

# Chemical Fluxes and Dynamics in River and Stream Ecosystems

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## Introduction

Rivers and streams have in common a unidirectional flow of water passing over a solid substrate. Thus, biogeochemical events that occur at a given location inevitably influence biogeochemistry downstream but have very little influence on biogeochemistry upstream. This is a profound contrast with lake ecosystems, wherein biogeochemical processes at a given location may influence later biogeochemical processes at any other location in the lake.

The unidirectional nature of flow in streams and rivers causes longitudinal chemical and biological gradients in these ecosystems. Examples include progressive biological conversion of coarse particulate matter to fine particulate matter in the downstream direction or accumulation of dissolved solids and nutrients in the downstream direction.

The continual passage of water through a reach of stream or river may suggest that biogeochemical processes occur mainly within a given parcel of water as it travels downstream. This would be incorrect, however, in that a high proportion of biogeochemical activity in streams and rivers is associated with organisms that maintain position within a stream channel or occupy habitats beyond the boundaries of the channel where the water is not moving rapidly. Thus, biogeochemical influences on the moving water of streams and rivers mostly originate from stationary habitats over which the water passes.

From the viewpoint of biogeochemistry, a stream or river consists of four major biogeochemical zones (Figure 1). Flowing waters of the channel are the most obvious zone, but only a small portion of total stream metabolism occurs within this zone.

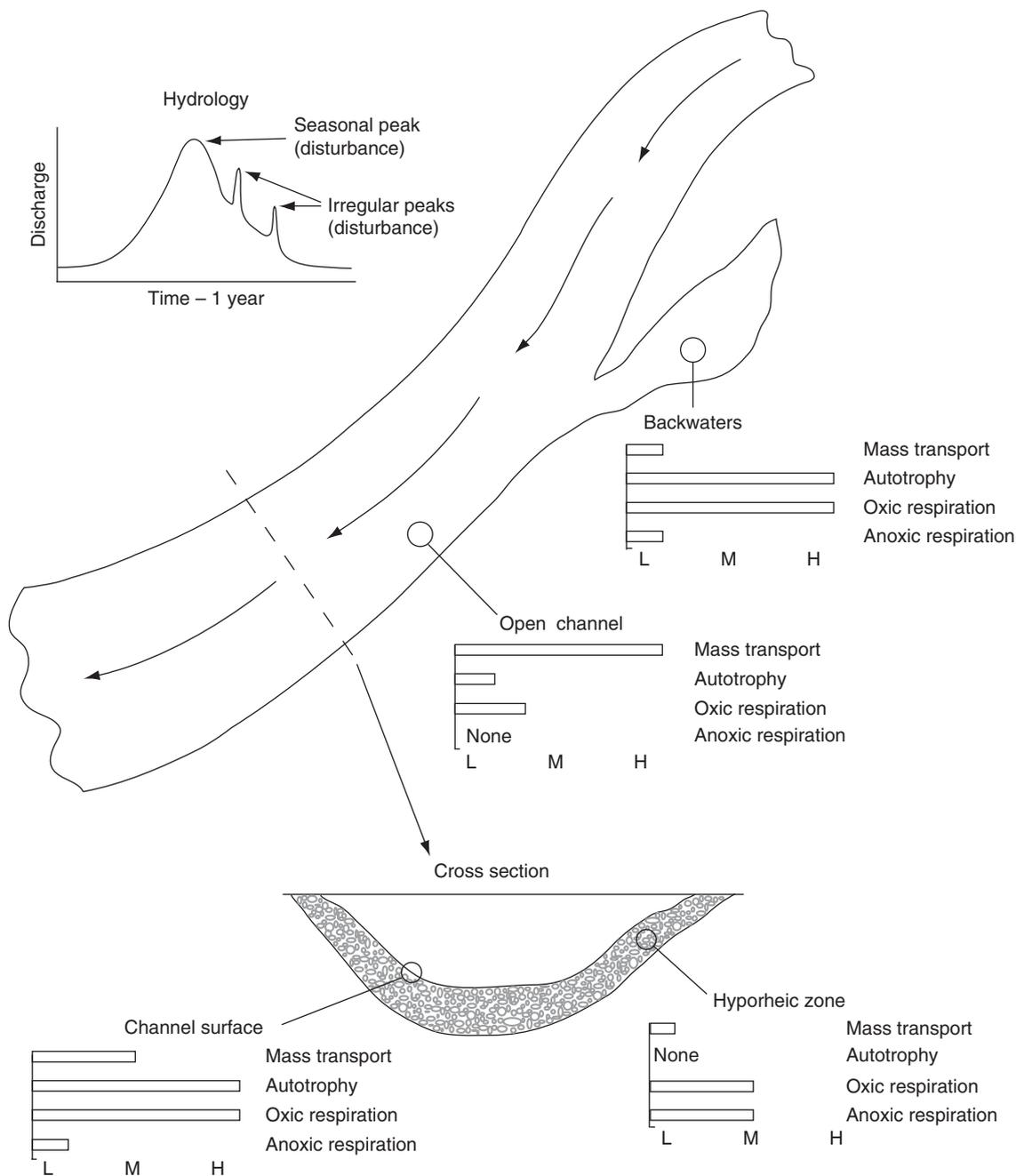
Autotrophs (algae) typically do not prosper when suspended in flowing waters because they are removed so rapidly that they cannot accumulate biomass. Under some circumstances, however, very low velocity allows suspended algae (phytoplankton) to become abundant in streams or rivers. Bacterial decomposers are better suited than algae for growth in flowing water in that they grow with sufficient speed that they can accumulate biomass by degrading some portion of dissolved and particulate organic matter in transit. Even so, the main microbial action in streams occurs on solid surfaces and not in the flowing water of the channel.

A second zone is the channel surface (rock, sand, or clay), along with any stationary organic debris that

it may contain (e.g., tree limbs, leaves). The solid surfaces are coated with bacteria, fungi, protozoans, and attached algae. These small organisms, along with the associated nonliving organic matter and mineral particles deposited onto the surfaces, can be called a 'biofilm.' The biofilm has both an autotrophic component (algae) and heterotrophic component (bacteria, protozoans), and supports a wide diversity of invertebrates that live within or near it. Biofilms of the channel typically are oxic because they are in direct contact with moving water, which efficiently distributes dissolved oxygen entering from the atmosphere, and because they often produce substantial oxygen through photosynthesis. Therefore, biofilms on the channel surface usually promote oxygen-based biogeochemistry and readily support photoautotrophs and heterotrophic eukaryotes (protozoans, invertebrates), which require oxygen. Interior regions of thick biofilms may be anoxic in some cases, however.

Beneath the channel is the hyporheic zone (Figure 1), which consists of all substrate below the channel that has a continuous exchange of water with the overlying channel. The hyporheic zone may be very well defined where the channel sediments are coarse, or may be nonexistent where the channel is lined with bedrock or fine clay. The hyporheic zone can be partly or completely hypoxic or anoxic, even when the channel water is saturated with dissolved oxygen. Because the particles that make up the hyporheic zone impede flow, movement of water through the hyporheic zone is much slower than movement of water in the channel. Furthermore, there is no photosynthesis in the hyporheic zone because it is dark. Therefore, water within the hyporheic zone may lose some or all of its oxygen, and oxygen concentrations often vary spatially within the zone.

The surfaces of particles within the hyporheic zone develop a biofilm, but its composition differs from that of the channel surface biofilm. No photoautotrophs occupy hyporheic biofilms. If oxygen is present, hyporheic biofilms will contain bacteria, protozoans, and fungi; invertebrates will live within or around the biofilm. Where concentrations of oxygen are low or nil, hyporheic biofilms are without eukaryotes; they are made up of the many kinds of bacteria that can metabolize actively in the absence of oxygen. Biogeochemically speaking, production of energy in the absence of oxygen occurs by oxidation involving electron acceptors other than oxygen, through bacterial metabolism.



**Figure 1** The four biogeochemical zones of a stream or river and a graphic indication for each of the magnitude of processes that influence biogeochemistry (L = low, M = moderate, H = high). Seasonal and irregular changes in flow that influence biogeochemistry are represented in the upper left.

Yet another biogeochemical zone of rivers and streams consists of backwaters, which include overflow zones that may be wet only seasonally or may be always wet but change volume markedly according to season. In addition, backwaters typically include irregularities along the sides of the channel that are in contact with waters of the channel but move very slowly or are completely stagnant (Figure 1). Because the movement of water within backwaters is either

slow or negligible most of the time, accumulation of biomass is possible. Therefore, backwaters may have phytoplankton blooms or dense macrophyte populations, develop large populations of small crustaceans and rotifers (zooplankton), and serve as a nursery for species of fish or invertebrates that must be away from strong currents in order to reproduce.

In addition to the linearity of flow and the presence of surprisingly diverse biogeochemical conditions in

streams and rivers, direct influences of the watershed and riparian corridor on biogeochemical processes in streams and rivers must be taken into account. Presence of riparian plants, as well as their type and seasonality, affects processes in streams through organic-matter subsidy (leaves, branches), addition of solid surfaces from wood or leaves falling into the channel, and shading of the water surface. In addition, the entire watershed transmits water containing organic matter and inorganic solids to stream channels through the soil with shallow groundwater and occasionally, during very wet weather, with surface runoff. Thus, the chemical feedstocks of a stream in its upper reaches consist almost entirely of organic matter from terrestrial vascular plants and dissolved or suspended inorganic solids from soils. As water ages longitudinally, the biogeochemical influences of the stream itself may grow substantially through biologically driven chemical transformations, but the chemical imprint of the watershed is always present.

Changes through time in the amount of flow in the channel (hydrographic change) also derive from the watershed and have strong effects on the biogeochemistry of streams and rivers. In almost all streams and rivers, there is a seasonal pattern of discharge that reflects the seasonality of precipitation or snowmelt in the watershed (Figure 1). The seasonal pattern can vary substantially from year to year, and the hydrograph also shows irregularities that reflect non-seasonal precipitation events (Figure 1). High flow, whether seasonal or irregular, moves the bed sediments, thus disturbing biofilms to depths of a few centimeters to as much as 10 or 15 cm, depending on the amount of flow. Surface biofilms that are buried or scoured subsequently are replaced by new biofilms when the flow has declined. Periods of high flow also remove biomass from backwaters and are responsible for most of the annual mass transport of both dissolved and suspended materials through the channel. Only the deeper parts of the hyporheic zone are minimally affected by high flows.

Humans influence the biogeochemistry of streams directly through water pollution and indirectly through manipulation of watersheds or alteration of atmospheric chemistry. Byproducts of human activity may include increased concentrations of nutrients, introduction of toxins, increase or decrease in the organic-matter subsidy reaching streams from watersheds, increase in sediment load, and alteration of the light climate through changes in the riparian zone. Also included under this general heading are physical changes in channels and construction of artificial impoundments, which break the longitudinal continuity of streams and rivers.

## Transport

Mass transport in flowing waters can be given as mass per unit time (e.g.,  $\text{kg d}^{-1}$ ) passing a given cross-section of the stream channel. Mass transport is the product of concentration (e.g.,  $\text{mg L}^{-1}$ ) and volume of flow at any given time (e.g.,  $\text{m}^3 \text{s}^{-1}$ ). Average mass transport for a day, month, or year can be calculated as the time-weighted average of mass transport measured at specific intervals.

Mass transport is often related to watershed area through calculation of specific yield, which is mass transport at a given point on the stream divided by the area of the watershed above that point. Units are mass per unit area per unit time (e.g.,  $\text{mg m}^{-2} \text{year}^{-1}$ ).

Flowing waters of very different size can be compared on a basis that is not directly influenced by size on the basis of specific yield or discharge-weighted mean concentrations. For example, the Amazon River has a huge mass transport of both dissolved and suspended substances, but its discharge-weighted mean concentrations are low, as are its specific yields.

Mass transport, discharge-weighted mean concentrations, and specific yields can be calculated for any substance that is carried by water. Transport involves both particulate matter (solids) and dissolved substances (dissolved solids and dissolved gases). For solids, two forms of transport are recognized: suspended solids (washload) and bedload (bed movement). Transport of solids is erratic because suspended solids may settle to the bed during periods of low discharge and then be mobilized when flows are high. At times of the highest flows, solids that have settled in areas of low velocity are lifted to become part of the suspended solids in transit, and larger particles that are part of the channel surface tumble along the bed, comprising the bedload. Thus, transport of particulate solids is difficult to quantify accurately.

Suspended solids include mineral particles (clay, silt, and sometimes sand) as well as particulate organic matter, most of which is nonliving (detritus). In addition, all of the elemental components of the suspended particles (silicon, iron, phosphorus, and other elements) as well as materials that are adsorbed onto small mineral particles (phosphorus, organic matter) would comprise part of the total transport in any estimate of transport for specific elements. The same would be true of bedload. For example, a comprehensive study of organic carbon transport would take into account particles of detritus, living organisms, organic coatings on suspended silts and clays, and organic matter attached to rocks in the bedload. Under specific circumstances, however, the transport associated with some of these components would be very small and could be ignored.

Transport of dissolved solids is more easily quantified than transport of particulate substances, and often is the dominant mode of transport for a given substance. Major dissolved solids in water often are quantified, as are less abundant dissolved substances of special interest in relation to biotic metabolism (Table 1). Some elements of very low concentration are also quantified in connection with studies of toxicity or nutrition. Dissolved gases also are quantified, but transport calculations must take into account atmospheric exchange, which can be a major influence on the inventory of any gas in transit.

Elements and compounds in solution may be changed in transit by abiotic processes (e.g., flocculation, chelation), but biotic processes are often dominant. For example, phosphorus and nitrogen could be taken up as nutrients by attached algae, dissolved organic carbon could be assimilated and converted to CO<sub>2</sub> by bacterial respiration, and dissolved oxygen could be produced by autotrophs and consumed by all organisms.

It is common to refer to substances that have a low rate of transformation relative to transport rate as

being ‘conservative,’ whereas constituents that have a high transformation rate are designed as ‘labile.’ In reality, no element is perfectly conservative, but some substances, such as calcium, magnesium, or chloride are transformed very slowly, and therefore are controlled mainly by transport processes. Other elements, such as carbon, phosphorus, or nitrogen, are in high demand biotically and may show high rates of transformation under biotic influence in relation to their transport rates (Table 1). For example, calcium (Ca<sup>2+</sup>) concentrations in a stream could remain relatively constant on a given day, whereas concentrations of dissolved oxygen or specific categories of carbon (e.g., organic carbon) might change substantially through time or spatially along the river in response to biological activity. Thus, concentrations of substances in rivers and streams are affected by transformation as well as transport.

Streams and rivers show drastic changes in concentration as discharge varies seasonally or in response to storms (Table 2). Concentrations of dissolved substances may either increase or decrease as discharge increases. Transport of suspended solids and

**Table 1** Biogeochemically important elements in flowing waters

<i>Element</i>	<i>Main dissolved forms</i>	<i>Lability</i>	<i>Comments</i>
Most abundant (>1 mg L <sup>-1</sup> )			
Ca	Ca <sup>2+</sup>	Low	Major salinity component
Mg	Mg <sup>2+</sup>	Low	Major salinity component
Na	Na <sup>+</sup>	Low	Major salinity component
K	K <sup>+</sup>	Low	Major salinity component
Cl	Cl <sup>-</sup>	Low	Major salinity component
C	H <sub>2</sub> CO <sub>3</sub> , HCO <sub>3</sub> <sup>-</sup> , DOC <sup>a</sup>	High	Supports photosynthesis
S	SO <sub>4</sub> <sup>2-</sup> , S <sup>2-</sup>	Moderate	Supports biotic redox conversions
O	O <sub>2</sub> <sup>b</sup>	High	Dominant electron acceptor (respiration)
Intermediate abundance (0.1–1 mg L <sup>-1</sup> )			
N	NO <sub>3</sub> <sup>-</sup> , NH <sub>4</sub> <sup>+</sup> , DON <sup>a</sup>	High	Commonly limits autotrophs
Si	H <sub>4</sub> SiO <sub>4</sub>	Moderate	Diatom nutrient
Low abundance, nutrients (0.001–0.1 mg L <sup>-1</sup> )			
P	H <sub>2</sub> PO <sub>4</sub> <sup>-</sup> , DOP <sup>a</sup>	High	Commonly limits autotrophs
Cu	Cu <sup>2+</sup>	Low	Toxic when high
Zn	Zn <sup>2+</sup>	Low	Toxic when high
Fe	Fe <sup>3+</sup> , Fe <sup>2+</sup>	Moderate	Supports biotic redox conversions
Mn	Mn <sup>4+</sup> , Mn <sup>2+</sup>	Moderate	Supports biotic redox conversions
Mo			
Low abundance, toxins (0.001–0.1 mg L <sup>-1</sup> )			
As	As <sup>3+</sup>	Low	
Cd	Cd <sup>2+</sup>	Low	
Cr	Cr <sup>3+</sup> , Cr <sup>6+</sup>	Low	
Pb	Pb <sup>2+</sup>	Low	
Hg	Hg <sup>2+</sup>	Low	Biomagnified in food chains
Ni	Ni <sup>2+</sup>	Low	
Se	Se <sup>4+</sup>	Low	
Ag	Ag <sup>+</sup>	Low	

Heavy metals and metalloids may be present mostly as oxides or hydroxides rather than being truly dissolved.

<sup>a</sup>DOC, DON, DOP = dissolved organic carbon, nitrogen, phosphorus.

<sup>b</sup>Oxygen is also present as O<sub>2</sub><sup>-</sup> in combination with other elements, such as carbon (e.g., CO<sub>2</sub>).

**Table 2** Percent change in concentration corresponding to a 100% (doubling) increase in discharge (flow) for the Orinoco River, Venezuela (data from W.M. Lewis and O.F. Saunders, 1989, *Biogeochemistry* 7: 203–240.)

Constituent	Change %
	Discharge
Water	+100
	Major inorganic dissolved solids
Ca <sup>2+</sup>	-16
Mg <sup>2+</sup>	-13
Na <sup>+</sup>	-16
K <sup>+</sup>	-7
HCO <sub>3</sub> <sup>-</sup>	-13
SO <sub>4</sub> <sup>2-</sup>	-19
Cl <sup>-</sup>	-19
H <sub>4</sub> SiO <sub>4</sub>	-3
	Nutrient inorganic dissolved solids
NO <sub>3</sub> <sup>-</sup>	-27
NH <sub>4</sub> <sup>+</sup>	11
H <sub>2</sub> PO <sub>4</sub> <sup>-</sup>	19
	Dissolved organic substances and fractions
DOC <sup>a</sup>	15
TDN <sup>a</sup>	4
TDP <sup>a</sup>	15
	Suspended solids and solid fractions
TSS <sup>a</sup>	74
PC <sup>a</sup>	41
PN <sup>a</sup>	4
PP <sup>a</sup>	62

Note that most inorganic dissolved solids show a dilution effect for increased discharge, whereas organic matter and organic fractions as well as particulate matter and particulate fractions show a purging effect (increase) in response to higher discharge.

<sup>a</sup>D = dissolved, T = total, P = particulate (except that H<sub>2</sub>PO<sub>4</sub><sup>-</sup>, P = elemental phosphorus), O = organic, SS = suspended solids.

rate of bedload movement typically increase exponentially with increasing flow because they are mobilized and maintained in motion by the energy of flow. In contrast, inorganic dissolved substances often decrease in concentration as flow increases because rain or snow contains lower concentrations of most constituents than does water in prolonged contact with soil. Thus, the presence of rain or snowmelt in superficial soil layers may temporarily dilute the concentration of these constituents. There are some exceptions, however. Dissolved organic matter often shows an increase in concentration on the rising limb of the hydrograph (when discharge of a stream or river rises in response to precipitation or snowmelt). This increase probably reflects mobilization of accumulated stocks of dissolved organic matter that are readily flushed from the superficial soil layers.

## Oxic Processes

Elemental components of protoplasm are removed from or added to water through the complementary

processes of photosynthesis, respiration, growth, and mortality. Components of protoplasm include all elements that are required to synthesize biomass (growth), many of which are listed in [Table 1](#).

Oxic photosynthesis is conducted by a subset of organisms, the photoautotrophs, which take up protoplasmic constituents from water. For example, an algal cell attached to a rock in a stream will remove from the passing water or biofilm carbon dioxide, phosphorus, nitrogen, and other substances that are needed to synthesize protein, nucleic acids, lipids, and carbohydrates, which are the main constituents of protoplasm. Thus, photoautotrophs convert dissolved gases and dissolved solids into biomass; conditions that favor autotrophs (large amounts of light reaching solid surfaces in the channel) magnify the uptake of elements that are required for synthesis of autotrophic biomass.

In oxygenated environments, such as the channel surface, the channel water, or backwaters of a stream or river, oxic respiration dominates; it is characteristic of all groups of organisms, including autotrophs, invertebrate consumers, and bacteria. Oxic respiration always involves conversion of organic matter to CO<sub>2</sub> and water, and is accompanied by synthesis and maintenance reactions within organisms, during which metabolic byproducts may be produced and released into the environment (excretion). Support for respiratory processes may also involve processing of food leading to elimination (fecal output), which releases both dissolved and particulate organic substances to the water, as does mortality of organisms through mechanisms not involving consumption.

The bacterial decomposers, which are abundant on solid surfaces in streams, degrade organic matter in an oxic environment not only as a means of acquiring protoplasmic constituents to increase their own mass, but also as a means of supporting respiration. Because respiration requires only organic carbon (CH<sub>2</sub>O) and not the other components of protoplasm (P, N, etc.), respiration by bacteria often is accompanied by large releases of protoplasmic components such as phosphorus and nitrogen. For this reason, the decomposition process can be referred to as mineralization; it is a source of nutrient elements for autotrophs, which take them up from water.

In summary, simultaneous occurrence of photosynthesis and oxic respiration on a daily basis in the oxidized portions of streams and rivers is accompanied by both uptake and release of protoplasmic constituents such as CO<sub>2</sub>, N, and P. These processes may not be balanced at any given moment in time. If not, a progressive accumulation or reduction in the concentration of a biomass constituent may be observed through time or along the length of a stream.

## Anoxic Processes

Anoxic metabolism is possible for many types of microbes (mostly bacteria) but not for other organisms. Anoxic metabolism can occur within thick biofilms, even when oxygen may be present on the surface of the biofilm, or within regions of the hyporheic zone where bacteria have depleted oxygen, the preferred electron acceptor for respiration.

Anoxic metabolism involves both respiration and growth. The effect of anoxic growth (which involves only microbes) is similar to the effect of growth under oxic conditions: organisms take up and retain elements that are needed for the synthesis of biomass. Because oxygen is absent, however, an oxidizing agent (electron acceptor) other than oxygen is needed to support respiration. Any substance that can readily accept electrons is a potential oxidizing agent. [Table 3](#) lists the substances that commonly accept electrons under anoxic conditions with the assistance of microbial metabolism. Thus, for example, nitrate has substantial oxidizing potential when oxygen is absent. Microbes use this oxidizing potential by converting nitrate (which has a nitrogen atom with a +5 oxidation state) to dinitrogen ( $N_2$ , oxidation state zero).

Electron acceptors are used by microbes in anoxic environments in a progressive sequence, beginning with the most effective oxidizing agents and moving to weaker oxidizing agents as the stronger oxidizing agents are exhausted. The sequential nature by which microbes use electronic acceptors in an anoxic environment leads to a progression of biogeochemical changes. First, oxygen is depleted. As oxygen is nearing depletion, oxidized manganese ( $Mn^{4+}$ ) and nitrate ( $NO_3^-$ ) will be converted to reduced manganese ( $Mn^{2+}$ ) and  $N_2$  gas. If respiration continues (which requires the presence of labile organic matter), oxidized iron ( $Fe^{3+}$ ) may be converted to reduced iron ( $Fe^{2+}$ ). In fact, prolonged anoxia accompanied

by a strong supply of organic matter may bring the anoxic environment through the entire sequence of biogeochemical changes indicated in [Table 3](#). In this case, methane is eventually produced from organic matter, which is used by microbes in highly reduced environments as an electron acceptor.

It is common in streams and rivers for biogeochemical changes in anoxic sediments not to pass through the entire sequence of potential changes indicated in [Table 3](#). Several factors may interrupt progression through the full sequence. For example, anoxic conditions in a hyporheic zone may be associated specifically with low stream flow. At high flows, the anoxic environment may be flushed with oxic water, thus reinitiating the sequence of changes from the beginning. In addition, an anoxic environment may contain only a small amount of labile organic matter for microbes to use. In this case, the progression of biogeochemical changes ceases when the labile organic matter is used up by the microbes. Also, some of the potential electron acceptors shown in [Table 3](#) may be present in very small amounts, which would prevent any significant biogeochemical changes involving these electron acceptors. For example, sulfate is present only in small quantities in many inland waters. Production of sulfide from sulfate under anoxic conditions involving little sulfate would be trivial.

Under anoxic conditions, conversions summarized in [Table 3](#) set the stage for a reversal of biogeochemical changes when oxygen reaches an anoxic environment. For example, if reduced iron is flushed from an anoxic hyporheic environment into a river channel, microbes will reoxidize the iron, extracting energy in the process. In general, the presence of reduced chemical forms in oxygenated zones is temporary; reduced forms are converted to oxidized forms either spontaneously or by microbial processes.

Because of the diversity and importance of redox reactions that are dependent on the oxidation state of a given biogeochemical zone, water samples from different zones may show very different chemical composition. A sample from the channel or a backwater, for example, might be rich in oxygen and oxidized chemical constituents, whereas a sample from an anoxic portion of a hyporheic zone in the same stream might be rich in some or all of the reduced chemical substances shown in [Table 3](#).

The importance of anoxic metabolism is related not only to the production of reduced chemical substances in the absence of oxygen, but also to the continued breakdown of organic matter by microbes even when oxygen is absent. Although it may seem that an anoxic environment is biologically hostile, microbial decomposition of organic matter continues

**Table 3** Chemical forms produced and consumed by oxidation and reduction (redox) reactions

<i>Primary forms</i>	
Oxidized	Reduced
$O_2$	$O^{2-}$ ( $CO_2$ )
$NO_3^-$	$N_2$
$Mn^{4+}$	$Mn^{2+}$
$Fe^{3+}$	$Fe^{+2}$
$CH_2O$	$CH_3O$
$SO_4^{2-}$	$S^{2-}$
$CH_2O$	$CH_4$

The pairs of constituents are shown in approximate order of transformation assuming progressively more reducing conditions (increasing electron availability).

under anoxic conditions because of the ability of many types of bacteria to use electron acceptors other than oxygen to support respiration.

## Overview

In a lake ecosystem, where the longitudinal component of flow is typically smaller than the circulation of water, the concept of element cycling is highly applicable. A nutrient such as phosphorus, for example, may pass from the water column into an autotroph such as an algal cell, be consumed by an herbivore, and then pass to a carnivore or be released from an herbivore or carnivore back to the water column as fecal output or excretion. In addition, phosphorus that becomes attached to detritus (e.g., fecal pellets) might pass to the bottom of a lake and subsequently be released back to the water column. Thus, cycling is an accurate means of describing the movement of a given substance within a lake.

In a stream, the cycling concept is more difficult to apply because of the dominance of longitudinal movement. Although longitudinal movement is constant, an element such as phosphorus may be taken up as biomass, thus converting it from the dissolved to the particulate (solid) form. In the dissolved form, phosphorus moves longitudinally, but in the particulate form it typically may not move if it becomes attached to a solid surface as part of an organism or perhaps even to a grain of sediment that is immobile at low flow. Subsequently, phosphorus comes into motion again as it is released in soluble form or when a high flow moves it in particle form. Because longitudinal movement is added to cycling between mobile and nonmobile forms, the concept of 'spiraling' has been applied to elements in streams. The spiraling concept can be quantified in terms of the average distance (spiraling length) that a given element travels when it moves through one full cycle of the high mobility/low mobility sequences. Elements that are in high biological demand have tight spirals, whereas those that are in lower biological demand have loose spirals.

The distinct biogeochemical zones of flowing waters, in combination with concepts related transport under the control of hydrology and watershed effects, including pollution, produce a mechanistic understanding of the chemistry of flowing waters and the underlying biogeochemical processes that affect chemistry as water travels through a drainage network. The concept of spiraling unifies the longitudinal movement under control of flow with the processes that control the

forms and transformations of elements in a stream or river.

## Glossary

**Anoxic** – Devoid of free oxygen.

**Backwaters** – Waters adjoining a stream or river channel that are sometimes inundated by the channel at high flow but typically have very low rates of water exchange or are completely separated from this channel.

**Biofilm** – The combination of bacteria, fungi, and algae, along with associated nonliving organic and inorganic particulate matter, that coats solid surfaces within a stream or river. Invertebrates live within or around biofilms.

**Conservative substance** – Any element or substance whose rates of biogeochemical transformation are low relative to rates of transport.

**Hyporheic zone** – Sediments containing water that is constantly exchanged with water in the channel of a stream or river.

**Labile constituent** – Any element or substance that has high rates of biogeochemical transformation in relation to its rates of transport.

**Nutrient spiraling** – Movement of any element or substance within a stream or river under the simultaneous influence of longitudinal flow and repeated temporary immobilization through incorporation into a particle, living organism, or nonflowing zone.

**Oxic** – Containing free oxygen.

See *also*: Chemosynthesis; Fluvial Transport of Suspended Solids; Photosynthetic Periphyton and Surfaces; Redox Potential; Riparian Zones; Streams.

## Further Reading

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