Lakes as Ecosystems

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Introduction of the Ecosystem Concept

Scientific studies of lakes began as early as the seventeenth century, but at first were descriptive rather than analytical. Toward the end of the nineteenth century, measurements and observations on lakes became more directed. For example, the thermal layering of lakes was attributed to specific physical causes, and such phenomena as the movement of plankton in the water column were the subject of hypotheses that were tested with specific kinds of data.

Comprehensive studies of lakes began with the work of Alphonse Forel (1841–1912) on Lac Léman (Lake Geneva), Switzerland, as well as other Swiss lakes. In a three-volume monograph (*Le Léman*: 1892, 1895, 1904), Forel presented data on a wide variety of subjects including sediments and bottom-dwelling organisms, fishes and fisheries, water movement, transparency and color, temperature, and others. Thus Forel, who introduced the term 'limnology' (originally the study of lakes, but later expanded to include other inland waters), demonstrated the holistic approach for understanding a lake as an environmental entity, but without application of an explicit ecosystem concept.

The conceptual basis for studying lakes as ecosystems was first clearly given by Stephen Forbes (1844–1930; Figure 1) through a short essay, *The Lake as a Microcosm* (1887). Forbes was professor of biology at the University of Illinois in Champaign, IL, USA, and director of the Illinois Natural History Laboratory (subsequently the Illinois Natural History Survey), which was charged with describing and analyzing the flora and fauna of Illinois. Forbes realized that it was not possible to achieve a full understanding of a lake or, by implication, of any other environmental system such as a stream or forest, simply from knowledge of the resident species. Forbes proposed that the species in a particular environment, when interacting with each other and with the nonliving components of the environment, show collective (system) properties. The microcosm that Forbes described today would be called an ecosystem, although this term did not come into use until 48 years later through the work of the British botanist A. G. Tansley. By current usage, an ecosystem is any portion of the Earth's surface that shows strong and constant interactions among its resident organisms and between these organisms and the abotic environment.

Forbes not only described accurately the modern ecosystem concept, but also identified ways in which critical properties of ecosystems could be measured and analyzed. He named four common properties of lakes, each of which provides a cornerstone for the study of lakes and other ecosystems, as shown in Table 1. Although Forbes's concepts have been renamed, they are easily visible in the modern study of lakes as ecosystems.

Although the essay by Forbes now is considered a classic in limnology and in ecology generally, it caused no immediate change in the practices of limnologists or ecologists. Like many important discoveries in science, it was a seed that required considerable time to germinate.

In studies of Cedar Bog Lake, Minnesota, for his Ph.D. at the University of Minnesota, Raymond Lindeman (1915–1942; Figure 2) gave limnologists the clearest early modern example of the study of lakes as ecosystems. Rather than focusing on a particular type of organism or group of organisms, which would have been quite typical for his era, Lindeman decided that he would attempt to analyze all of the feeding relationships ('trophic' relationships) among organisms in Cedar Bog Lake. Thus, his Ph.D. work extended from algae and aquatic vascular plants to herbivorous invertebrates, and then to carnivores, and conceptually even to bacteria, although there were no methods for quantifying bacterial abundance at that time. Lindeman's descriptions of feeding relationships were voluminous but straightforward to write up and publish, but he sought some more general conclusions for which he needed a new concept.

Lindeman took a postdoctoral position with G. Evelyn Hutchinson at Yale University in 1942. Hutchinson had become a limnologist of note through his quantitatively oriented studies of plankton and biogeochemical processes in the small kettle lakes near New Haven. He would in subsequent decades become the world's most influential limnologist, and part of his reputation grew out of his contributions to the field of biogeochemistry, an important tool of ecosystem science.

Hutchinson made suggestions that no doubt were critical to Lindeman's groundbreaking paper, *The Trophic Dynamic Aspect of Ecology* (1942, published in the journal *Ecology*), which now is recognized as a landmark in limnology and in ecology generally.

Lindeman proposed a way of converting the tremendous mass of highly specific information for Cedar Bog Lake into a format that would allow comparisons with any other lake or even with other kinds of ecosystems. Building on the work of the German limnologist August Thienemann and the British ecologist Charles Elton, Lindeman organized the feeding relationships as a feeding hierarchy within which each kind of organism was assigned to a specific feeding level (trophic level). He then proposed that the feeding relationship represented by any given link in the food web be quantified as an energy flow. Thus, the total energy flow from level 1 (plants) to level 2 (herbivores) could be quantified as the summation of energy flows between all pairs of plants and herbivores; a similar estimate could be made for all other pairs of trophic levels. In this way, the flow of energy across the levels of the food web could be expressed in quantitative terms.

The first important conclusion from Lindeman's energy-based approach was that each transfer of energy between trophic levels is governed by the second law of thermodynamics, which requires that significant energy loss must occur each time energy is transferred. Thus, Lindeman demonstrated why food webs have relatively few trophic levels: progressive dissipation of energy as it passes through the food web from the bottom (plants) to the upper levels (upper-level carnivores) ultimately provides insufficient energy for expansion of the food web to further levels. Also, analysis of a food web in this way sets the stage for calculating efficiencies of energy transfer, comparison of efficiencies across different ecosystem types, and the identification and analysis of bottlenecks restricting the flow of energy within the food web.

The contributions of G. Evelyn Hutchinson in the 1940s on the biogeochemistry of carbon in lakes also must be counted as landmarks in the development of ecosystem science. Even so, ecosystem science was scarcely represented in the research agenda of ecologists or in the academic curriculum as late as 1950. Penetration of the ecosystem thinking into research, teaching, and public awareness occurred first through the publication of a textbook, *Fundamentals of Ecology* (1953), written by Eugene P. Odum, and especially through the second edition of the same book (1959), written by E. P. Odum and Howard T. Odum. The Odums visualized ecology as best viewed from the top down, with ecosystems as a point of departure and studies of ecosystem components as infrastructure for the understanding of ecosystems.

The ecosystem perspective has not displaced the more specialized branches of ecology that deal with particular kinds of organisms or specific kinds of physical phenomena, such as studies of water movement, optics, or heat exchange. Rather, ecosystem science has had a unifying effect on studies of ecosystem components (Figure 3). Study of a specific ecosystem component produces not only a better understanding of that component, but also a better understanding of the ecosystem, which is a final objective for the science of an ecosystem type, such as lakes.

Figure 1 Stephen A. Forbes. Reproduced from the Illinois Natural History Survey website, with permission from the Illinois Natural History Survey.

Table 1 Four key properties of ecosystems identified by S. A. Forbes, along with their modern nomenclatural counterparts and some examples

| Forbes concept	Modern nomenclature	Modern studies
Web of interactions	Food-web dynamics	Food-web complexity and efficiency
Building up and breaking down of organic matter	Ecosystem metabolism	Total ecosystem photosynthesis and respiration
Circulation of matter	Biogeochemistry	Dynamics and cycling of carbon, nitrogen, and phosphorus
Distribution of organisms along gradients	Community organization	Vertical and horizontal patterns in the distribution of fishes, invertebrates, and algae
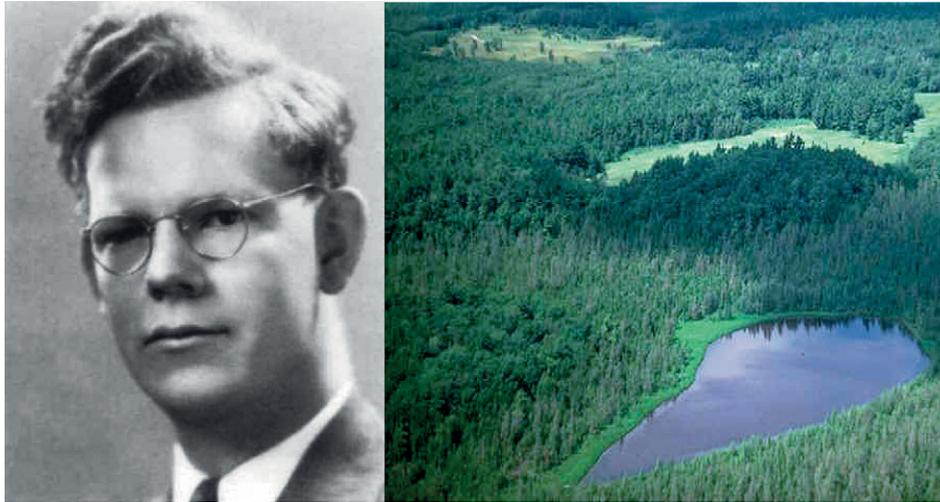
Figure 2 R. L. Lindeman and his famous study site, Cedar Bog Lake, MN. Reproduced from People of Cedar Creek website, with permission from Cedar Creek Natural History Area.
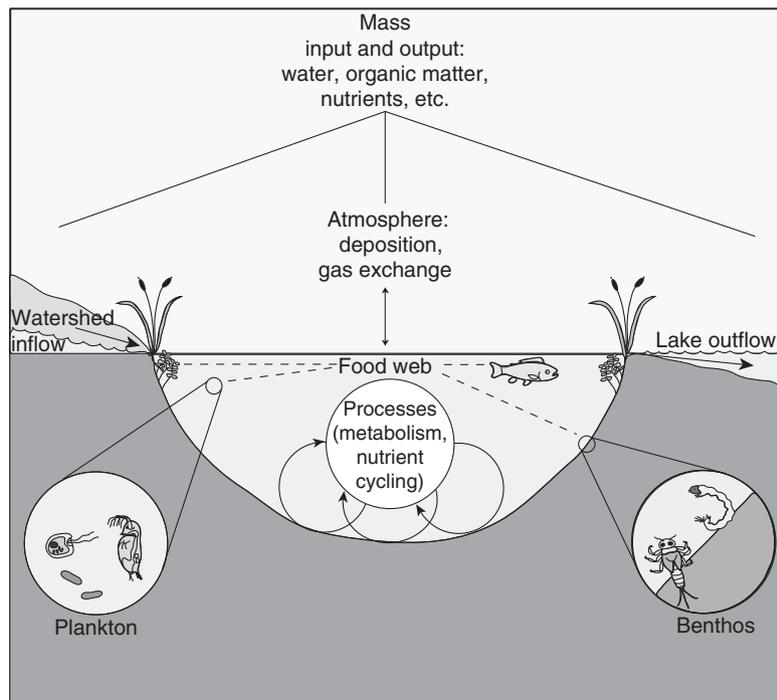

Figure 3 Ecosystem diagram of a lake.

Metabolism in Lakes

The dominant anabolic component of metabolism in lakes is photosynthesis based on carbon dioxide and water plus solar irradiance as an energy source. The dominant catabolic component is aerobic respiration based on the oxidation of organic matter with oxygen as an electron acceptor. Conversion of solar energy to stored chemical energy in the form of biomass seldom reaches 1% efficiency in lakes because of losses inherent in the wavelengths that can be intercepted by photosynthetic pigments, inefficiency in the interception process, and thermodynamic losses in the conversions leading to the production of biomass. Respiration also involves thermodynamic losses. Therefore, the solar energy source greatly exceeds photosynthetic output, and cellular capture of the

energy released from organic matter by respiration greatly exceeds the energy stored in the organic matter.

Aerobic photosynthesis is characteristic of the aquatic vascular plants, attached algae, and phytoplankton of lakes and is universal wherever light and oxygen are present. Aerobic respiration is characteristic of aerobic autotrophs as well as consumers and most bacteria; it occurs wherever oxygen is present (Table 2). Other categories of metabolism occur under either of two more restrictive conditions: (1) where light penetrates into an anaerobic zone, and (2) where there is an interface or mixing between oxidizing and reducing conditions, as is common near a sediment–water interface.

A study of whole-ecosystem metabolism would require consideration of all of the metabolic categories listed in Table 2. The dominance of aerobic photosynthesis and aerobic respiration, however, often allows ecosystem studies to focus on these two metabolic components. In open water, photosynthesis and respiration are often measured with a vertical series of paired transparent and darkened incubation bottles filled with lake water; rate of decline of oxygen in the dark bottles indicates respiration rate, and rate increase of oxygen in the transparent bottle indicates net photosynthesis. In unproductive lakes, uptake of ^{14}C-labeled CO_2 can be used as an even more sensitive indicator of photosynthesis. Where macrophytes or attached algae are important, as is often the case in small lakes, separate measurements must be made of their photosynthesis, typically by the use of enclosures. The metabolic rates of microbes in deepwater sediments can be inferred from the rate of oxygen loss from the hypolimnion of a stratified lake, or can be measured with enclosures.

Annual rate of photosynthesis and respiration per unit area (typically given as mg C m^{-2} year^{-1}) is the most commonly used metabolic statistic for lakes. A complete metabolic accounting would also include processing of organic matter entering a lake from the surrounding terrestrial environment, primarily through stream flow.

Total annual net production of autotrophs (production in excess of respiration) is a measure of the capacity for a lake to generate biomass at higher trophic levels (Figure 4).

Also, the time-course of production, which shows seasonal and nonseasonal variation, is often a useful point of departure for the analysis of mechanisms that control biotic functions in a lake. Factors that may suppress production include deep mixing of the water column, exhaustion of key nutrients, grazing, and hydraulic removal of biomass.

Photosynthesis and respiration often respond differently to a specific physical or chemical change.

Food-Web Analysis

Modern food-web analysis follows the example given by Lindeman. The sophistication of the analysis is much greater today than it was in 1942, however, and the uses of food-web analysis have diversified as well.

At the base of the food web is organic matter generated within a lake or coming to a lake from its watershed and atmosphere above (Figure 5). All of these sources of organic matter can be quantified, as explained in the preceding section, but require the application of several methods and must take into account both spatial and temporal variability in the synthesis or transport of organic matter.

Quantification of linkages in the food web begins with feeding relationships between autotrophs (primary producers) and herbivores (primary consumers). Analysis of gut contents is one method for establishing the linkage between a specific kind of consumer and one or more plant foods. A linkage

Table 2 Summary of metabolic processes in lake ecosystems

| Metabolic process	Energy source	Capabilities			Occurrence conditions in lakes
		Eukaryotic plants	Cyanobacteria	Other bacteria	
Aerobic photosynthesis	Solar	Yes	Yes	No	Universal, photic, oxic
Anaerobic photosynthesis	Solar	No	No	Specialists	Occasional, photic, anoxic
Aerobic chemosynthesis	Inorganic oxidation	No	No	Specialists	Common, oxic/anoxic interfaces
Aerobic respiration	Organic oxidation	Yes	Yes	Yes	Universal, oxic
Anaerobic respiration	Inorganic or organic reduction	No	No	Yes	Common, oxic/anoxic interfaces
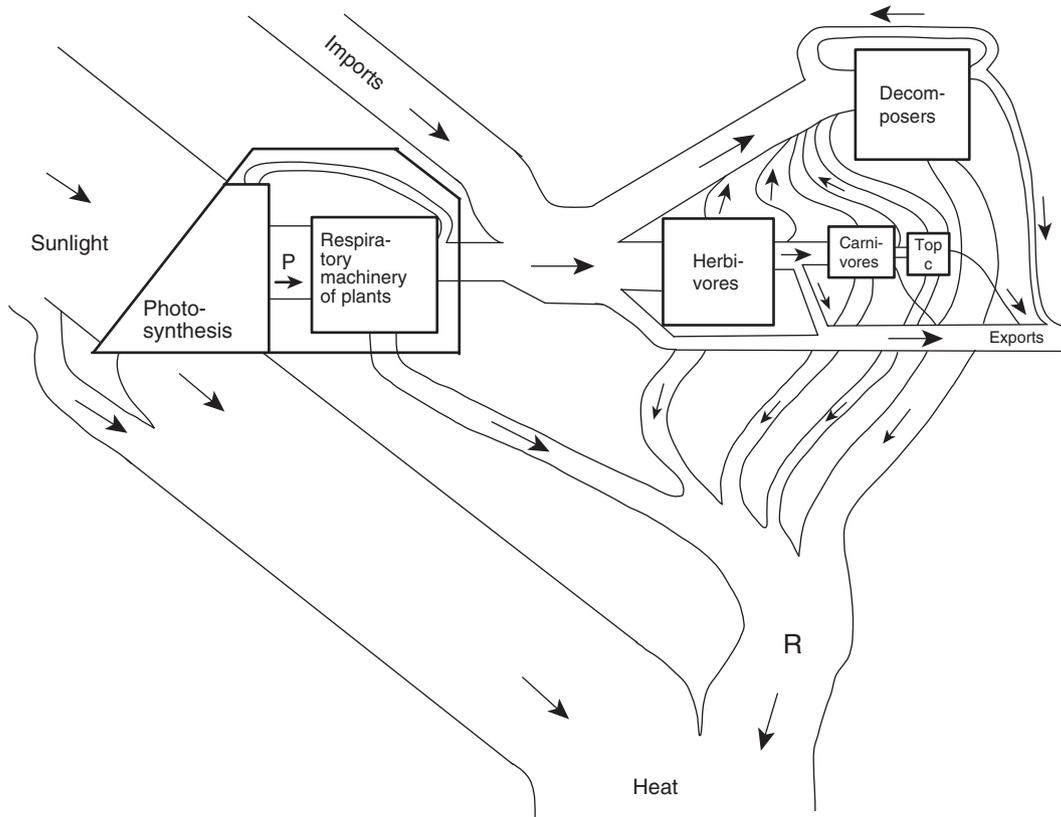
Figure 4 Example of an early metabolic (energy-flow) diagram for an aquatic ecosystem. Reproduced from Odum H T (1956) *Limnology and Oceanography* 1: 102–118, with permission from the American Society of Limnology and Oceanography.

drawn in this way has two disadvantages, however: (1) it is not quantitative because food items often cannot be identified fully, and (2) it is subject to errors of interpretation caused by the ingestion of foods that are not assimilated or only partially assimilated through the gut wall. The first problem can be overcome either by the use of feeding experiments or by the quantification of growth rate of the consumer, with some empirically-based assumptions about the growth efficiency of the consumer. The second problem can be resolved by experimental use of tissue labels (typically isotopes) or, more efficiently, by the use of stable isotopes as passive tracers (i.e., relying on the natural abundance of stable isotopes to infer food sources). Because primary producers of different categories may differ substantially in their concentration of the stable carbon isotope ^{13}C, analysis of ^{13}C content of protoplasm from the consumer may allow a quantitative estimation of the relative importance of several possible foods contributing to the synthesis of biomass by the consumer.

Above the level of primary consumers are carnivores, which may be secondary, tertiary, or even quaternary consumers, depending on their food source.

Measurements of growth rate, along with gut-content analysis and use of passive or active tracers, can be applied to carnivores just as they are to herbivores. Within the carnivore trophic levels, however, the assignment of consumers to a specific trophic level may be difficult because carnivores often consume foods belonging to more than one trophic level. The stable nitrogen isotope ^{15}N is useful in assigning a species to a fractional position on the food web because ^{15}N shows increasing tissue enrichment from one trophic level to the next.

When completed, a food-web analysis shows the efficiency of energy transfer from one level to the next. Because of the thermodynamic limits on efficiency and the typical observed efficiency, which are a matter of record, a food-web analysis based on energy shows whether particular linkages are unusually weak or strong by comparison with expectations. Such observations in turn lead to hypotheses about mechanisms of control for energy transfer within the food web. For example, modern ecosystem theory includes the concept of 'trophic cascades' involving 'top-down' and 'bottom-up' effects on trophic dynamics, which is easily applicable to lakes. Change in one trophic level
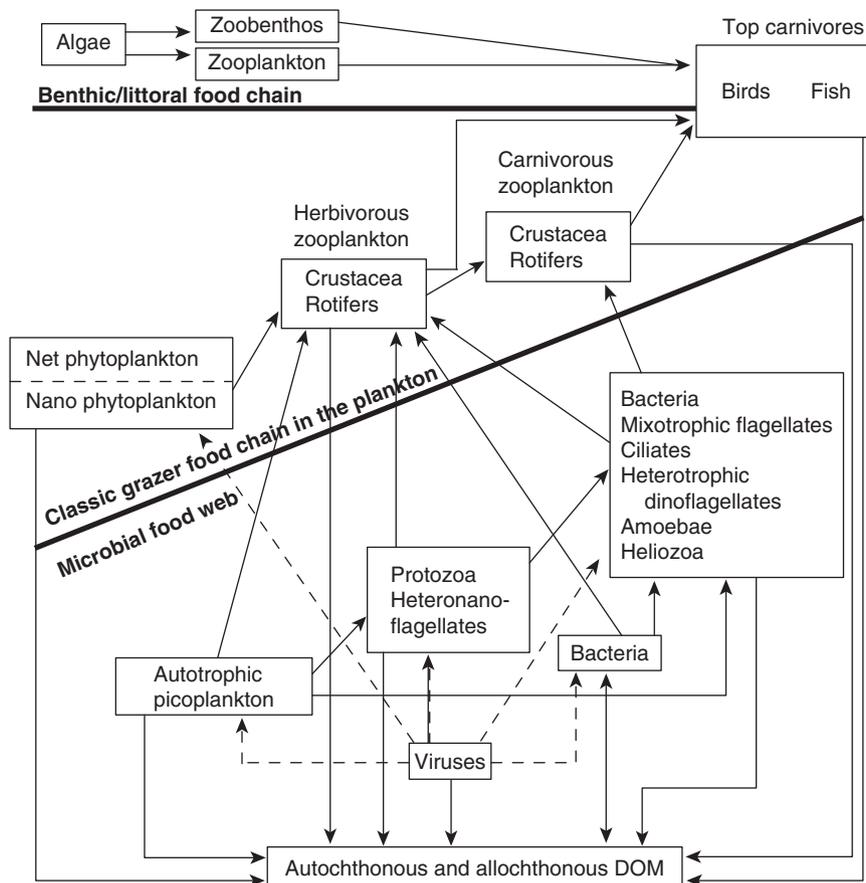
Figure 5 A modern diagrammatic view of a lacustrine food web, including both microbial and nonmicrobial components (from Weisse and Stockner, 1993 as modified by Kalff, 2002; with permission).

may be visible in other trophic level, in the manner of a cascade (**Figure 6**). Top-down effects pass from any trophic level to the next trophic level below. For example, an unusual abundance of algal biomass in a lake could be traced to unusually efficient removal of herbivores through predation at such a rate as to leave algae mostly uneaten (a top-down effect).

Similarly, bottom-up control passes from any trophic level to the next level above. The inability of an oligotrophic (nutrient-poor) lake to grow substantial amounts of plant biomass, e.g., exerts a bottom-up effect on all higher trophic levels by restricting the amount of energy that is available at the base of the food chain.

Trophic-dynamic analysis also leads to other fundamental questions involving the structure of biotic communities. For example, food webs might or might not be more productive or more efficient with a high diversity of herbivores than with strong dominance from a very successful, specific type of herbivore. Such questions bear not only on the analysis of natural ecosystems, but also on ecosystem management.

Biogeochemistry

Many of the functional attributes of lake ecosystems can be analyzed through biogeochemical studies. While metabolism and trophic dynamics are viewed in terms of energy flux, biogeochemistry typically is viewed in terms of mass flux. As with energy analysis, the foundation is basic physics: mass is neither created nor destroyed (under conditions that are compatible with the presence of life). The conservation of mass leads to the mass-balance equation, which can be given as follows for an ecosystem: $I - O = \Delta S$, where I is input of mass of a particular type (carbon or phosphorus, for example), O is output of mass, and ΔS is change in storage of mass. Input and output pathways for lakes are either hydrologic (flow) or atmospheric (deposition or gas exchange). Over the short term, change in storage may involve changes in concentration of mass in the water column, but over the long term, change in storage mostly reflects accumulation of mass in sediments. Any element can be a target for biogeochemical studies, but the most frequently
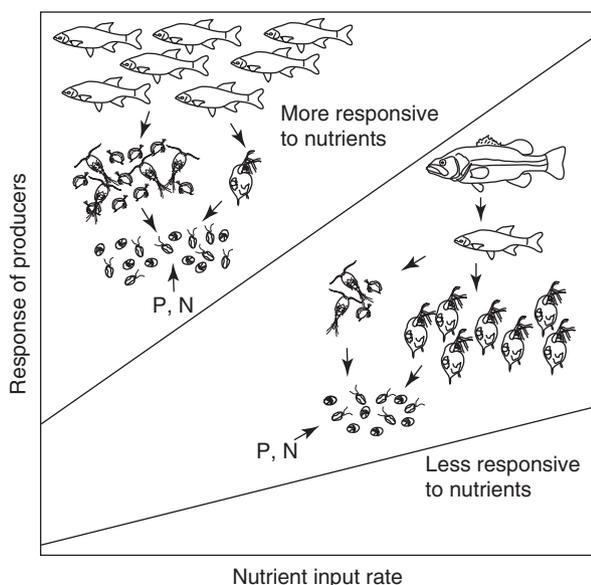
Figure 6 Contrasts in nutrient response for lakes that have strong control by top carnivores (lower line) and lakes that have weak control by top carnivores (upper line). The top carnivore exercises top-down control by suppressing smaller fish that eat large grazing zooplankton. Survival of more large zooplankton holds phytoplankton in check, thus weakening response to plant nutrients (P, N). Reproduced from Carpenter S R (2003) *Regime Shifts in Lake Ecosystems*, with permission from the International Ecology Institute, Oldendorf/Luhe, Germany.

Figure 7 Compartment matrix for analysis of carbon cycling in the water column of a lake.

studied biogeochemical processes in aquatic ecosystems involve carbon, phosphorus, and nitrogen.

The mass-balance equation applies not only to the entire ecosystem, but also to compartments within the ecosystem (Figure 7). For example, carbon in the water column could be partitioned into compartments, each of which would have its own mass-balance equation. Some of these compartments would have a high turnover rate, while others would not. The dynamics of compartments explain restrictions on specific biological processes such as photosynthesis, and account for differences in individual lakes or categories of lakes, such as those that differ greatly in nutrient supply.

Studies of the carbon cycle are ideal complements to studies of lake metabolism and food webs. CO_2, which is the feedstock for photosynthesis, enters aquatic autotrophs either in the form of free CO_2 ($CO_2 + H_2CO_3$) or bicarbonate (HCO_3^-). CO_2 is converted to organic matter by the reduction process of photosynthesis. Either within an autotroph or through consumption of autotroph or other biomass by consumers or decomposers, reduced carbon is reconverted to its oxidized form as CO_2 through aerobic respiration.

Organic carbon resides not only within organisms, but also in water or sediments in dissolved or nonliving particulate form. Dissolved organic carbon derives from the watershed, atmosphere, or organisms within the lake. Watershed contributions to dissolved organic carbon in lakes are composed to a large extent of humic and fulvic acids, which are the byproduct of the degradation of organic matter within soils. Humic and fulvic acids are refractory (resistant to breakdown), although they are slowly decomposed by microbes and can be broken down by ultraviolet light in a water column. Humic and fulvic acids are generally present in concentrations of $1-10 \, \mathrm{mg \, l^{-1}}$ in lakes and, when present at concentrations above $5 \, \mathrm{mg \, l^{-1}}$, generally impart a brown or orange color to the water.

Organic compounds that are released to the water column of lakes by the resident organisms vary greatly in composition. All soluble organic compounds present in organisms can be found in the water column at measurable concentrations. Thus, a careful analysis of lake water would show a wide variety of amino acids, carbohydrates of varying complexity, and other metabolites of organisms. These compounds enter the water column through leakage (excretion), death, or the production of fecal matter. As might be expected, the turnover rate for metabolites is generally high because most of these compounds are labile (easily used), in contrast to humic and fulvic acids.

Particulate organic matter present in a water column may be either living or nonliving. Frequently, these two compartments are physically joined, as all nonliving particulate organic matter in water is colonized by bacteria and, under some conditions, fungi.

Most of the carbon attributable to living organisms is accounted for by phytoplankton and zooplankton; fish and bacteria make smaller contributions in the sense of mass but have important ecosystem effects. Carbon is continually stored in sediments, which accumulate at rates often about 1 mm per year, much of which is organic. As sediments become buried by additional sediments, their decomposition slows because of the lack of oxygen and chemically hostile conditions for active metabolism of bacteria. Thus, while some of the organic matter in sediments is remobilized into the water column, other organic matter in the sediments becomes long-term storage.

A study of mass flux and storage, when viewed in terms of ecosystem compartments and subcompartments, tells a story about the mechanisms by which a lake functions. For example, lakes may differ greatly in the terrestrial contribution to carbon processing and carbon storage, and also may differ greatly in speed of carbon turnover in specific living and nonliving compartments.

The cycling of phosphorus in lakes has been studied intensively, because phosphorus is one of the two elements (nitrogen is the other) most likely to be critically depleted by aquatic autotrophs. Thus, phosphorus at the ecosystem level is commonly viewed as an ecosystem regulator; lakes in which it is abundant (eutrophic lakes) have potential to produce high amounts of plant biomass (phytoplankton, attached algae, or aquatic vascular plants) and have water-quality characteristics that are often viewed as undesirable (low transparency, green color, potential for odor production, and severe loss of oxygen in deep water). In contrast, lakes having low supplies of phosphorus (oligotrophic lakes) may show constant suppression of plant growth through phosphorus scarcity. Such lakes have much lower amounts of carbon in the water, higher transparency, often appear blue, and retain oxygen in deep water consistent with the requirements of fish and other eukaryotes.

Because the phosphorus requirement of plants is only approximately 1% of dry biomass, scarcity of phosphorus can be offset by relatively modest increases in the phosphorus additions to a lake. Addition of 1 kg of phosphorus per unit volume or area, e.g., could easily generate 100 kg of dry mass or 500 kg of wet mass of autotrophs. Thus, mobilization of phosphorus by humans has the potential to change lakes and has done so throughout the world wherever human populations liberate phosphorus through waste disposal, agriculture, and disturbance of soil. For this reason, the study of trophic state (nutrient status) has received more attention than any other ecosystem feature of lakes. The practical application of modeling or analysis of trophic status in lakes arises through the desire to prevent changes in trophic state or to reverse changes in trophic state that have already occurred, which requires ecosystem-level understanding of the lake and particularly of its nutrient budgets.

Lakes may also be limited by low concentrations of the forms of inorganic nitrogen that are readily available to aquatic autotrophs (ammonium, nitrate). In this case, nitrogen limitation rather than phosphorus limitation may control plant growth. In fact, the two types of nutrient limitation may occur sequentially across seasons or across years in a single lake.

Nitrogen cycling in lakes is much more complicated than is phosphorus cycling because nitrogen has a gaseous atmospheric component that phosphorus lacks, and because nitrogen exists in seven stable oxidation states within a lake, which sets the stage for the use of nitrogen as a substrate for oxidation reduction reactions supporting microbial metabolism (**Table 2**). Like phosphorus, nitrogen enters lakes through the watershed and, in small amounts, with precipitation. Unlike phosphorus, nitrogen also enters lakes as a gas by diffusion at the air–water interface in the form of N_2. N_2 is so inert chemically that it cannot be used as a nitrogen source by most organisms. Certain prokaryotes have the ability to use N_2 by converting it to ammonium, which then can be used in organic synthesis, provided that a substantial energy supply is available. This process is called nitrogen fixation, in that it converts the gaseous nitrogen to a solid that is soluble in water (ammonium). The dominant nitrogen fixers in lakes are the cyanobacteria. Not all cyanobacteria fix nitrogen, but certain taxa that have a specialized nitrogen-fixing cell (heterocyst) grow commonly in lakes that show nitrogen depletion.

Nitrogen fixers escape the limitation of growth associated with nitrogen depletion, thereby gaining an advantage over other autotrophs. Thus, lakes that are enriched with phosphorus but showing nitrogen depletion often have nuisance growths of nitrogen-fixing cyanobacteria, which produce all of the expected symptoms of nutrient enrichment, and sometimes also produce toxins. There is currently much interest in predicting and preventing the development of circumstances that lead to large and persistent blooms of nitrogen-fixing cyanobacteria.

Nitrogen is a multiplier element, just as phosphorus is. It constitutes approximately 5% of dry mass in plants. Therefore, when it is added to lakes, provided that phosphorus is added at the same time, it supports a 20-fold multiplication of dry plant biomass.

A detailed documentation of the carbon, nitrogen, and phosphorus cycles for a lake produces an understanding of factors that regulate the metabolic rates of lakes and the accumulation of biomass of various

kinds in lakes. These ecosystem phenomena have numerous practical applications, ranging from interest in biomass production (e.g., fish) to interest in constraining water quality within boundaries that are either natural or that favor human purposes.

Community Organization

As foretold by Forbes, ecosystems have a strong degree of spatial organization involving the arrangement of organisms according to abotic constraints based on factors such as amount of irradiance, concentration of dissolved oxygen, or substrate characteristics. The requirement for irradiance is especially important because it dictates the distribution and growth potential for aquatic autotrophs. Phytoplankton grow strongly only within the euphotic zone, which corresponds approximately to water receiving at least 1% of the solar irradiance available at the water surface. Thus, vigorously growing phytoplanktons often are confined to the upper part of the water column (epilimnion and sometimes metaliminon). The same principle applies to periphyton and rooted aquatic plants, which can occupy substrates only over portions of the sediment that are exposed to at least 1% surface irradiance. The gradient of irradiance is controlled by the transparency of the water.

Spatial organization of animal communities and microbial communities is dictated partly by physical conditions and partly by the distribution of autotrophs. Crustacean zooplankton, e.g., may migrate large distances vertically in the water, hiding in deep water during the daytime but rising to feed within surface waters at night. The zooplankton of the littoral zone differs from that of open water, in that the littoral zone offers food types (periphyton especially) that are not available in open water. Distribution of fishes may be dictated in part by the presence of structure associated with littoral zone. The effect of structure may even be related to life history in that immature or small fish may seek the structure of the littoral zone for shelter from predation.

Because organisms conduct the business of an ecosystem, an understanding of their habitat requirements, reflected as spatial organization, leads to explanations of the total abundances of certain categories of organisms, the failure of certain organisms to fare well in one lake but not in another, and the consequences of habitat disturbances of natural or human origin.

Synthetic Analysis of Ecosystems

Synthetic analysis of ecosystems often involves the statistical study of empirical information, particularly if the objective is to test a particular hypothesis. A quantitative overview of multiple ecosystem functions or of the intricate detail for an ecosystem component typically involves modeling as a supplement to other types of quantitative analysis. When computers first became available, it was anticipated that ecosystem science would ultimately be driven almost entirely by mechanistic models that would predict ecosystem responses to natural or anthropogenic conditions. These expectations were not realized. Ecosystems, like other complex systems such as climate or economics, are moderately predictable from modeling that combines a modest number of well-quantified variables addressed to a specific question, but typically are unpredictable on the basis of large number of variables addressing more general questions. Even so, modeling of numerous variables in an ecosystem context can be useful in setting limits on expected outcomes or showing possible outcomes of multiple interactions that cannot be easily discerned from the study of individual variables. Therefore, modeling is useful in promoting the understanding of ecosystems.

Conclusion

Lakes first inspired the ecosystem concept, and have been a constant source of ideas about ecosystem structure and function. Ecosystem science as applied to lakes, is supported by and is consistent with, other kinds of ecological studies that are directed toward specific organisms, groups of organisms, or specific categories of abiotic phenomena in lakes. The strength of ecosystem science lies in its relevance to the understanding of all subordinate components in ecosystems, and to its often direct connection to human concerns in understanding and managing lakes.

Glossary

Biogeochemistry – Scientific study of the mass flux of any element, compound, or group of compounds within or across the boundaries of an ecosystem or any other spatial component of the environment. Mass flux within an ecosystem is often designated as nutrient cycling or element cycling.

Cycling – A biogeochemical term referring to the movement of elements or compounds within an ecosystem or any other bounded environmental system.

Ecosystem – Any portion of the earth's surface that shows strong and constant interaction among its resident organisms and between those organisms and the abotic environment.

Lake trophic state – Fertility of a lake, as measured either by its concentrations of key plant nutrients (especially phosphorus and nitrogen) or the annual production of plant biomass (aquatic vascular plants and algae). Trophic-state categories include oligotrophic (weakly nourished), mesotrophic (nutrition of intermediate status), and eutrophic (richly nourished).

Mass flux – Movement of mass per unit time, often in ecosystem studies expressed as mass/area/time.

Stable isotope – Any isotope of an element that does not decay spontaneously.

Trophic dynamics – Fluxes of energy or mass caused by feeding relationships, including rates of grazing by herbivores on plant matter, rates of predation by carnivores on other animals, or rates of decomposition of organic matter by microbes.

See also: Carbon, Unifying Currency; Microbial Food Webs; Modeling of Lake Ecosystems; Nitrogen; Phosphorus; Regulators of Biotic Processes in Stream and River Ecosystems; Trophic Dynamics in Aquatic Ecosystems.

Further Reading

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