivation

Growth of nuisance algal blooms (a consequence of eutrophication) can be controlled by reducing an essential nutrient to limiting concentrations. Internal sources of P can be decreased by phosphorus precipitation and inactivation which removes P from the water column and suppresses its release from sediment (Cooke and Kennedy 1981a, b, Cooke et al. 1982). That is accomplished in lakes by introduction of an aluminum salt which binds P as an aluminum phosphate precipitate or (more often) in an aluminum hydroxide floc. Lakes that experience significant internal P loading may be the rule rather than the exception (Cooke et al. 1986).

Originally, aluminum treatment of lakes was analogous to that in water treatment plants, i.e. aluminum sulfate (alum) was the aluminum salt, and dosage was calculated from water volumes and desired P removal. Today's technology combines the application of alum and sodium aluminate (not pre-mixed) to maximize Al dose, create a seal on sediment P release which is not redox active, and to control Al toxicity by maintaining pH 6-8. Effects of aluminum treatment upon P precipitation and inactivation, lake water chemistry, and the autotrophy of lakes are predictable. Aluminum treatment is an increasingly popular technique for lake restoration.

Following depletion of oxygen, hypolimnetic respiration continues by chemically reducing alternate TEAs in the order of decreasing Eh. Anaerobic respiration is an important component of lake secondary productivity. Products of anaerobic respiration become reactants in bacterial chemolithotrophic and chemoorganotrophic processes. The heterotrophic microflora of a eutrophic lake supports a substantial

fraction of higher trophic level requirements via benthivory (Sanders et al. 1989). In many lakes, the redox system is dominated by reduction of ferric to ferrous iron. P-binding capacity of a lake is directly related to iron (Fe) content. Hypolimnetic Fe:P ratios exceeding 3 are desired to promote iron phosphate precipitation during turnover (Stauffer 1987).

Allotrophy is not controlled by nutrient inactivation; nor is oxygen depletion due to respiration of allochthonous DOM and POM. Little consideration has been given to sulfate loading and potential long-term impacts of aluminum sulfate treatments. The magnitude of sulfate loading during an alum treatment may adversely interact with the iron cycle through anaerobic respiration (Fig. 6). Increased availability of sulfate as a TEA is likely to increase the fraction of anaerobic respiration carried by the sulfur cycle, and increase production of hydrogen sulfide. This would have a direct toxicity impact (sulfide is more toxic than ferrous iron). Furthermore, hydrogen sulfide and ferrous iron react, forming insoluble ferrous sulfide (Doyle 1968). Hence, the lake's P-binding capacity would decrease at the same time the redox system shifted to sulfide predominance.

Nitrate can have substantial benefits, including enhancement of denitrification and favoring non-nuisance green and diatom species over Cyanobacteria (Shapiro 1983, Klemer and Konopka 1989). Use of aluminum nitrate may retain beneficial properties of alum while avoiding consequential impacts of sulfate loading. Preliminary tests indicate similar  $\text{Al(OH)}_3$  floc formation and effects, and slightly higher floc specific gravity (Kortmann, unpubl. data). Unlike sulfate, the nitrate load is not conserved by the ecosystem. Rather it favors nonbluegreen species and ultimately leaves the ecosystem as nitrogen gas via dissimilatory nitrate reduction.

Use of ferric nitrate could increase P-binding capacity, increase Fe:P ratio at overturn, and have a greater effect on net sedimentation of newly imported P than an alum application. Injection of ferrous chloride through hypolimnetic aerators is an example of an integrated aeration-nutrient inactivation approach (Walker et al. 1989). At Lake Waramaug, water from the hypolimnion is withdrawn, put through several holding cells, and returned to the metalimnetic-hypolimnetic interface (Kortmann et al. 1991). Ferrous iron generated by anaerobic respiration in the hypolimnion is used (after its reoxidation to ferric iron) to precipitate P. In the treatment system at Lake Waramaug, ammonia nitrogen is oxidized to nitrate, which serves as an alternate TEA to stabilize the (anoxic) oxidation-reduction potential. These anaerobic aeration treatments have resulted in significant reductions in TP and  $\text{NH}_4^+$ -N concentrations (up to 65 and 69%, respectively) and reductions in Cyanobacteria bloom frequency and intensity (Kortmann et al. 1991). The use of lake-generated iron as a P-precipitation agent during layer aeration is currently being tested. The ferric

phosphate precipitate would be subject to subsequent redox reactions. Hence, it may be desirable to use an Al-based compound (e.g., aluminum nitrate) to inactivate sediment P release, while using a ferric compound (e.g., ferric nitrate) to increase long-term water column P sedimentation rate. Use of iron and nitrate based materials for nutrient inactivation increases respiratory capacity via desirable alternate TEAs. Alum surrogate materials which may be useful for nutrient inactivation include aluminosilicates, ferric nitrate, ferric oxides, aluminum nitrate, and calcium hydroxide or calcium carbonate (in hard water lakes). Further research is warranted.

### Aeration

Oxygen loss is a consequence of autotrophication (aka eutrophication) due to increased respiratory demand for TEAs. Oxygen supply is often exhausted in eutrophic lakes, resulting in anoxia, sediment-P release, habitat suitability decline, and accumulation of anaerobic respiration products and ammonia (reactants in chemosynthesis). Aeration treats those consequences by increasing the rate of dissolved oxygen input (hence increasing aerobic respiratory capacity). Aeration affects almost all aspects of the lake: nutrient cycling, heat distribution, bacteria, phytoplankton, zooplankton, zoobenthos, and fish. Aeration can control eutrophication consequences, the expression of trophic state (i.e., trophic quality).

Three basic aeration approaches are available: artificial circulation, hypolimnetic aeration, and layer aeration. Artificial circulation increases dissolved oxygen (DO) input by preventing (or destroying) thermal stratification. It tends to favor green algal species over bluegreens, and aerobic fauna. Artificial circulation is most useful in lakes which are not nutrient limited (Cooke et al. 1986).

Hypolimnetic aeration has been used in many deep lakes to overcome anoxia, improve coldwater habitat, and control sediment P release. Sizing of airflow has been a historic difficulty. Nearly every hypolimnetic aeration case exhibited mean hypolimnetic DO concentrations below  $2 \text{ mg l}^{-1}$  at some time during stratification (McQueen and Lean 1986, McQueen et al. 1986). This has been attributed to a variety of factors including aerator induced BOD and overestimated solute phase transfer efficiency. DIC increment rate demonstrated a threefold increase in respiration during one application (Kortmann et al. 1988). Quantification of respiratory oxygen demand using carbon dioxide increment and respiratory quotient (RQ) improved reliability of sizing methods (Kortmann et al. 1988, 1993). More recently the importance of allochthonous loading and nonrespiratory contributions to the total oxygen demand have been demonstrated (Kortmann et al. 1993).

A depth-discrete artificial circulation technique (layer aeration) has been developed which utilizes

photosynthetic oxygen production (noncyclic photophosphorylation) to offset demand in deeper, tropholytic waters. This method maintains a thermally stratified depth profile while reducing internal P loading and restoring coldwater fishery and zooplankton refuge habitats (Kortmann et al. 1993). Sizing of hypolimnetic or layer aeration methods involves identification of both respiratory and nonrespiratory oxygen demands (of both autochthonous and allochthonous origin; Kortmann et al. 1993).

### *Biomanipulation (Trophic Level Manipulation)*

Manipulation of biomass at a particular trophic level to induce a change in the expression of trophic state (trophic quality, control of eutrophication consequences, nutrient influx not reduced) is an emerging technology with substantial promise for the future of lake management. The principle of trophic level manipulation is that increasing the biomass of a higher trophic level (recipient) induces an increased rate of energy transfer to it from the next lower level and hence lower biomass of that lower (donor) level. Trophic level manipulation alters biomass and secondary productivity rates. The most direct example is introduction of grazer biomass (e.g., grass carp) which consumes macrophyte biomass more rapidly. Hence, macrophyte biomass is reduced (but not necessarily macrophyte productivity). Nonpredatory losses from grass carp to detritus is accelerated, and temporal production is altered. Nutrient cycling may intensify, favoring pelagic phytoplanktonic autotrophy over littoral autotrophy. Another approach relies on the response of several trophic levels. Adding piscivore biomass decreases zooplanktivore biomass, which increases zooplankton biomass (via reduced predation), which decreases phytoplankton biomass (via increased grazing). This concept of cascading trophic interactions is supported by substantial literature (Carlson and Schoenberg 1983, Carpenter et al. 1985). In practice, the approach seems to produce inconsistent results. Perhaps this inconsistency may be due, in part, to lack of considering allotrophy as well as autotrophy, and detrital dynamics of the food web. Indeed, the conceptual model of trophic structure in a typical lake (Carpenter et al. 1985) omitted detrital components entirely.

Trophic level manipulation (as discussed so far) relies on recipient control; the receiving level controls donor level (e.g., grazers control phytoplankton). However, in nature, donor control usually prevails (resource control). Furthermore, the trophic dynamic structure (producer-grazer-predator-predator) operates at a relatively low efficiency. Only 10-15% of available energy from the donor trophic level is incorporated into biomass of the recipient level. The balance is not lost from the ecosystem.

Energy (in organic matter) that is not assimilated by the recipient trophic level goes into the detrital dynamic structure via nonpredatory losses. The detrital dynamic structure makes this energy available to the food web through heterotrophic bacteria, chemolithotrophic bacteria, etc. This is not a minor component of the ecosystem. Indeed, bactivory can account for most trophic energy transfer at the primary consumer level (e.g., 50-80% of areal grazing, and up to 98% of grazing at some depths (Sanders et al. 1989). Ecosystem trophic efficiency is actually closer to 60%. Increasing the biomass of higher trophic levels will tend to increase the rate at which nonpredatory losses enter the detrital dynamic structure, and will tend to accelerate production of bacteria. In turn, it supports greater bactivory by flagellates, ciliates, rotifers, and some cladocerans, and supports greater biomass at higher levels. It also increases competition between bacteria (heterotroph and chemolithotroph) and phytoplankton (photolithotroph) for available resources such as phosphorus (required by both bacteria and phytoplankton for their biochemical machinery).

Lake ecosystem food webs involve integrated trophic and detrital dynamic structures, which interact via nonpredatory losses and bactivory. Biomanipulation via piscivore stocking may tend to accelerate delivery of nonpredatory losses to the detrital structure. If detrital biomass (or the rate of secondary production by detritus) increases, the next higher trophic level (bactivore) may increase by a donor controlled mechanism. Also, detrital heterotrophs require nutrients (e.g., TP) for respiration of organic matter (autochthonous and allochthonous). Hence, donor control mechanisms are also implicated in biomanipulation, at all levels.

Perhaps these energetic mechanisms account for some of the (apparently) variable success of biomanipulation. The relative proportions of trophic and detrital energy exchanges are likely driven by the proportions of allochthonous vs. autochthonous organic carbon. Hence, an ecosystem organism may express a more allotrophic (heterotrophic) or autotrophic nature depending on areal lake:paralimnion ratios and the character of the watershed. Perhaps trophic manipulation by piscivore stocking is more successful in lakes where autotrophy strongly dominates allotrophy. Perhaps trophic top-loading accelerates nonpredatory losses and secondary productivity by detritus too much in some lake ecosystems (e.g., where TEA availability limits respiration). Further biomanipulation research is needed, which measures biomass changes, and exchange rates, at all trophic levels (including the detrital dynamic structure).

### *Mechanical Harvesting*

Removal of macrophyte biomass by mechanical harvesting also controls the consequences of eutro-

phication (increased littoral autotrophy). In a sense it is analogous to adding a grazer (man) to reduce macrophyte biomass. However, it removes a crop entirely from the ecosystem, without the nonpredatory losses associated with increased biological grazing. Mechanical harvesting removes autochthonous organic carbon, and can reduce subsequent consequences (e.g., respiratory demand). Nutrient export is also increased, albeit by a relatively small amount when compared to the primary nutrient source (sediment P).

### *Other Consequence Controls*

Sediment oxidation (Ripl 1976) is essentially an enhancement of dissimilatory nitrate reduction. It provides a desirable alternate TEA (nitrate) while modifying ambient conditions (pH) to favor facultative anaerobes which perform denitrification. The principles were described previously in discussions regarding nutrient inactivation by alum surrogates and the conversion of lake-generated ammonia to enhance denitrification. Additional consequence control methods include sediment covers for macrophyte control (physically isolating sediments), seasonal drawdown (susceptible population control), rotovation, etc.

## Treatment of Symptoms

We categorize methods which directly kill nuisance target organisms as treatments of symptoms (aquatic algicides and pesticides). They do not reduce nutrient influx or increase nutrient export. These methods do not manage the consequences of eutrophication by controlling trophic quality. Indeed, they often have additional adverse lake ecosystem consequences. Symptom treatments are used after a problem exists (e.g., Cyanobacteria bloom); they do not prevent problem conditions from developing (as do eutrophication controls and consequence controls).

Copper sulfate is a very commonly used algicide. Its dosage rate is regulated on the basis of its toxicity to higher organisms (e.g., fish). Lake community effects are generally not considered. The LC50 (50% mortality dose) for phytoplankton is 0.10-1.50 mg Cu l<sup>-1</sup>, zooplanktonic Crustacea 0.06-0.09 mg Cu l<sup>-1</sup>, zooplanktonic Rotifera 1.1-1.7 mg Cu l<sup>-1</sup>, and Salmonids 0.01-0.10 mg Cu l<sup>-1</sup>, (Demayo et al. 1982). When a copper sulfate treatment effectively kills a phytoplankton population it will undoubtedly also kill nontarget organisms.

Trophic level exchanges are again involved, but here these interactions include the immediate delivery of a large biomass as nonpredatory losses, an abrupt increase in detrital respiratory demand, severely reduced grazing, etc. Repeated use of algicide becomes necessary because trophic level control is perturbed.

Repeated copper sulfate treatments also load the system with sulfur, shifting redox systems to less desirable alternate TEAs (hydrogen sulfide production) with subsequent toxicity impacts and loss of iron (P-binding capacity).

Adverse impacts of algicide and herbicide use can be reduced by temporal application (e.g., early herbicide application before biomass has accumulated), focused application (e.g., depth-discrete algicide application during early stages of bloom formation), etc. However, when possible, controlling eutrophication consequences should be preferred over treating nuisance organisms.

## General Discussion—Summary

Lakes are complex ecosystems in which all living organisms collectively interact with physical and chemical processes of the environment. There are fundamental differences between autotrophication, allotrophication, and lake succession; differences important to selection of effective restoration methods. The process of eutrophication (synonymous with autotrophication as used here) has frequently been erroneously equated with lake succession, allotrophication, etc., and also has the connotation of pollution. In this introduction to lake ecosystem energetics we have distinguished between autotrophication and allotrophication, biomass and productivity, detrital and trophic dynamic structures. We have examined interactions between the flow of energy and matter, and how these can affect trophic quantity and quality. Finally, we discussed several energetic relationships of lake management techniques.

Fig. 11 presents a simplified flux diagram illustrating elements of the eutrophication process and consequences (modified after Mortimer 1969). The most direct effects of lake management methods are superimposed.

- Watershed management, dilution, flushing, and hypolimnetic withdrawal are methods for the control of eutrophication. These methods either reduce nutrient influx directly, or reduce nutrient influx relative to hydrology, flushing rate, and morphometry.
- Harvesting removes biomass of primary producers without nonpredatory loss effects.
- Biomanipulation manipulates biomass of selected trophic levels. Productivity can remain high even though biomass is low (if grazing rate is high). Biomanipulation tends to increase secondary production and the delivery of NPLs to detritus.
- Aeration increases oxygen influx, supporting greater secondary production and breakdown

- of increased organic production. Aeration increases aerobic respiratory capacity.
- Nutrient inactivation, sediment oxidation, aeration, and anaerobic aeration (i.e., Eh maintenance) all reduce internal nutrient reflux.
  - Algicides tend to decrease secondary production, increase the breakdown of increased organic production and increase internal nutrient reflux.
  - Sediment removal tends to be a method for control of lake succession, not eutrophication.

Lake ecosystem energetics is involved in all lake restoration methods. Life is energy.

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