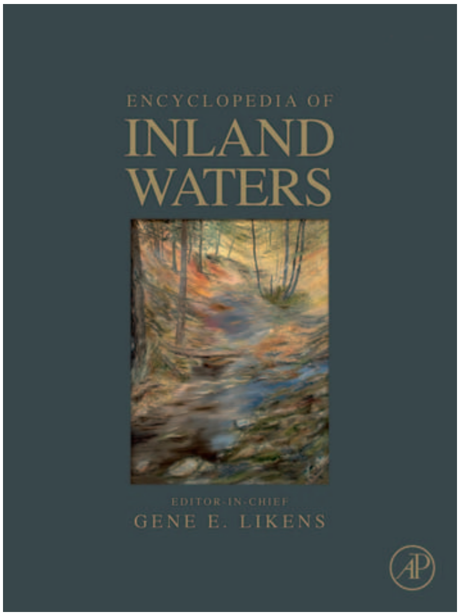

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Carbon, Unifying Currency

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Introduction

A unifying feature of all life on Earth is that it is based on a central element: carbon. The transformation of C from one form to another, either from inorganic to organic as in photosynthesis or from organic to inorganic as in respiratory or decomposition processes, basically defines the actions of living organisms and thus plays a unique and fundamental role. For this reason, carbon is often used as the unifying currency with which to quantify the rates of basic metabolic or ecological processes, from individual cells to whole ecosystems. The transformations of carbon in its various forms also serve to establish relationships among ecosystems, for example linkages between lakes and their surrounding land.

Historically, the examination of the functioning of aquatic ecosystems as a system of interconnected flows of material and/or energy was strongly influenced by the pioneering work of H.T. Odum. It also served as the conceptual framework of the International Biological Programme of the 1960s. This view emerged in contrast to a more species-based prior approach, in which interactions between species are central to the understanding of lake ecological dynamics. Instead, a carbon flow approach generally considers only the major biological compartments (i.e., bacteria, phytoplankton, zooplankton, etc.), without special regard to the identity of the species composing the particular assemblages present. By aggregating individual species into coarse functional groups, the approach subsumes variability among taxa to the benefit of greater generality and predictability.

The aim of this chapter is to describe briefly the functioning of freshwater ecosystems as systems of interconnected carbon pools and carbon flow processes, and to examine the main drivers determining them. While the emphasis is on lakes, the same general principles apply to other types of inland aquatic systems, such as small streams and rivers.

Carbon Pools

As a chemical constituent of living matter, carbon typically represents about half of the mass of organic material of aquatic organisms. Despite this constancy however, carbon pools are very unevenly divided among lake constituents and generally follow an inverse relationship with body size: in any freshwater ecosystem, there is much less carbon contained in fish than in bacteria.

In lake waters, the largest reservoirs of carbon are generally found as dissolved constituents, both organic (DOC) and inorganic (DIC). DOC is a largely uncharacterized amalgam of hundreds of individual compounds with molecular weights varying from simple carbohydrates to highly complex molecules of different aromaticity (cite other chapters, McKnight?). The concentrations of DOC in freshwaters vary enormously from $<0.5\,\mathrm{mg\ C\ l^{-1}}$ in freshwater springs to over $300\,\mathrm{mg\ C\ l^{-1}}$ in hypersaline ponds of endorheic areas. However, for the vast majority of lakes (>85%), DOC concentrations vary within a much narrower range, between 1 and $20\,\mathrm{mg\ C\ l^{-1}}$. Dissolved inorganic carbon concentrations in freshwater lakes varies within a similar range, typically between 0.5 and $15\,\mathrm{mg\ C\ l^{-1}}$. In inland saline waters however, it can reach much higher concentrations.

The amount of carbon contained in the living biomass of water column organisms is generally small when compared with those of the other pools and will depend on the biological productivity of the systems. For the pelagia, particularly in oligotrophic waters, heterotrophic bacteria will comprise the largest living organic carbon pool, followed sequentially by phytoplankton, zooplankton, and fish. For benthic organisms, macrophytes can accumulate large quantities of carbon over the growing season. The approximate turnover time of several taxonomic groups are listed in Table 1.

Although not operating on the same time scale as the dissolved or biological carbon pools, the largest carbon reservoir of lakes is preserved within the accumulated bottom sediments. Depending on the age of the lake ecosystems (a few thousand to several million years), lakes can permanently store enormous quantities of carbon (e.g., L. Tanganyika alone contains several hundred gigatons of carbon in its sediments, i.e., within the same order of magnitude as the biomass of terrestrial plants in the entire biosphere). Even in lakes that were created following the last glaciation, lake sediments often contain as much carbon as the soils of their watersheds.

A Simplified Carbon Cycle for Inland Waters

Carbon enters inland aquatic ecosystems from several pathways and in different forms (Figure 1). It can

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enter from the atmosphere as carbon dioxide by simple diffusion across the air–water interface. There will be a net transfer from the atmosphere to the water when the partial pressure of CO_2 in the water is lower than that of the atmosphere. In general, this occurs only in eutrophic systems where the photosynthetic demand for CO_2 is large. In most oligo and mesotrophic systems, their surface waters tend to be oversaturated with CO_2 with respect to the atmosphere and therefore act as net sources. Other carbon sources entering through the atmosphere are volatile organic carbon compounds (VOCs), such as terpenes and other isoprene derivatives, as well as other organic material scavenged by dust particles. Their biological significance is largely unknown.

The major pathway for carbon to enter lakes is through stream and groundwater inflows as both inorganic (DIC: carbonate and bicarbonate ions plus dissolved CO_2) and organic fractions (particulate (POC) and dissolved (DOC)). In most aquatic systems, bicarbonate (HCO_3^-) and carbonate (CO_3^-) ions are the main source of alkalinity and are generated through weathering reactions of the dissolved CO_2, derived from the decomposition of soil organic matter, with various minerals contained in the parent rock material. Organic carbon inputs in streams largely originates from the incomplete decomposition of soil and terrestrial plant material into soluble compounds (DOC). Over large spatial scales, the amount of DOC exported from catchments to lakes will depend on the productivity of the terrestrial landscape as well as on the local hydrological flow path. Thus, although chemically very different, both the inorganic and organic fractions have ultimately the same origin: terrestrial primary production.

Table 1 Approximate turnover time for different taxonomic groups

Taxonomic group	*Turnover time*
Bacterioplankton	Hours to days
Phytoplankton	Days
Zooplankton	Days to weeks
Benthic invertebrates	Days to weeks
Fish	Months to years

Once it has reached the lake, only a portion of the carbon inputs will undergo transformation before it leaves the system through its outflow. For example, carbonate alkalinity (CO_3^- and HCO_3^- ions) is largely conservative in lakes except in cases where some primary producers (e.g., macrophytes) can use bicarbonate ions as inorganic substrates when dissolved CO_2 is scarce, or when carbonates precipitate as in marl lakes. Organic carbon inputs however have a much different fate. Most (typically 90%) of the organic carbon enters lakes as dissolved, while the particulate remainder is composed mostly of detrital terrestrial plant and soil material. Although the dissolved organic matter can be quite old and therefore suggestive of a high degree of recalcitrance, the conditions prevailing in aquatic systems are more conducive to rapid transformation. Thus, a significant portion of the DOC received by lakes will be transformed in situ by the combined action of photochemical reactions and microbial utilization. Although some of the DOC used by microbes can make its way into bacterial biomass and subsequent assimilation into organisms of higher trophic levels, most of

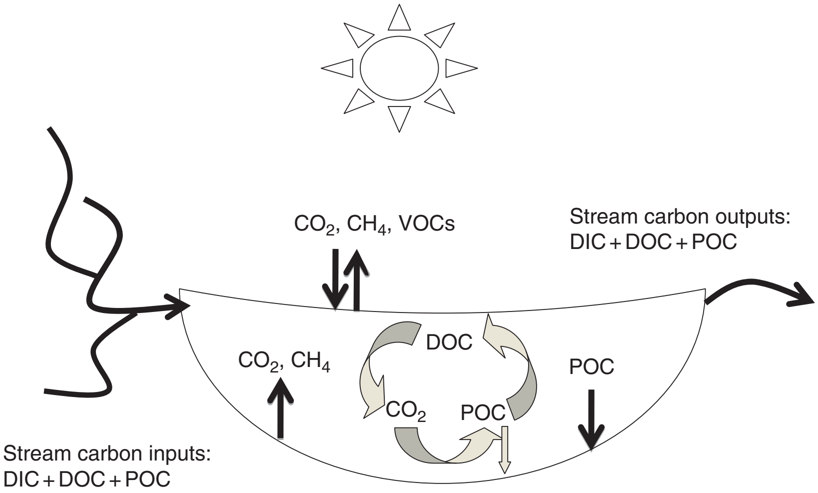

Figure 1 A simplified carbon cycle for inland aquatic ecosystems.

it will simply be respired and released as carbon dioxide. Depending on the direction of the pCO_2 gradient at the air–water interface, this CO_2 will either evade to the atmosphere or be available for photosynthetic assimilation by the phytoplankton and benthic plants. In anaerobic conditions of the sediments or the hypolimnion, organic matter degradation can lead to methanogenesis, thereby increasing the CH_4 partial pressure relative to that of the atmosphere. In many instances, methane can be oxidized to CO_2 before reaching the air–water interface but in strongly anoxic conditions, carbon can evade lakes as methane gas. In general however, methane flux is small (less than 1%) compared with the flux of carbon dioxide.

The photosynthetic assimilation of CO_2 also constitutes a major pathway of carbon transformation in lakes. The stoichiometry of carbon fixation by aquatic photoautotrophs generally follows the empirical reaction equation:

$$106\ CO_2 + 106\ H_2O + 16\ NH_3 + H_3PO_4 \leftrightarrow (CH_2O)_{106}(NH_3)_{16}(H_3PO_4) + 106\ O_2$$

in accordance with the so-called Redfield ratio (C:N:P = 106:16:1), which refers to the average elemental composition of aquatic biomass. The reverse reaction (i.e., to the left) corresponds to aerobic respiration. When oxygen is depleted, such as in sediments or in the hypolimnion of certain lakes, decomposition processes are achieved through alternate reactions, such as sulfate, nitrate, iron, or manganese reduction, as well as through methanogenesis.

In the broadest sense, all biological carbon transformations can be characterized as either a production or a respiration process, both of which apportioned among autotrophs and heterotrophs alike. Depending on the level of aggregation of the aquatic compartments under study, production and respiration processes in aquatic systems can be quantified at any scale: from individual cells to entire ecosystems, or for broad single compartments such as bacteria, phytoplankton, benthic plants, zooplankton, benthos, or fish.

The Predictability of Carbon-Based Aquatic Processes

In aquatic science as in other fields, the utility of a scientific construct is ultimately measured by the degree to which successful predictive theories can be built around it. In this regard, the description of aquatic processes in terms of carbon flow patterns has been remarkably reproducible.

Patterns of Organic Matter Production

Primary production by lake phytoplankton is largely determined by the concentration of its primary limiting nutrient, phosphorus. Except in hypereutrophic systems (total phosphorus concentration >150 μg P l^{-1}) where light can become limiting, the positive relationship between phytoplankton production and phosphorus is approximately proportional, implying that a doubling in phosphorus normally gives rise to a doubling in phytoplankton production. In contrast, benthic primary production is negatively related to phosphorus concentration because the increase in phytoplankton abundance decreases light penetration to the surface of the sediments. In general, the contribution of benthic primary producers to the overall production of the lake ecosystem declines with increasing lake trophic status. Conversely, it can represent most of the lake's productivity, particularly in shallow oligotrophic systems.

While secondary production (that is the production of consumers) is also ultimately regulated by nutrients, several factors modulate the ecological efficiency with which autochthonous carbon production is converted to secondary production. Thus, empirical relationships between secondary production and phosphorus are generally weak. In addition, recent evidence suggest that organic carbon of terrestrial origin, particularly particulate organic carbon, plays some role in sustaining the growth of higher trophic level organisms. Nevertheless, and in spite of this terrestrial load-secondary production shunt, the ecological efficiency between trophic levels is generally low in lakes (<10%). Existing models of invertebrate production in lakes are based largely on temperature and on the biomass of individuals.

Patterns of Organic Matter Oxidation

In lakes that can be considered in a long term equilibrium with the nutrients they receive, carbon accumulation will be in the form of sediment accumulation. Because sedimentary carbon burial is small relative to in situ primary production, it implies that most of it is respired either in the water column or at the sediment surface. Thus, respiration will be largely a function of external organic C input and in-system primary production and of the factors controlling production itself, nutrients. Although autotrophic respiration accounts for a sizeable fraction (about 30%), most of the respiration will be heterotrophic and, within the heterotrophic component, 80% is microbial. On average, benthic respiration represents only about 15% of the total respiration of the 'typical' lake ecosystem but can be much larger in shallow unstratified lakes. However, this proportion is not constant along the trophic gradient, with the contribution of benthic processes lower in more eutrophic systems.

It is now well established that for the water column compartment, respiration generally exceeds gross primary production, a condition termed net heterotrophy. For this situation to be sustained, it requires an external subsidy of organic carbon that is metabolized in situ. This pattern is found mostly in oligotrophic to mesotrophic environments. In eutrophic systems, the autochthonous net primary production is usually sufficient to counterbalance the excess respiration generated by the metabolized exogenous organic carbon.

Glossary

International biological programme – A decade long (1964–1974) large scale program to coordinate ecological studies of the world's major biomes.

Lake Tanganyka – A very large lake in Central Africa; L. Tanganyka is the second largest lake in the world by volume.

Partial pressure – The total gas pressure of a mixture of gases is the sum of the partial pressures exerted by each individual gas.

Autotrophs – An organism that produces all, or nearly all of its complex organic molecules from simple inorganic compounds and energy from either light (photoautotrophs) or by exploiting chemical reactions (chemoautotroph).

Heterotrophs – An organism that requires complex organic molecules from other sources. Consumer organisms are all heterotrophs.

Stoichiometry – The quantitative measure of the ratios of chemical reactants and products in a chemical reaction. Compositional stoichiometry refers to the ratios of elements in a given substance or an organism.

Redfield ratio – The ratios (or compositional stoichiometry) in planktontic marine organisms. Coined in honor of A. Redfield who wrote extensively on this subject.

Autochthonous – Organic matter that was produced in the system of interest. Contrast it to allochthonous, which refers to organic matter that was produced elsewhere (for example in the watershed) and imported into the system of interest.

See also: Alkalinity; Dissolved CO2.

Further Reading

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