LIMNOLOGY OF RIVERS AND LAKES

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Contents

Summary
Limnology deal with the study of fresh waters contained within continental boundaries. Limnology evolved into a distinct science only in the past century, integrating physical, chemical and biological disciplines to became able to describe and manage freshwaters ecosystems. Although inland water bodies are well below the oceans size, they are complex systems and they can't be fully understood if studied without taking into account the complex interrelations between physical, chemical and biological aspects This paper offers an overview of the basic principles of limnology. Particular attention has been devoted to the integration of physical, chemical and biological information, highlighting how abiotic and biotic compartments deeply interacts to determine lakes and rivers evolution. Thus this text has the ambition to improve the mutual understanding between the different disciplines dealing with the specific compartments of freshwater ecosystems.

1. Introduction

The science studying the water bodies located on the surface of the continents is called limnology (from the Greek λίμνη (*limne*) = lake and λόγος (*logos)* = study. It is considered as a part of ecology. It covers the biological, chemical, physical, geological, and other attributes of all inland waters, both running as in rivers (lotic ecosystems) and standing as in lakes (lentic ecosystems). The study of rivers, springs, streams and wetlands, lakes and ponds, both fresh and saline, natural or man-made is included in limnology. The term limnology was firstly proposed by François-Alphonse Forel (1841–1912) when publishing his researches on Lake Geneva. Because of its practical value, the interest in the discipline rapidly expanded, and in 1922 August Thienemann (a German zoologist) and Einar Naumann (a Swedish botanist) co-founded the International Society of Limnology (SIL, *Societas Internationalis Limnologiae*).

2. Inland waters and the water cycle

Most of inland water bodies are freshwater and they account only for a small fraction (~0,02%) of the whole hydrosphere. Some more freshwater (~1%) is groundwater and the ~2% of the hydrosphere is confined as ice in polar caps and in glaciers. Most of the water on Earth (~97%) is made up by seawater (Shiklomanov, 1999). In spite of the uncertainty of these estimates, without doubt the usable freshwater allowing for the existence of life on the continents is a very small fraction of the hydrosphere. The mechanism supplying new freshwater to continents as the water flows away from them is the water cycle (Figure 1). The sun provides the energy that keeps the water cycle moving through the evaporation of oceanic and inland surface waters and the evapotranspiration of terrestrial vegetables. Water vapor than progressively condensate in the atmosphere, eventually returning to the ground as rain or snow. The oceans lose for evaporation more water than they get back through precipitations and the opposite occurs in the continents. Thus the water flow through the continents is maintained. The residence time of water in the compartments of the cycle are very different. A certain mass of water can stay about ten days in the atmosphere, it will remains few weeks in the rivers and reside years or centuries in lakes and several centuries in groundwater (Trenberth et al. 2007).
In spite freshwater covers a small fraction of the Earth's surface, they are important quantitative components of the carbon cycle at either global or regional scales. Lakes, rivers, and reservoirs traps roughly half of carbon entering inland aquatic systems from land. A small fraction of such carbon is buried in aquatic sediments, a larger part is returned to the atmosphere as gas exchange while the remaining is delivered to oceans (Cole et al. 2007).

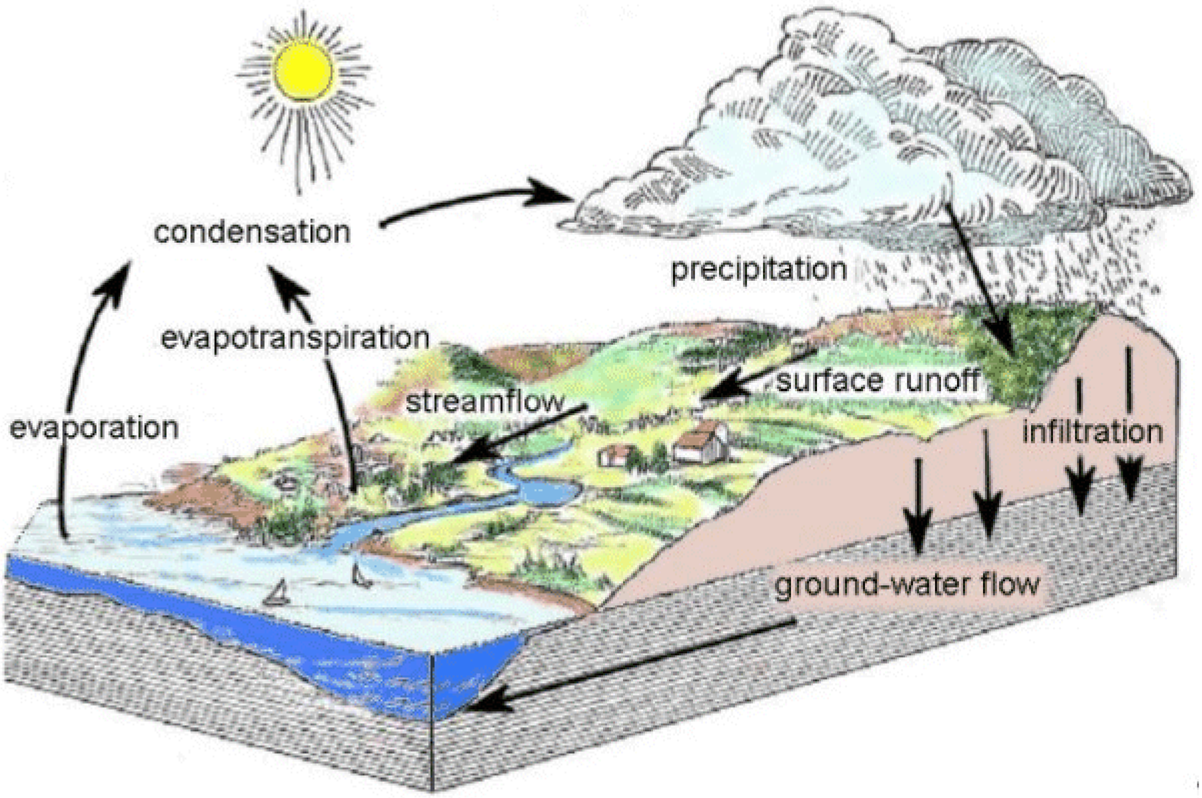


Figure 1. The water cycle

2.1. Physical properties of water

The water molecule is formed when two atoms of hydrogen establish a covalent bond with one atom of oxygen (Figure 2). In the covalent bond electrons are shared between atoms. In the water molecule the sharing does not have equal strength: the oxygen atom attracts electrons more strongly than the hydrogen atoms. As a consequence, in the water molecule the charges are asymmetrically distributed. The molecules that have partially negative or positive edges are called bipolar. This property makes water a good solvent for many substances. The positive region of a water molecule attracts the negative of another molecule, creating an hydrogen bond (dashed in Figure 2). In this bond the hydrogen atom is shared by two oxygen atoms: the donor atom is that to which hydrogen is more closely tied and the acceptor (that with partial negative charge) is the one attracting the shared hydrogen atom. The hydrogen bond is significantly weaker than the covalent bond but when many hydrogen bonds are acting together they constitute the strong cohesive force that gives water a high surface tension.

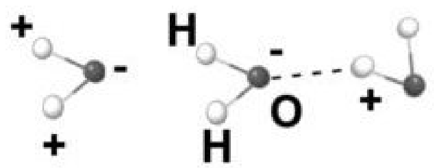


Figure 2. Structure of water molecule.

When the temperature falls and ice forms, the movements of the molecules are greatly reduced, and they bind together forming a rigid crystalline structure, allowing for large intermolecular voids (Figure 3). Because of this, a defined volume can accommodate less iced water molecules than liquid water molecules.

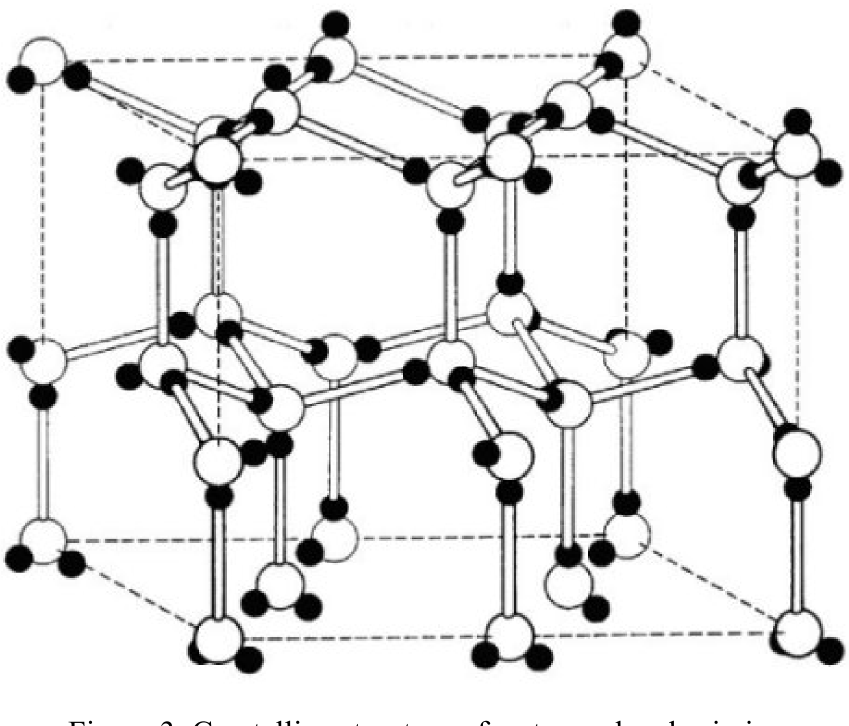


Figure 3. Crystalline structure of water molecules in ice.

The molecular structure of water gives it unique physical characteristics affecting the movements of water masses in lakes. Water maximum density is at 3.98° C: the water at lower temperature is less dense, i.e. lighter, so that a cube of ice (0°C) of 1 dm side weighs 85 grams less than a cube of water of same size at 3.98° C. Above this value, water becomes less dense (lighter) with increasing temperature (Table 1).

Temperature (°C)	**Density** (g dm^{-3})
0 (solid)	915.0
3,98	1000
20	998.2
40	992.2
60	983.2
80	971.8
100 (gas)	0.6

Table 1. Change of water density as a function of temperature.

Also the specific heat, i.e. the amount of heat (in calories) necessary to raise by 1°C the temperature of 1g of water is a physical characteristics unique to water. It is = 1, the highest among all solids and liquids, with the exception of liquid ammonia. For this reason water is an accumulator of heat, ensuring that the aquatic environment is thermally more stable than the ground. The thermal fluctuations in lakes are, therefore, gradual with changing seasons. Also the interval between the extreme daily values is much more reduced in water than in air, thus making the underwater climate thermally rather uniform. Exhaustive information on the structure and properties of water can be found in Eisenberg & Kauzmann (2005).

2.2 Inland waters dynamics

Waters moves into the cavities of the Earth's crust transporting solutes and suspended matter from and to neighbouring ecosystems, exchanging heat and gases with the atmosphere. By gravity the water flows in rivers along the lines of maximum slope with a current speed that tends to decrease from the mountains to foothills, although deviations from this rule are possible due to variation of other parameters also influencing the current velocity (e.g., flow increase for a tributary input). The current velocity of a mountain stream is around 3 ms^{-1} (about 10 km h^{-1}), that of a river in the plain is less than 1 ms^{-1} and in a lake the flow velocity decreases to values close to 1 cm s^{-1}. In rivers the kinetic energy of moving water is the main force fostering the exchanges with the neighbouring environment and determining the life conditions in the ecosystem.

Reaching the lake, the river bed widens considerably and the current velocity decreases rapidly. So the water movement in lakes is no longer promoted by gravity but depends on other energy sources: the heat supplied by solar radiation and the mechanical energy supplied by wind. These determine the movement of water masses and, therefore, the exchanges between them and the atmosphere. Because these sources of energy suffer obvious seasonal variations and are influenced by the regional climate, the lake waters chemistry (particularly the oxygen availability) and the activity of organisms living in the lake is highly dependent on seasonal thermal events of the lake itself.

Rivers and lakes, according to the different water flow velocity are called, respectively, lotic ecosystems (running water) and lentic ecosystems (still water).

Lakes need a river or at least an underwater spring to exist. This obvious succession prompt to deal with rivers first, but most of the concepts related to water physics and chemistry and aquatic food webs will be illustrated in details in the chapters dealing with lakes (chapter 4 on).

3. Running waters: the rivers

3.1 River morphology

Meteoric water flowing down slopes ends up merging to form small streams which then channel into a river. Because of the kinetic energy of the moving water, the river develops various landforms through channel processes. It is outside the aim of this text to discuss in detail the river landforming activity, already illustrated in Matsuda (2004).
For the purpose of this book it is enough to recall some basic terminology constituting the necessary context for river ecology illustration.
As shown in Figure 4, the area supplying water into a river is the drainage basin (db). The boundary between drainage basins is a water divide (wd). A river system is composed of the main stream (ms) and many tributaries (t). However, in many cases several tributaries have similar length and flow, and it is difficult to find which is the main stream. The main fluvial processes are **erosion**, **transportation** and **sedimentation**. In the upper area of a drainage basin, where current velocity is higher, erosion predominates and valleys composed of channels and slopes are formed. The materials swept downstream are the sediment load, produced mainly by weathering of the rocks composing slopes. Sediment load is deposited to form an alluvial plain. The channel patterns forming in alluvial plains can be braided, meandering and straight. The channel patterns and forms bring about the river morphology, decided by many inter-related factors such as discharge, water velocity, slope, depth and width of the channel, and riverbed geology.

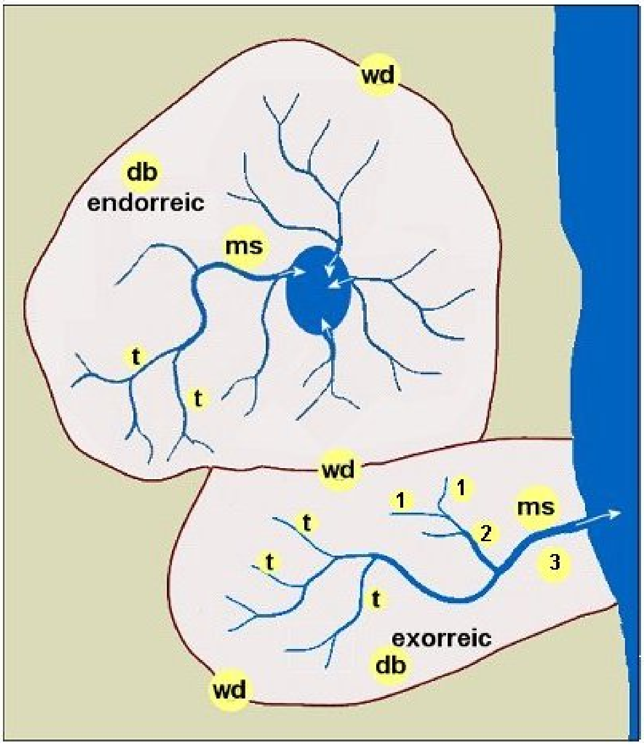


Figure 4: The hydrographic net: drainage basin (db), water divide (wd), main stream (ms), tributaries (t); first (1) second (2) and third (3) order stream.

3.2 River ecology: zonation

The current speed, the riverbed geology and granulometry, the flow rate, the extent of flooding and the amount of allochthonous materials carried by rivers profoundly affect the nature and functioning

of the biological component.
The current speed is a key factor for organisms living in the river. It also partially controls a number of environmental parameters (as temperature, oxygen, type of substrate, type of resources). The current speed generally decreases from upstream to downstream, and this gradient also characterizes the main factors governing life in rivers.

Temperature and oxygen
Close to the source the stream waters are turbulent, with a low and quite constant temperature. Flowing downstream, the water temperature becomes more and more dependent on air temperature. Thus the annual excursion, which does not exceed 5 °C in the alpine zone, can reach 15 °C after a few kilometers. In the plain the thermal behavior of a river of slow current differs little from that of a stagnant environment so that in summer the river can sometimes show a thermal stratification (see chapter 4.2).
The factors controlling the oxygen concentration in water are illustrated in chapter 4.5. Rivers turbulence promotes exchanges between air and water, ensuring an oxygen concentration in running waters always close to saturation. In rivers of slow current velocity the reduced turbulence limits the water oxygenation reducing the contact between water and atmosphere. Here the oxygen concentration is more dependent on organisms' metabolism. The photosynthesis can cause oversaturation during the day while the respiration may cause oxygen deficiency during the night, particularly at the bottom of the river, where microbial decomposition of organic matter can be very active.

Matter transport
The flowing water can carry large amounts of different materials from the surrounding environment. In addition to mineral particles, also the organic matter from plants and animals is collected by streams. Since the autochthonous vegetal production is often close to zero in rivers, allochthonous plant material provides more than 90% of energy input of a stream, making the heterotrophic metabolism the prevailing one.
During the transport by river the organic matter is attacked by fungi, bacteria and protozoa and is broken into fragments by invertebrates, particularly by insects larvae. Other invertebrates (larvae of diptera, chironomids, oligochaetes, molluscs) then filter out the smaller particles. The size of organic particles decreases more and more along the flow of the river. Further downstream the allochthonous supply tends to decrease and the presence of macrophytes, benthic algae and phytoplankton reduces the importance of heterotrophic contributions. Parallel to the reduction of the longitudinal velocity, an alluvial bottom made by sand, silt or clay, replaces the erosive bottom, made by boulders, pebbles and gravel.
In the upper part the riverbed is very irregular and uneven, ensuring a variety of shelters for organisms, abundant and diversified diets and a good oxygenation.
Despite the reduced current velocity, the sandy bottoms of the piedmont rivers are less favorable to life due to the very low organic matter content and their instability, so that can be resuspended even by very weak currents. The silt-clay bottom of the river plain, by contrast, is generally more stable because it incorporates small size particles acting as ligands (colloidal organic matter). The fauna includes many different organisms able to easily penetrate the fine sediments. This substrate is sometimes poorly oxygenated and often unstable and it can accommodate a considerable biomass of detritivore invertebrates, although the population is often not much diversified.

Ecological zonation of the watercourses
Depending on its average width, the watercourse it is defined as brook, stream, creek or river. In addition a distinction is often made between the upper part (mountain stream or river), the middle part (piedmont river) and the lower part (river plain). Rivers can be classified according to the morphological, physical and ecological conditions along the river length.
A simple geomorphological classification of rivers is based on the changes of flow at the

confluence of the rivers. It is assumed that the confluence of two rivers in the same category leads to the formation of a water course of a higher category. So two rivers without tributaries (order 1) at the point of their confluence form a stream of higher order (order 2). The confluence of two streams of order 2 leads to a stream of order 3. Finally, a river originating when streams of order 1 and 2 merge together is always of order 2. Nevertheless this classification is unsatisfactory from the ecological point of view.

A classification of running waters providing more valuable ecological information is based on the actual composition of biological communities inhabiting the river. The existence of a succession of fish populations along the river length has been known since a long time, allowing to define four zones named according to the prevailing fish species. The first is the salmonids zone, inhabited by trout (*Salmo trutta fario*) and grayling (*Thymallus thymallus*). Downstream there is the cyprinids zone, where the barbel (*Barbus Barbus*) is found, followed by the bream zone (*Abramis brama*). At the river end there is the flounder zone (*Pleuronectes flesus*), in the area where fresh water and sea water mix.

The river slope and width are, together with some ecologically relevant factors such as temperature, the important parameters regulating the species succession. But peculiar local conditions may alter the succession pattern: a sharp narrowing of the river bed, a sudden jump in the slope or an immission of cooler water are all factors likely to cause changes in the expected sequence.

Moreover, the distribution areas do not allow to have the same characteristic fish species for the whole of Europe. Grayling, for example, tends to be replaced by a cyprinid, the roach (*Leuciscus souffia muticellus*) in Southeast Europe. In England, the area with minnows (*Phoxinus phoxinus*) follows the areas with trouts.

A more general ecological zonation has been proposed (Illies, 1961) to distinguish in rivers two main ecosystems: rhitron and potamon.

The rhitron is characterized by an average monthly temperature never exceeding 20°C, an high oxygen concentration and very turbulent waters. The river bed is composed of boulders, pebbles and gravel sometime alternating with sand or mud. The organisms characteristic of rhitron have specific morphological adaptations to life in very turbulent waters and prefer cold and well oxygenated waters. Plankton is rare or more often absent.

The potamon waters have a monthly average temperature exceeding 20°C and they can occasionally suffer an oxygen deficiency. The current is very slow and the flow tends to be laminar. The bottom is mainly sandy or muddy. The typical organisms living in potamon withstand large temperature changes or prefer fairly warm waters, they can tolerate weak oxygen concentrations and prefer calm waters. The plankton can be abundant.

Within these two categories, three zones can be distinguished taking into account the invertebrates, particularly insects, living at the river bottom.

A third category was later added corresponding to the zone of spring: the crenon. It should be noted that the boundaries between the ecological zones are often confluence points of rivers.

Rhitron and potamon correspond to salmonid or cyprinid zones described above.

Vannote et al. (1980) developed the River Continuum Concept (RCC), a classification model for flowing water in addition to the classification of individual sections of rivers after the occurrence of indicator organisms. The model is based on the concept of dynamic equilibrium in which streamforms balance between physical parameters (width, depth, velocity, and sediment transport) taking also into account biological factors. The river zonation into rhithron and potamon and the ecological changes occurring along the watercourse, which will be illustrated in the next chapters, are summarized in Figure 5.

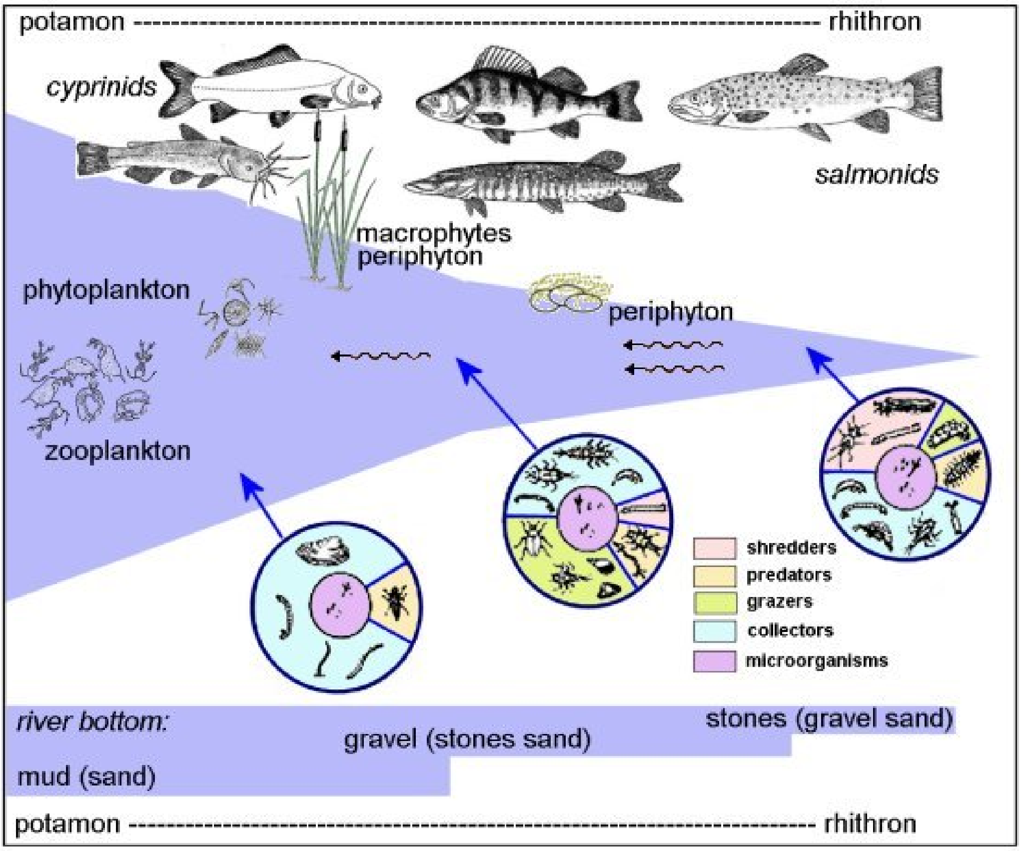


Figure 5. Zonation of river and ecological changes occurring along the watercourse.

3.3 Springs and upper river

The **springs** are places where the groundwater reaches the surface emerging from the soil. This generally occurs when the impermeable layers above which the rainwater absorbed by soil flows get close to the surface. Because of their underground origin, spring waters are characterized by a quite stable temperature, a low oxygen concentration and a low organic matter content.

These stable environmental conditions allow for the life of organisms with strict ecological requirements such as the worm planarian alpina (*Crenobia alpine*) in the cold mountain springs or the diptera of the genus *Scatella* in Iceland hot springs.

The springs are the interface between groundwater and surface water and they host the interstitial fauna, consisting of small animals living in groundwater and in subsurface cavities. Among them are found harpacticoid copepods, blind cyclopids adapted to darkness and other small crustaceans belonging to different genera are found.

According to the way the water emerges from the ground three different types of springs are recognized.

Rheocrene springs are formed on steep slopes and straight away originate a small stream.

Few organisms colonize the rheocrene springs immediately after their emergence. However, quickly sessile algae (periphyton) cover the stones and a typical vegetation colonize the edges of the stream. In alpine and subalpine regions mosses of different genera. (*Philonotis, Cratoneuron* and *Fontinalis*) are particularly important. Grasses, saxifragas (*Saxifraga* Sp) and sedges (*Carex* sp.) flank the mountain springs. The fauna includes many benthic herbivore or detritivore organisms. In mountain areas the larvae of Ephemeroptera and Chironomidae are the most common.

Limnocrene springs are found at the bottom of ponds and lakes. The biological communities of limnocrene springs are those of the surrounding lacustrine environments.

Helocrene springs, finally, are found at outcrops of the graundwater and give rise to wetlands, ponds and bogs. Unlike other sources, they offer highly variable conditions particularly as for temperature. Amphibians and many insect larvae adapted to weak currents inhabit this ecosystem.

The **upper river** has fast current, turbulent flow, intense erosion and low temperatures. The high water turbulence limits the development of vegetation. Higher plants are absent, although some species such as a buttercup (*Ranunculus fluitans*) can develop in the calmer zones of the river. Nevertheless some mosses (*Fontinalis, Hypnum*) and some algae can form dense mats on the stones hosting invertebrate herbivores. The abundant allochthonous supply of organic matter provides energy for the development of detritivorous organisms. The good oxygenation of the water allows the development of predator invertebrates with high energy requirements.
The coarse bottom of the river provides shelter to many organisms, often avoiding the direct exposition to strong currents. The insects can be very abundant, in particular the stonefly, the mayfly, trichoptera and diptera. Other invertebrates such as crustacea, molluscs, worms and hydracarina can be found there. The benthic invertebrates colonizing the upper zone of the river can reach densities from hundreds to thousands individuals per square meter.
The upper reach of the river is dominated by salmonids, and in particular by the trout (*Salmo trutta fario*), adapted to cold (5-10°C) and well oxygenated waters. The trout is 15-30 cm in length, is carnivorous, feeding on aquatic invertebrates and on fry of other fish. In the fall it goes upstream up to almost 2000 m a.s.l. to spawn.
The bullhead (*Cottus gobio*) is 10-20 cm in length, it share the environment with trout and has a very similar diet. Differently from trout, it is a bad swimmer, has nocturnal habits hunting the invertebrates at the stream bottom. In the salmonids zone the minnow (*Phoxinus phoxinus*) is also common, a small cyprinid about ten centimeters long. These fishes require an oxygen concentrations of 8-12 ml L^{-1}.
In the parts of the river where the water is less turbulent and becomes slightly warmer in summer (10-15°C), the grayling (*Thymallus thymallus*) gradually replaces the trout. Other fish species are present here, as the gudgeon (*Gobio gobio*) and species of the genus Chondrostoma and Leuciscus. These species tolerate oxygen concentrations of 5-7 ml L^{-1}.

3.4 Middle and lower river

Reaching the bottom of the valley the river loses its power, and its bed is here coarse sand and gravel, alternating with a finer substrate covered with vegetation. The mosses and filamentous algae are accompanied by higher plants rooted in the river bottom, such as the buttercup (*Ranunculus fluitans*), the milfoil (*Myriophyllum* sp.), the *Potamogeton fluitans* and the *Elodea canadensis*. In slow current zones *Callitrichum* sp. is also present.
The summer temperature often reaches 20°C and in sandy bottoms the quite homogeneous benthic fauna includes fossorial organisms, filter feeders or carnivores. In periphyton rich areas the grazer organisms dominate, such as larvae of mayflies and dipterans. The gammarids are abundant in the mosses and larvae of Odonata *(Gomphus, Calopteryx)* and good invertebrate swimmers are quite often found near the river shores.
The river is no longer inhabited by salmonids with the exception of rainbow trout (*Oncorhynchus mykiss*), introduced from the U.S. across Europe. This part of the river is the typical barbel area (*Barbus Barbus plebejus*). This cyprinid is an omnivorous fish feeding on benthic animals and plants. Other cyprinids found here are the bream, the chub and the roach. Carnivorous fishes such as perch (*Perca fluviatilis*), pike (*Esox lucius*) and eel (*Anguilla anguilla*) are also present.
In summer the temperatures of slowly flowing waters can exceed 20°C. As the river carries a considerable load of suspended particles, the water has low transparency and reduced light penetration, limiting the macrophytes and periphyton growth. The autotrophic production is ensured by the phytoplankton and by macrophytes colonizing the banks in stagnant waters. Anoxia is not rare at the sediment – water interface particularly in summer.
The benthic fauna living in these conditions includes organisms resistant to low oxygen

concentrations such as oligochaetes, especially tubificids. Among the insects, the dipterans, especially chironomids larvae, are the most abundant in the lower part of the river. The grazer organisms, abundant in the middle part of the river, are sparse while the detritivores and filter feeders are abundant.
Along the river banks the invertebrate community consists of Megaloptera larvae (*Sialis* sp.), Odonata, Coleoptera and crustaceans (*Asellus*), leeches, snails (*Limnea, Planorbis*), bivalves molluscs (such as *Dreissena polymorpha*). The zooplankton fauna is dominated by rotifers while the microcrustaceans (Copepods and Cladocera), forming the most important component in lakes, are mostly benthic species in the rivers.
The fish characteristic of the lower river is the carp (*Cyprinus carpio*), a cyprinid mainly feeding on benthic invertebrates and aquatic plants. This river stretch hosts tolerant fishes such as the roach (*Rutilus erythrophtalmus*), the rudd (*Scardinius erythrophtalmus*), the tench (*Tinca tinca*) and the catfish (*Ameiurus melas*). The pike (*Exos lucius*) is common, but only when the oxygen concentration is high enough. The fish community is comparable to that of mesotrophic lakes.
At the river mouth freshwater and marine water mix following the tides and many marine fish can be occasionally found in this brackish water zone. In particular, this is the case for migratory anadromous fishes swimming up rivers to spawn.
These fishes are sturgeon (*Acipenser sturio*), allice shad (*Alosa fallax*), salmon (*Salmo salar*), sea lampreys (*Petromyzon marinus*) and river lamprey (*Lampetra fluviatilis*). The populations of these species decreased dramatically as a result of overfishing, the dams impeding their migration and the destruction of spawning areas. Other marine species sometimes go upstream without reproducing. This is the case of mullet (*Mugil* sp.) and flounder (*Plaichthys flesus*). A review of concepts in large river ecology is available in Allan (1995) and in Johnson et al. (1995).

4. Still water: the lakes.

4.1 Lakes origin

The lakes are cavities in the soil collecting waters conveyed to them by rivers from the catchment area, by atmospheric precipitations and supplied by groundwater. These cavities may have been produced in the Earth's crust by catastrophic events occurred in distant geological era (tectonic and volcanic lakes) or in relatively recent times (landslide lakes). The cavities may have originated in the most recent geological era by slow changes in the Earth's crust (glacial lakes, plain lakes, coastal lakes, karstic lakes) (Hutchinson, 1957; Wetzel, 2001). According to their origin, lakes are classified as:

Tectonic lakes: the movements and fractures of the deeper layers of the Earth's crust determined the opening of basins where water is collected (Figure 6). The oldest lakes of the planet originated in this way. It is the case of Lake Ohrid (Albania and Macedonia), the oldest lake in Europe formed between 4 and 10 million years ago, situated in karstic area. Also of tectonic origin are the great lakes in Africa (Tanganyika, Nyasa, Rodolfo) and in Asia, as lake Baikal, one of the largest, deepest and oldest of Earth (20-30 millions of years).

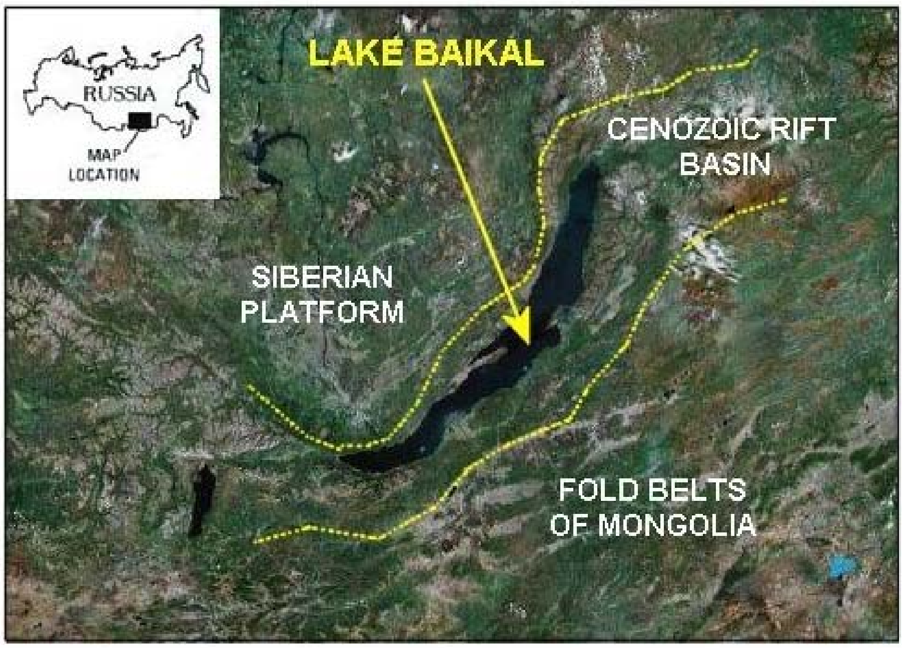


Figure 6. Lake Baikal, Siberia.

Volcanic lakes: they are hosted in the craters (Figure 7), single or several interpenetrating, of extinct volcanoes (crater lakes) or in depressions formed by the subsidence of the magma chambers of inactive volcanoes (caldera lakes). Of volcanic origin are also the barrier lakes formed by the consolidation of lava flowing across a valley.

Figure 7. Crater lakes inside a large crater (San Miguel, Azoras).

Landslide lakes: formed as a result of catastrophic events for the deposition at the bottom of a valley of debris from a collapsed valley wall. (Figure 8).

Figure 8. Landslide damming a river and forming a ew lake.

Glacial Lakes: the landforming activity of glaciers was very active in originating lakes during the glaciations of the Quaternary period, ended roughly 10,000 years ago. The downhill flow of glaciers transformed V-shaped valleys into U-shaped valleys through the glacial erosion processes. The moraine material deposited on the floor and at the edge of the valley originated the basins hosting a moraine-dammed lake (glacial lakes). When retreating, glaciers left behind underground or surface chunks of ice that later melted leaving a depression containing water (North American cattle lakes). At the head of a valley a concave amphitheatre open on the downhill was often formed by glaciers erosion. When the concavity is filled up by water a cirque lake is formed.

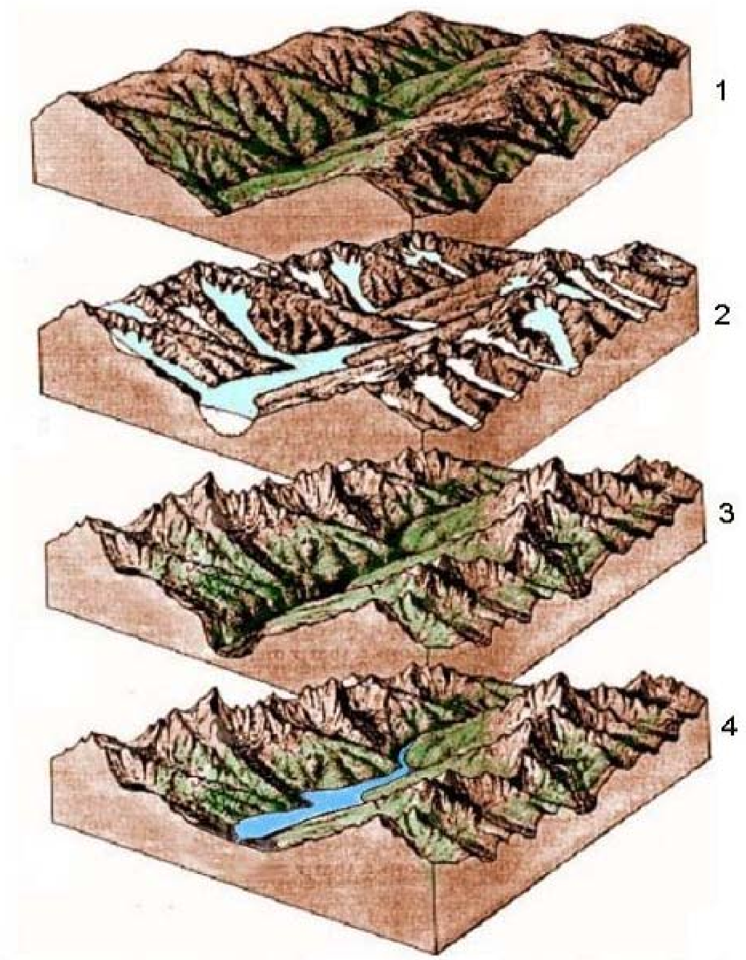


Figure 9. V-shaped valley (1) modified by glacier (2) resulting in a U-shaped valley (3) eventually dammed by moraine and filled by water forming a lake (4).

River originated lakes: lakes can result from the erosive force of rivers. As riverine erosion occurs, sediments are resuspended and deposited downstream in the process. Large rivers can deposit sediments in such a way that dams tributary streams forming new lakes (lateral lakes). At river bends, turbulence and sediment deposition can build up. This sediment can cause the river path to divide and may actually dam a river meander which is thus segregated from the main river. The resulting water body is called an oxbow lake (Figure 10).

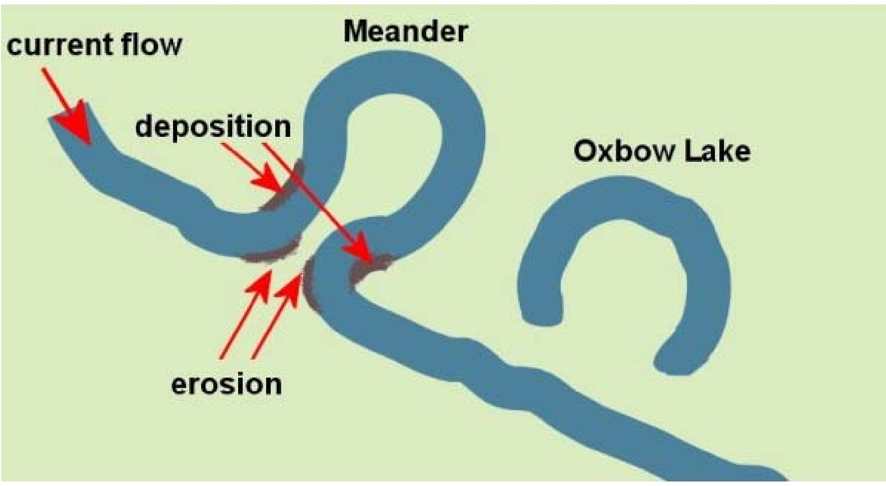


Figure 10. Erosion and deposition processes eventually separate a meander from the main river bed originating an Oxbow lake.

Coastal lakes: often form along irregularities in the shoreline of the sea by deposition, promoted by currents, of sediments in bars protruding above the mean sea level and eventually isolating a fresh or brackish water lake. (Figure 11).

Figure 11. Coastal lake (Lake Varano, Italy).

Karstic lakes: in regions of calcareous ground the running-over waters dissolve the carbonate constituting the rocks. The cracks in limestone rocks are thus attacked and widened by the waters dissolving the carbonate. In this way funnel-shaped cavities are formed (sinkholes) that are gradually widened and that often end in a cave. The eroding water flow can weaken the ceiling of the cave till it break. The cavity thus formed can accumulate waters originating a sinkhole lake (Figure 12).

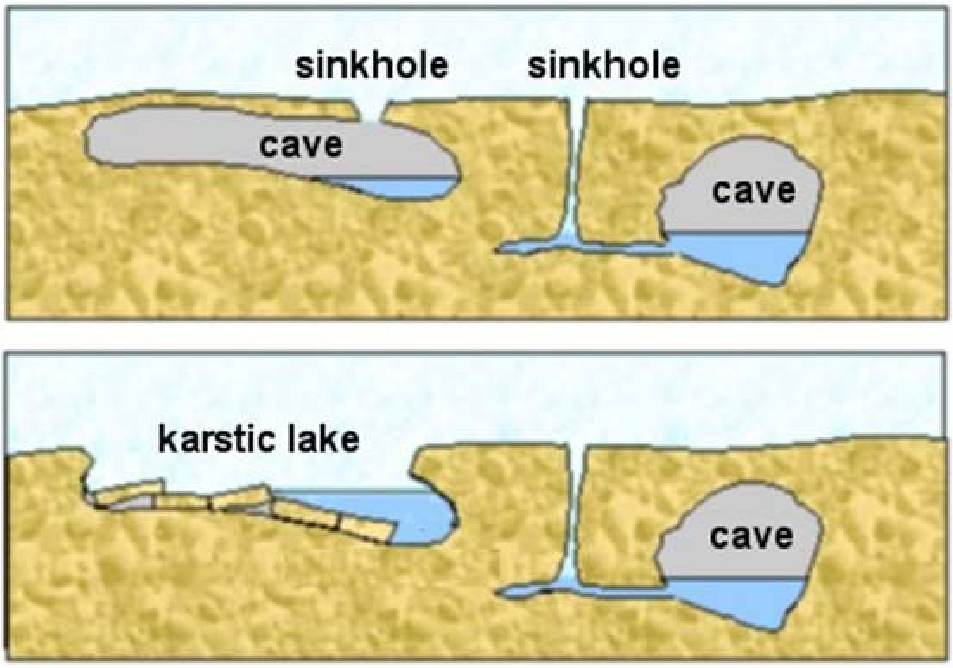


Figure 12. Formation of a karstic lake.

Artificial lakes: these are man-made lakes, intercepting the course of rivers with dams to store water for drinking or energy production purposes . The cavity hosting the lake could also have been dug for some mining enterprises (quarry lakes). These are often fragile environments, managed considering them simply as water tanks. This simplification ignores the complexity of the processes taking place in a lake, and usually results in a rapid deterioration in the quality of the newly formed lake.

A list of the largest lakes (average area greater than 100 km²) of Europe can be found at the address: http://en.wikipedia.org/wiki/List_of_largest_lakes_of_Western_Europe

4.2 Energy penetration in lakes

Figure 13 shows the spectrum of the solar radiation reaching lakes surface and the effect of different wavelengths on organic matter and living organisms. The radiation of higher energies changes the atomic or molecular structure of matter. With decreasing energy content, ie in the range of visible light, the radiation energy is used for photosynthesis, the biochemical reactions leading to organic matter production by autotrophic organisms. Thus the radiation in the visible range 400-700 nm and is called Photosynthetically Active Radiation (PAR). The long wavelength radiation interacts with water molecules, transferring them its energy and determining the water heating.

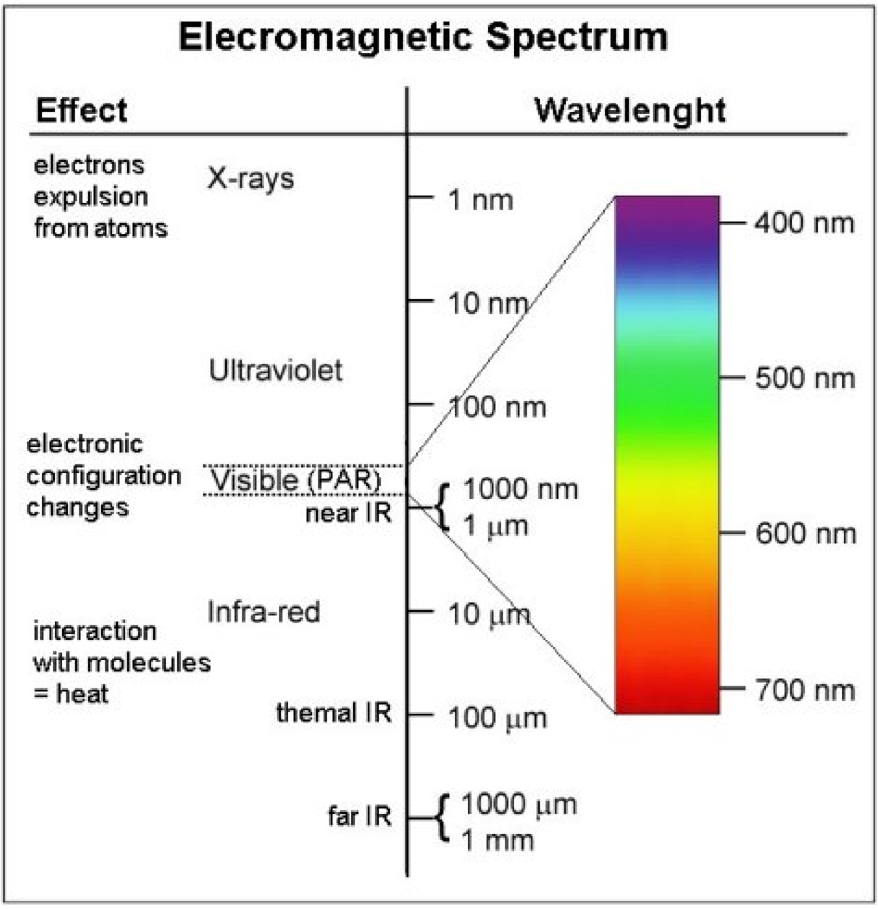


Figure 13. Spectrum and activity of solar radiation reaching the biosphere.

The amount of solar radiation reaching the surface of lakes varies depending on the transparency of the atmosphere, latitude and altitude of the lake. When it reaches the lake surface, the radiation is partly reflected, returning to the atmosphere, and partly refracted, penetrating in the water.
The percentage of incident radiation reflected depends on the sun position according to day time and season, i.e. the incidence angle. The percentage of radiation reflected is minimum when the sun

it at zenith and maximum when the sun is near the horizon
The incident radiation penetrating water is refracted, thus changing direction and decreasing its speed moving through a denser medium. The refractive index of water is about 1.33 and is greater than 1 because the water is more reflective than the air. For this reason light rays cross water more vertically than air, thus shortening down and dusking in the underwater world.
After penetrating through water, the radiation is transmitted only to a certain depth. The gradual absorption limiting light penetration is due to water itself and to the dissolved substances (determining water color) or suspended particles reflecting light (diffusion).
The relationship between the radiation intensity at surface (I_0) and at depth z (I_z) is given by:

$$I_z/I_0 = e^{-kz} \; \textit{(1)} \text{ or by the equivalent } I_z \ln - \ln I_0 = -kz \; (2)$$

where e is the base of natural logarithms (ln).
The parameter k is the extinction coefficient, expressing the percentage of surface incident light reduced by a water layer one meter thick. The higher k is, the more rapidly the radiation intensity decreases with depth.

If at the lake surface the PAR is 1200 µmol m^{-2} and is 600 µmol m^{-2} at 5 m depth, from equation *(2)* we have:

$$k = -(\ln I_Z - \ln I_0)/z = -(\ln 600 - \ln 1200)/5 = 0{,}1386 \text{ m}^{-1}$$

In other words, assuming to be 100 the radiation at the surface, from equation *(1)* the amount reaching 5 m is:

$$I_Z = I_0 \, e^{-kz} = 100 \, e^{-0{,}1386 * 5} = 50$$

that is only the 50% of surface radiation reaches 5 m depth.
The maximum depth to which aquatic vegetals (algae and macrophytes) can live is that reached by at least 1% of surface radiation. This depth is taken as the lower limit of the photic or euphotic zone, that is the water layer where the autotrophic production is possible. The dark portion of the lake is called aphotic zone. From the extinction coefficient of a lake the extent of its euphotic zone can be calculated from equation *(2)*. In the example above the lake, with k = 0.1386 m^{-1}, the depth of 1% of incident radiation will be:

$$z = -(\ln I_Z - \ln I_0) / 0{,}1386 \text{ m}^{-1}$$

that is:

$$z = -(\ln 0{,}01 - \ln 1{,}00) / 0{,}1386 \text{ m}^{-1} = 33{,}2 \text{ m.}$$

Such a lake is a very clear one, as it's evident from figure 14, which compares the attenuation curves of the light radiation of an eutrophic, an oligotrophic and a ultraoligotrophic lake.

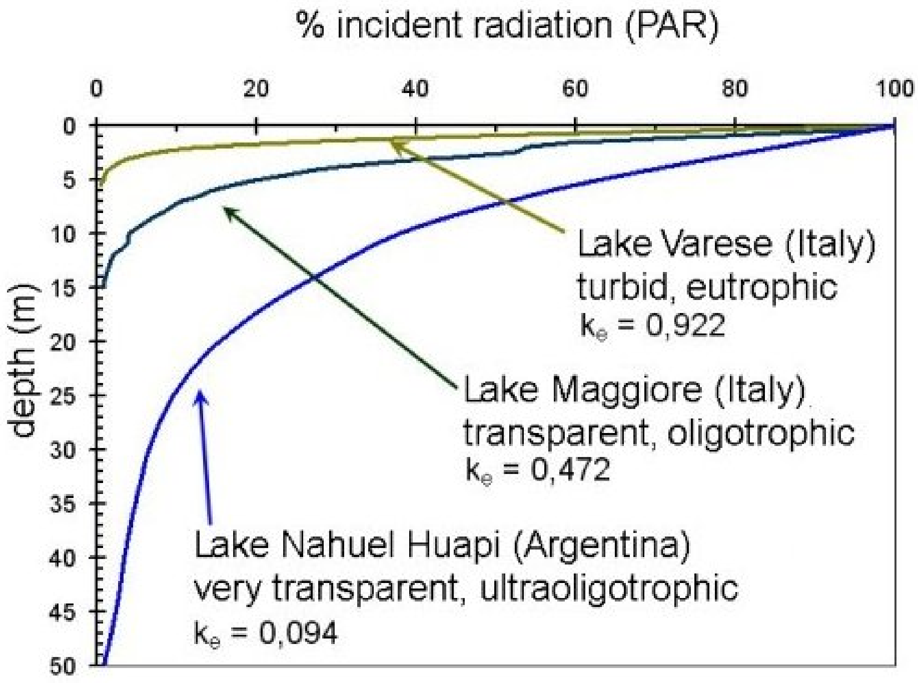


Figure 14. Attenuation curves of light radiation showing the different transparency in lakes of different trophic condition.

Not all wavelengths are attenuated in the same way as water absorbs some wavelengths more than others (Table 2).

	Wavelength (nm)		Extinction coeff. (m^{-1})
	720	(IR)	1,04
PAR	680	(red)	0,455
PAR	620	(orange)	0,273
PAR	580	(yellow)	0,078
PAR	520	(green)	0,016
PAR	460	(blu)	0,0054
PAR	400	(violet)	0,0134
	380	(UV–A)	0,0255

Table 2. Extinction coefficients of light in distilled water for visible radiation and the adjacent wavelengths (Hutchinson, 1957).

The window of maximum transparency of water is in the blue region, and since the blue-green light is less absorbed, this is the dominant color in the depths. But suspended and dissolved substances (plankton, detritus particles, humic acids and other solutes) alter the absorption spectrum of water determining the light, or underwater optical climate, characteristic of each lake.
As the light does not penetrate very deep in a very productive lake, then the red wavelength is dominant. Vice versa, in an unproductive lake the red radiation extinguishes quickly and in the deeper layers, where it can still get light, short-wave radiation (blue and green) are the dominant ones. Ultraviolet radiation, in particular, penetrates very little because even in unproductive lakes it is rapidly absorbed by dissolved organic matter (O'Sullivan and Reynolds, 2005).

Lake water transparency
Particles and solutes present in a lake determine its transparency, which is assessed with the Secchi disk, a simple instrument firstly used in 1865 by abbot A. Secchi. It is a white disk, usually metallic,

20-30 cm in diameter, tied to a rope. The Secchi disk is lowered in water and the depths of its disappearance and reappearance are measured (Figure 15). The average between the two measures is the transparency of a lake, defined as Secchi disk disappearance depth.

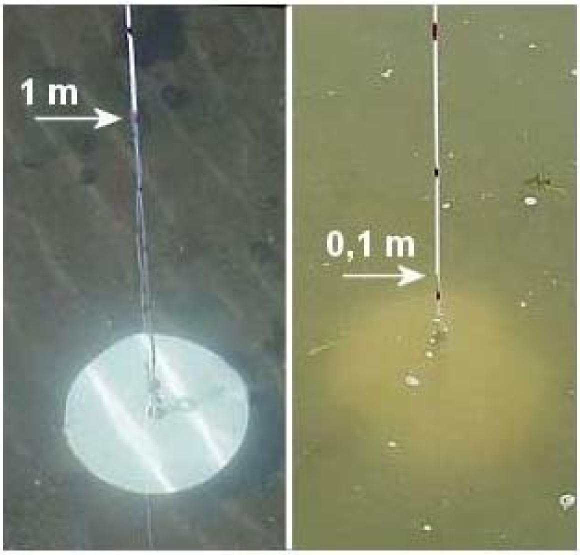


Figure 15. Secchi disk in a transparent (left) and in a turbid lake (right). The arrows indicate the water level.

The transparency of highly productive lakes may be less than 1 m, while in less productive lakes it can be more than 10 m. For example, in Lake Baikal it is about 40 m. In the northern hemisphere the transparency of a lake is maximum in winter (minimum of production) and minimum in summer-autumn, i.e. during the production period (Figure 16). The thickness of the euphotic zone is, very roughly, 2-3 times the Secchi disk transparency.

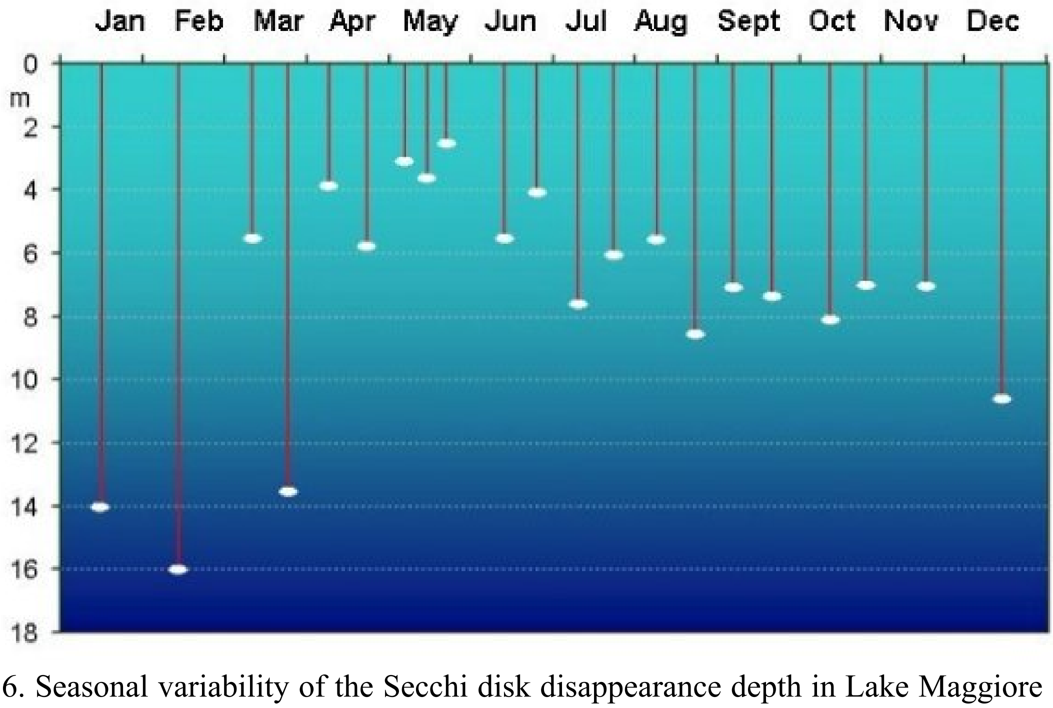


Figure 16. Seasonal variability of the Secchi disk disappearance depth in Lake Maggiore (Northern Italy).

The true, or intrinsic, color of a lake is given by colloids and solutes. It is evaluated in the laboratory, measuring the absorption spectrum of a filtered lake water sample.
The apparent color of a lake perceived by an observer depends on the presence of suspended particles, both living and nonliving, and by external conditions (color of the sky, surrounding

vegetation). In shallow lakes the apparent color can also depends on bottom sediments color. Iron compounds, such as ferrous sulfate and ferric oxide, can make a lake reddish or yellowish. Lakes receiving waters draining forests or peat lands are rich in humic substances, which can lead to brown or even blackish waters. The color of a lake can also change with the seasonal cycle, depending on biological phenomena such as the growth of algal populations different in species and density. Planktonic organisms can determine the apparent color of the waters where they live, with extraordinary results when there is an explosive growth (bloom) of phytoplankton. Some species of *Haematococcus*, *Euglena*, *Planktothrix*, can give to alpine lakes the appearance of "pools of blood". Also *Bacteria* can produce in lakes rich in sulfur or in brackish waters intense colors of different hues. In the past the lake apparent color was evaluated, in " Platinum color units ", comparing the water color with a color scale from standard solutions of Pt and Co salts.

4.3 Water mass movements in lakes

Reaching the lake, the river bed widens considerably and the current speed quickly drops to the point that lake water movements are no longer due to gravity. They now depend on other energy sources such as the heat supplied by solar radiation and the mechanical energy supplied by wind. These energies determine the movement of lake water masses and, therefore, the exchanges between them and the atmosphere. Because these energy sources are obviously affected by seasonal variations and are influenced by the climate of the region, the lake chemistry (in particular oxygen availability) and the activity of organisms inhabiting the lake are both highly dependent on the seasonal thermal cycle of the lake itself (Dodds, 2002).

4.3.1 Thermal energy and lakes circulation

The hydrodynamic of a lake is complex because of the complex interactions between water and the forces moving it. Considering the heat content, affecting the density of lake waters and therefore their buoyancy, it is transferred:

- by radiation, when the energy transfer occurs via electromagnetic waves, without matter transfer
- by conduction, when heat is transferred through thermal energy exchange from one molecule to the next one, without mass movement. This is possible when there is a temperature gradient between water masses
- by convection, when the heat transfer takes place through displacement of warm water from one site to another of the water body. This is the prevailing course of heat transfer in fluids.

Solar radiation warms up the uppert water layers and the heat transfer in deep layers mainly depends on convection and on the wind. The heat transfer in the lake determines its temperature at any season as a result of the lake heat balance, i.e. the difference between the input and loss of heat. Measuring lake temperature from surface to bottom, one can get very different thermal profiles along the course of the year. The water column can have the same temperature from surface to bottom or can show an evident thermal gradient.

In the temperate zone, a hypothetical lake 20 meters deep will progressively lose heat during winter, reaching by the end of the season a temperature close to 4° C at any depth. The wind activity can easily mix surface and bottom waters that have now the same density. The spring circulation thus established transfers the surface water, in contact with the atmosphere and thus well oxygenated, towards the lake bottom, charging of oxygen the whole water column (Figure 17 A)

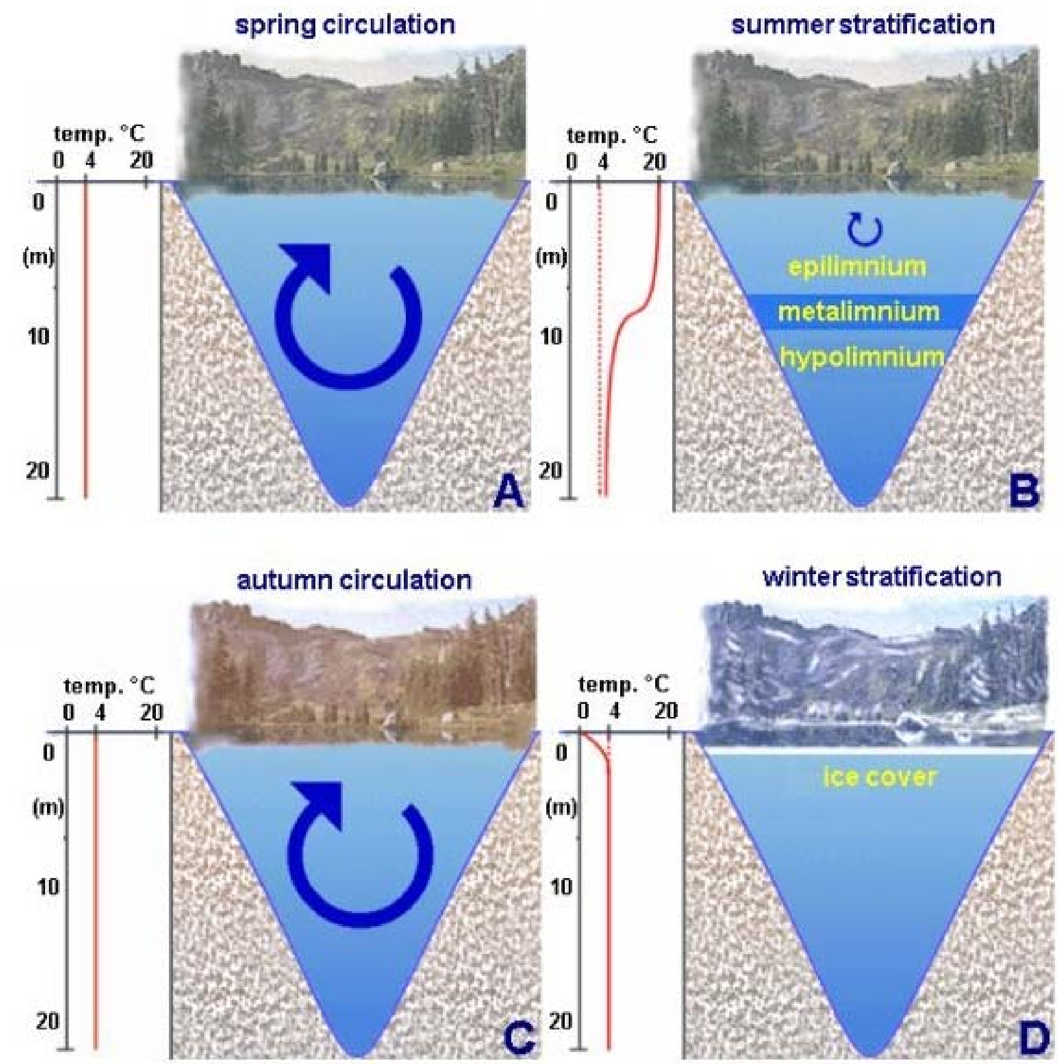


Figure 17. Temperature profile and section of a lake during the circulation, in spring and autumn, and stratification, in summer and winter.

As spring proceeds (Figure 17 B), the increasing amount of heat conveyed by solar radiation rises the surface water temperature. The mechanical work of wind may mix surface waters (warmer and less dense) with those immediately below (colder and therefore denser), thus gradually distributing the heat from the upper layers to the deeper ones. However, as the warm season goes on, a thermal, and therefore density, gradient sets up between surface and deep water. This gradient soon becomes high enough to prevent the wind from mixing the waters. In this way, in the warm season, the warmer surface layer (epilimnion) will be separated from the uniformly cold deep layer (hypolimnion) by a transition layer (metalimnion). Here the temperature rapidly drops with increasing depth and when a temperature difference greater than 1°C per meter is reached, a thermocline sets up. This is defined as the horizontal plane passing through the inflection point of a vertical temperature profile. This situation of summer stratification prevents the oxygen exchange between surface and deep layers. If the lake is very productive, the microbial oxidation of organic matter can completely consume the dissolved oxygen in deep waters, leading to an anoxia condition, incompatible with the life of many aquatic organisms.
In autumn (Figure 17 C) the surface water cools up, becoming denser and sinking towards the bottom. The epilimnion thickens and the metalimnion grows increasingly thin. The temperature difference between epilimnion and hypolimnion gradually reduces. As in spring, the wind mixing intensifies till producing a complete circulation (autumn circulation). The lake temperature is now

about 4° C and the dissolved oxygen is evenly distributed along the water column.
In winter (Figure 17 D) water density decreases after the further cooling. The water density anomaly results in an unstable inverse thermal stratification, with a colder surface layer above a deeper water layer at 4°C. If ice forms, it covers the lake surface because its density at 0° C is about 9/10 that of water. Ice can stabilize the winter inverse thermal stratification thus setting up the winter stratification.
According to their mixing features lakes can be classified as:
Holomictic (*holos* = whole): lakes that completely mix because they reach uniform temperature and density from top to bottom. Full circulation can occur once or twice a year, and such lakes are called, respectively, **monomictic** or **dimictic** (as the one described before). There are also **polymictic** lakes, i.e. lakes mixing several times a year. This is the case of lakes too shallow to develop thermal stratification. Their waters can mix from top to bottom throughout the ice-free period. Polymictic lakes can be cold polymictic lakes (i.e., ice-covered in winter), and warm polymictic lakes (i.e., without winter ice-cover). There are also **oligomictic** lakes, where mixing is irregular, not occurring every year. The great deep subalpine European lakes are of this kind.
Amictic (*a* = without): lakes that never circulate. Amictic lakes are usually ice covered throughout the year. This is the case of polar lakes, close to the North and South Poles. Although high mountain lakes are exposed to temperatures mostly below freezing, they often have an ice free surface for a short time in summer. These lakes are isothermal once a year and then have one full circulation (monomictic lakes).
Meromictic (*meros* = part): lakes where bottom water never mix with surface water. In these lakes dissolved substances accumulate at the bottom, increasing the water density above the value attributable to temperature alone. The more superficial layers, where mixing is possible, constitute the mixolimnion while the deep layers, never mixing, are the monimolimnion. The intermediate layer, where there is a sudden change in density at the upper edge of bottom layer accumulating salts or dissolved organic matter, is called chemocline (or pycnocline). Meromixis can be:
- **ectogenic** when external events transport salt water into a freshwater lake or vice versa;
- **crenogenic,** when a saline spring at the bottom of the lake introduces in it water rich in salts;
- **biogenic,** when salts from organic matter decomposition in sediments or from carbonates precipitation due to pH changes promoted by photosynthesis accumulate in the deeper layers.

In the first two cases, the meromixis is a natural phenomenon. In the third case, however, the introduction of excess organic matter in a lake is anthropogenic, either directly (urban sewage inputs into the lake) or indirectly, as a result of eutrophication. Whatever the cause of meromixis is, with the segregation the deep layers lose the ability to come in contact with the atmosphere to grab oxygen. As a consequence, they quickly become anoxic because the decomposition (oxidation) of organic matter by bacteria rapidly exhausts the oxygen of the bottom layers. In the monimolimnion, therefore, only the anaerobic bacterial microflora is active. In relatively shallow meromictics lakes, where solar radiation reaches the chemocline but anoxia prevents algal photosynthesis, abundant bacterial assemblages performing anaerobic photosynthesis and producing a significant amount of organic matter often develop.

To evaluate the extent to which global climate change is affecting the thermal evolution of a lake it is necessary to know the **annual heat balance** of the lake. This is the amount of heat contained in the lake annually, expressed as joules (or calories) per unit area. The thermal birgean budget of a lake, named after the American limnologist Birge, is calculated summing up the caloric content of each of the ***n*** water layers constituting a lake, each of area A and depth z. The caloric content of each layer is computed as

$$\frac{A_n \times z_n \times (\text{max summer temp}_n - \text{min winter temp}_n)}{\text{Area lake}}$$

The **overall thermal stability** of a lake is measured by the amount of wind work required to remove the thermal stratification of the water column till the complete mixing, overcoming the resistance due to density differences. According to another approach, the thermal stability is evaluated from the work required to maintain a lake omeothermic. Whichever is the approach, the thermal stability is an expression of how strongly the hypolimnetic waters are segregated.

4.3.2 Wind and water movements

If the heat transfer in a water body would occur only by thermal conduction, already at 3 m depth the annual temperature excursion would be only one tenth of that at the surface.
But wind, flowing on the lake surface, leaves part of its energy to the water which it comes in contact with, triggering a turbulent water movement.
In natural environments, however, water masses flow can be:
- laminar (low speed, uniform and one way motion)
- turbulent (high speed, multi-directional motion and chaotic).

In fluid mechanics, the type of flow depends on the viscosity and density of the fluid, its velocity and the section of the pipeline through which the liquid flows. It is indicated by the Reynolds number (Re):

Re = (density x velocity x pipeline section) / viscosity

If Re <1000 laminar flow occurs, when Re> 1000 the flow is turbulent.
In lakes, assuming the water column depth as the pipeline section, a speed of few mm per second already induces a turbulent flow.
In turbulent flow, water particles leave the section where the current exceeded the critical speed and penetrate into the surrounding water mass, transporting their own chemical and thermal properties. In this way turbulent convective motions start up, transferring the thermal properties of the impending water layers to some 10 m depth. The circular motions known as vortices are the result of turbulent flow.
The wind-promoted turbulent flow generates the waves, the surface seiches, the internal seiches and the surface currents.

Waves are successions of oscillations of water surface of variable size and regularity, conveying windward the energy released by the wind without causing large horizontal water displacement. The distance covered by wind above a water body before reaching the shore is called fetch. The larger the fetch, the greater the chance of large waves to develop. The surface waves affect the lake thermal condition. The wind and the shaking of surface waters cool them up, changing the thermal equilibrium with the underlying water layers. The wave forms because the wind friction on the water forces it to ripple. The ripple size depends on the strength of the wind, on the extension of the lake surface affected by wind (fetch) and on the duration of the blast. The wave parts are the crest (the highest point of a wave), the trough (the hollow between two waves), the wavelength (the horizontal distance between two successive crests or troughs), the wave height (the vertical distance between crest and trough), and the wave frequency (the number of waves passing through a point in a certain time interval) (Figure 18).

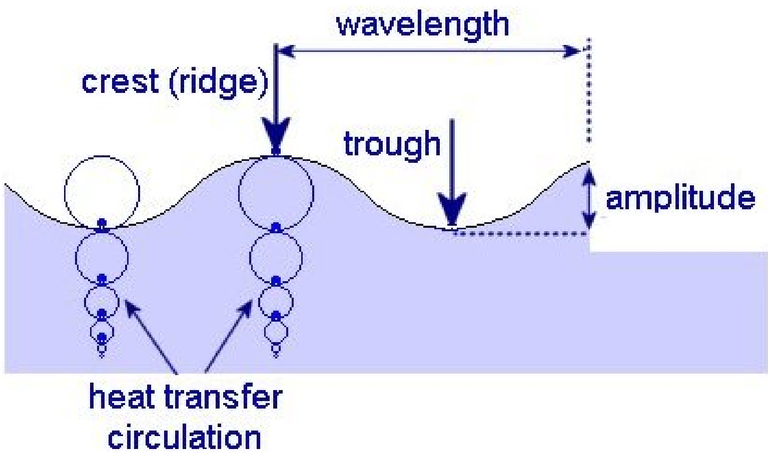


Figure 18. Features of a wave.

The wave moves forward the energy but not the water. The motion of a water drop during the passage of a wave follows a circular path from the starting point back to the end of the wave. These trajectories are most evident near the surface. They decrease with depth, disappearing at half-wavelength below the surface.

The surface seiches

Surface seiches originate when the wind blows constantly in the same direction, pushing the water leeward and producing a windward depression. When the wind drops, the water accumulated flows back by gravity, triggering an oscillation gradually decreasing due to friction and gravity force (Figure 19). The seiches involve the entire water column, although their maximum amplitude shows up at surface as small changes of lake level, leaving rhythmically dry ("seiche" in French, hence the word) the lake shore. The basic seiche has a single node (uninodal seiche), but harmonics of the oscillation can occur, exhibiting several nodes (multinodal seiche).

The period of the uninodal seiche (*t*) can be estimated from a formula that equates it to twice the length of the lake in the direction of the tilt (*L*), divided by the square root of the product of the average lake depth (*z*) and the gravity acceleration (9.8 ms^{-2}).

$$t = 2L/\sqrt{gz}$$

The extent of a seiche depends on the morphology and dimensions of the lake. Seiches have been observed and studied for hundreds of years. In Lake Geneva, Switzerland, one of the first lakes where seiches were studied an uninodal period of about 74 minutes and a binodal period of about 35 minutes was recorded. The observed uninodal periods in Lake Garda and Lake Maggiore, Italy, are approximately of 40 minutes with an amplitude of several centimetres. The seiches causing a regular water movement generate a small water current (of the order of cm sec^{-1}) alternatively changing direction.

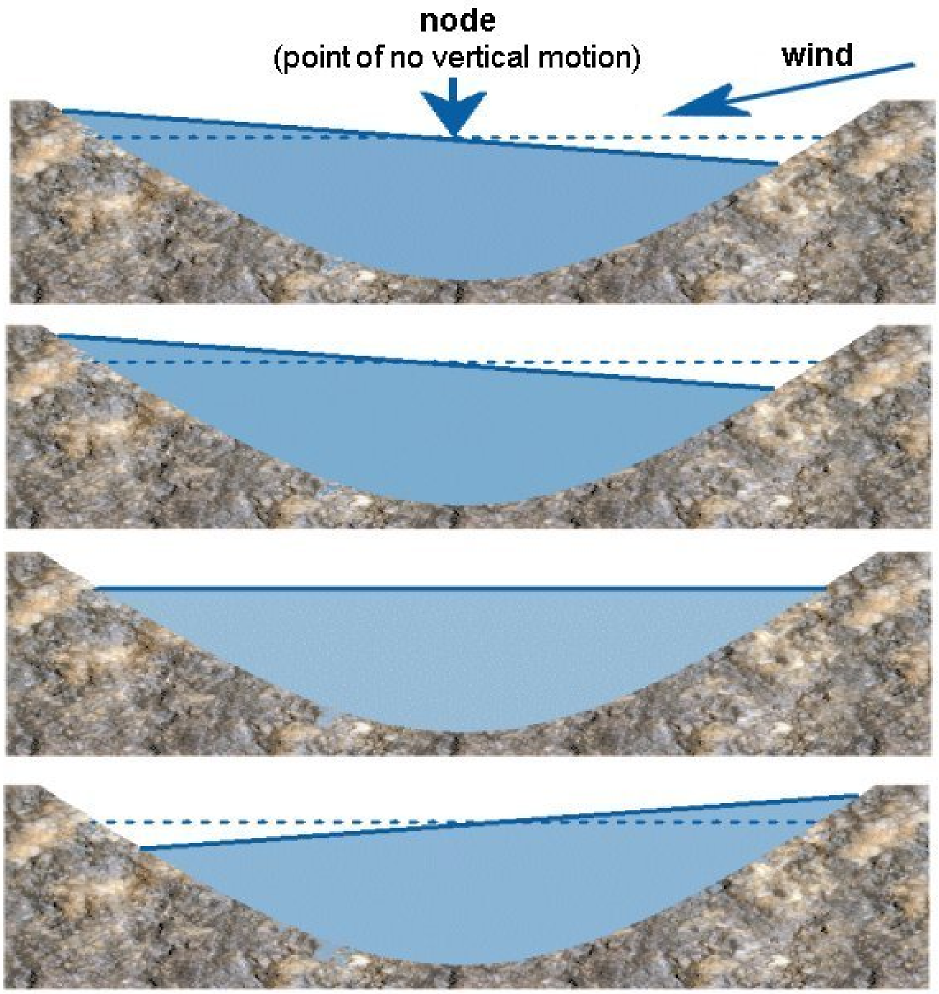


Figure 19. Uninodal surface seiches.

The internal (underwater) seiches

The internal seiches (Figure 20) are due to the "accumulation" of water masses produced by a wind blowing in the same direction for a time span long enough. Internal seiches occur during thermal stratification. The lake layers separated by the thermocline oscillate one relative to the other. The phenomenon is not evident at the lake surface but it becomes evident as a periodic variation of the thermocline depth. The necessary data are gathered from continuous measures of the temperature vertical profile with a chain of sensors. The massive water movements and the turbulent exchanges occurring during internal seiches produce at the border between epi and hypolimnetic layers, a periodic exchange of waters very different in thermal and biological characteristics. The consequent transport of heat and dissolved substances can significantly affect the distribution and the production of phyto- and zooplankton.

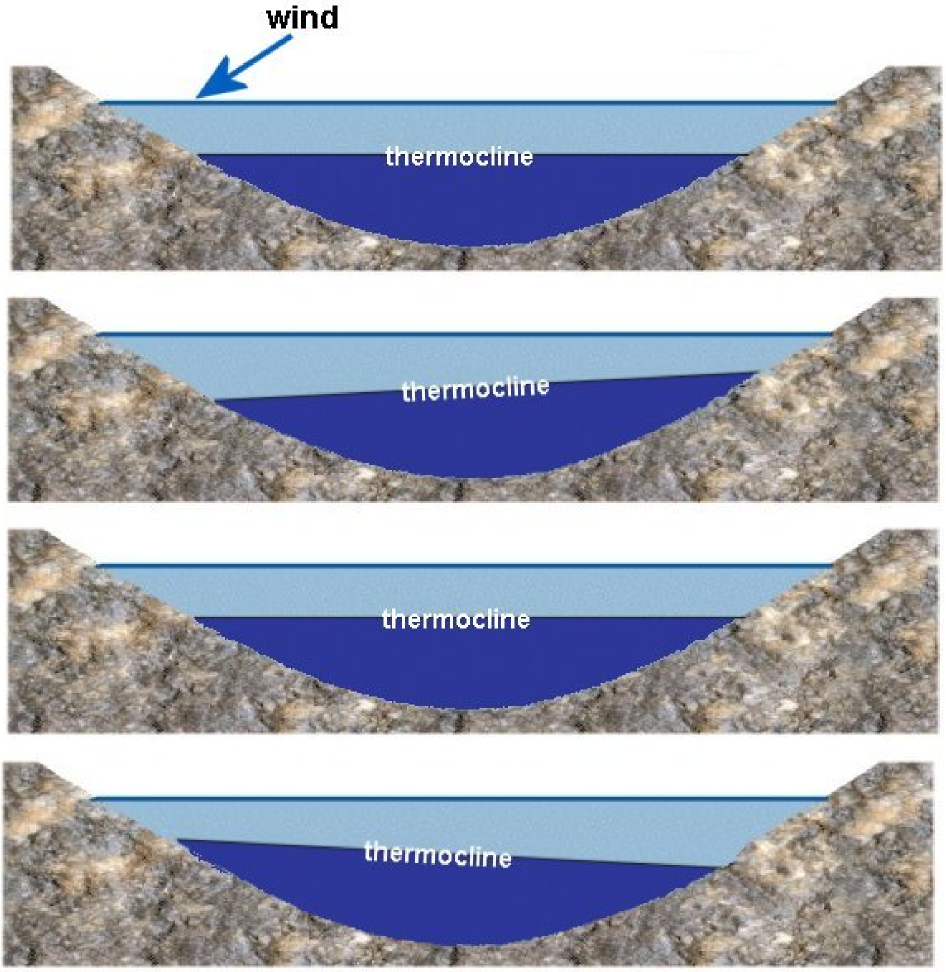


Figure 20. Evolution in time of internal seiches.

Internal seiches are usually larger and of longer periods than surface seiches and can be several meters high. The resulting current flow rhythmically back and forth in opposite directions and are one of the most important causes of movements of the deep layers of lake water. The period of internal seiches can be computed, considering the lake as divided in two homogeneous layers with different densities, from:

$$t = \frac{2L}{n \times \sqrt{\dfrac{g(d_b - d_a)}{\dfrac{1}{b} - \dfrac{1}{a}}}}$$

where L is the lake length at the thermocline, a and b are the thickness of the epilimnion and hypolimnion respectively, d_a and d_b is, for each layer, the water density at the average layer temperature, g is the acceleration of gravity, n is the number of nodes of the seiche. From this relation it is clear that the period is directly proportional to the lake length and increases with decreasing density difference of the two layers.

To give an idea of the size of the phenomenon, the observed uninodal periods in Lake Geneva (surface 345.31 km^2) and in Lake Baikal (surface 31,722 km^2) are approximately 96 and 900 (binodal) hours, respectively.

In large lakes (hundreds km^2) the movement of internal seiches is not merely a pendulum swing because the water masses involved are affected by Coriolis force. The result is a circular path with the flow directed, in the northern hemisphere, towards the coast.

An online Seiche Calculator is available at the website of University of Delaware at the URL: http://www.coastal.udel.edu/faculty/rad/seiche.html

The Lagmuir currrents

Winds with speed between 10 and 25 km h^{-1} induce large-scale counter-rotating helical vortices known as Langmuir circulation. The alternating convergence and divergence zones of the Langmuir currents are visible by the appearance of streaks of foam or scum on the lake surface in the direction of the wind. These streaks are originated by the transport and accumulation of suspended particles and dissolved matter by the spiral water movement (Figure 21). The diameter of the spiral approximately equals the epilimnium thickness. Langmuir circulation is largely responsible for the mixing of the surface layer and the deepening of the epilimnion.

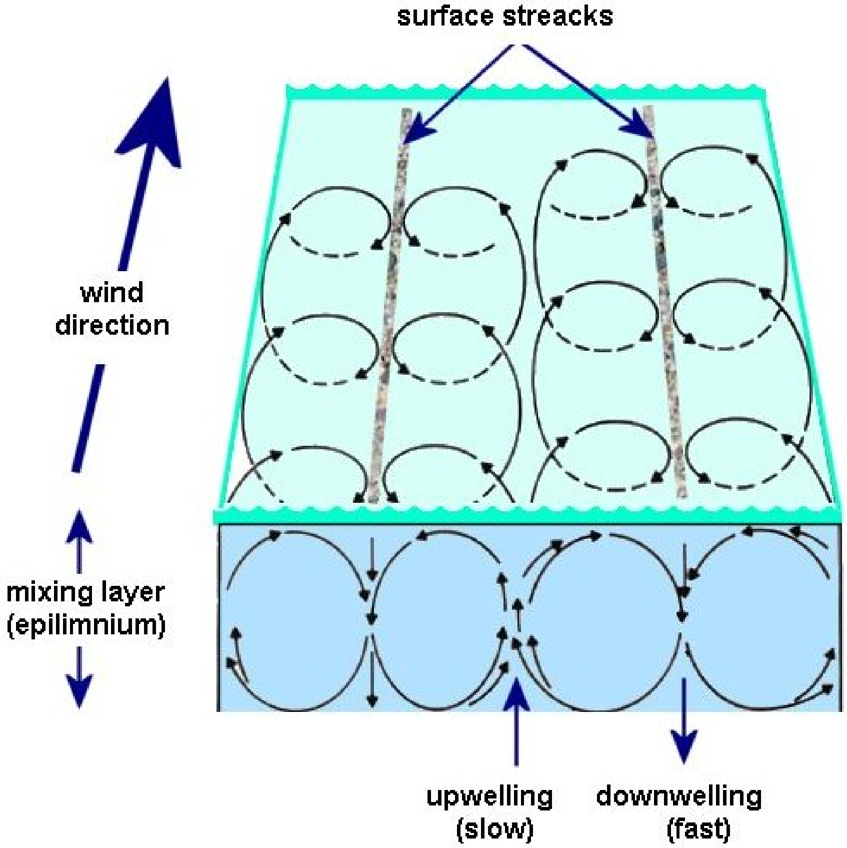


Figure 21. The spirals of Lagmuir: diagram of their formation and surface streaks production.

The surface current drift

These are non periodic water movements caused by water dragging in the direction of the wind of the uppermost surface layers, with transport of subsurface waters, although it rapidly decreases with depth.

The current velocity is, roughly, about 2% of the wind velocity, but it is widely variable depending on the lake morphology. The current promoted directly by wind action differs greatly from lake to lake and no generalization is possible.

The water thus displaced is replaced by other coming from the surrounding lake zones and from the deeper layers, shielded from direct wind action. This originates counter-currents mixing the upper layers till the depth affected by wind. They can disrupts the equilibrium of water layers, triggering a water movement that continues even when the wind has ceased.

Wind independent currents can be found also in deep layers and are generated by tributary rivers. Since their waters are generally colder (particularly in summer) and denser because of the suspended material, they slide along the lake bottom to the depth where river and lake densities are equal. For riverine waters the thermocline can be a sliding surface which limits the mixing of river and lake water to epilimnetic layer.

Surface currents can cause sediment resuspension in shallow lakes and in littoral zones, increasing the water turbidity and reducing the light penetration and, consequently, the volume of the productive zone. In addition, the resuspension reintroduces in the water column the nutrients, previously segregated in bottom sediments. In this way the resuspension can contribute maintaining or developing lake eutrophication.

4.4 Lakes zonation

According to light and temperature distribution in a lake, zones with different characteristics can be located which are commonly used in limnological context (Figure 22).

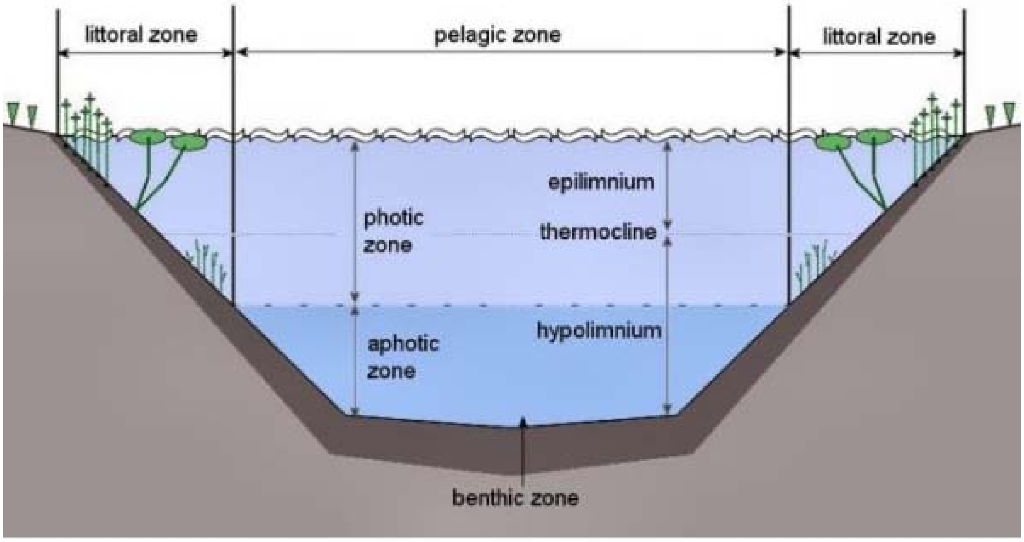


Figure 22. The zones of a lake.

Littoral zone: is the portion of the lake horizontally extending from the shore to the point impending the bottom area where submerged macrophytes and bentic algae can live. This is the part of the lake bottom reached by solar radiation, included in the photic zone.
Pelagic zone: is the portion of the lake above the depths not reached by solar radiation.
Photic or euphotic zone: is the layer of water vertically extending from the surface to the depth reached by 1% of surface solar radiation.
Aphotic zone is the part of the water column not reached by solar radiation.
Epilimnion / hypolimnion: water layers overlying / underlying the thermocline.
Thermocline or metalimnion: is the layer of water where the temperature changes of 1°C per meter.
Benthic zone: is the portion of the lake located at the water-sediment interface. In the aphotic zone it is often called profound benthic zone.

4.5 Oxygen and other gases distribution in lakes

Aquatic organisms as well use for their metabolism atmospheric gases. But these have low solubility in water so that the gas availability is lower for aquatic than for terrestrial organisms.

	Partial pressure	Concentration (mg L^{-1})			
		0°C	10°C	20°C	30°C
O_2	20,99%	14,5	11,1	8,9	7,2
N_2	78,0%	22,4	17,5	14,2	11,9
CO_2	0,03%	1,005	0,7	0,51	0,38

Table 3. Partial pressure of the main gases of the atmosphere and their solubility in water at different temperatures at atmospheric pressure.

Oxygen

Oxygen is present in water at low concentrations that, in some cases, can quickly reduce to zero establishing conditions incompatible with the life of the majority of organisms except some bacteria. The oxygen solubility in water is mainly affected by lake temperature and decreases with increasing temperatures (Table 3).

The amount of atmospheric oxygen that can dissolve in lake waters up to saturation depends also on lake altitude, because the decrease in barometric pressure with increasing altitude reduces the partial pressure of oxygen in the atmosphere. Moreover, the solubility of oxygen depends on the humidity since the water vapor forming at the lake surface dilutes the concentration of other atmospheric gases, reducing their partial pressure.

Also biological activities affect oxygen concentration in lakes. Biological production (photosynthesis, performed by plants) releases oxygen into the water, while biological decomposition (carried out by heterotrophic bacteria) consumes it. Such activities can alter the relative oxygen saturation of water, rising or lowering it with respect to the theoretical value for some temperature and pressure conditions. Thus the oxygen vertical distribution depends on turbulence and on lake temperature on the one side and on biological activities on the other.

During cold seasons, when vertical mixing is possible because of a lack of thermal structure and increased wind stirring, lakes are replenished with oxygen (Figure 23 A and B) . In the warmer seasons, in oligotrophic (i.e. non productive) lakes surface waters, despite the lower concentrations, may remain as well saturated as deep waters (Figure 23 C). The oxygen concentration is essentially uniform along the water column, exhibiting an orthograde profile. On the contrary, in eutrophic (i.e. very productive) lakes, surface waters can even be supersaturated while in deep waters oxygen consumption due to biological decomposition may lead to serious oxygen depletion (Figure 23 D). The oxygen concentration decreases with depth showing a clinograde vertical distribution. If vertical mixing occurs in autumn, also the eutrophic lake is again replenished with oxygen (Figure 23 A and B). In eutrophic lakes freezing in winter the ice cover may significantly inhibit the replenishment of oxygen, leading to anoxia at the bottom layers (Figure 23 F).

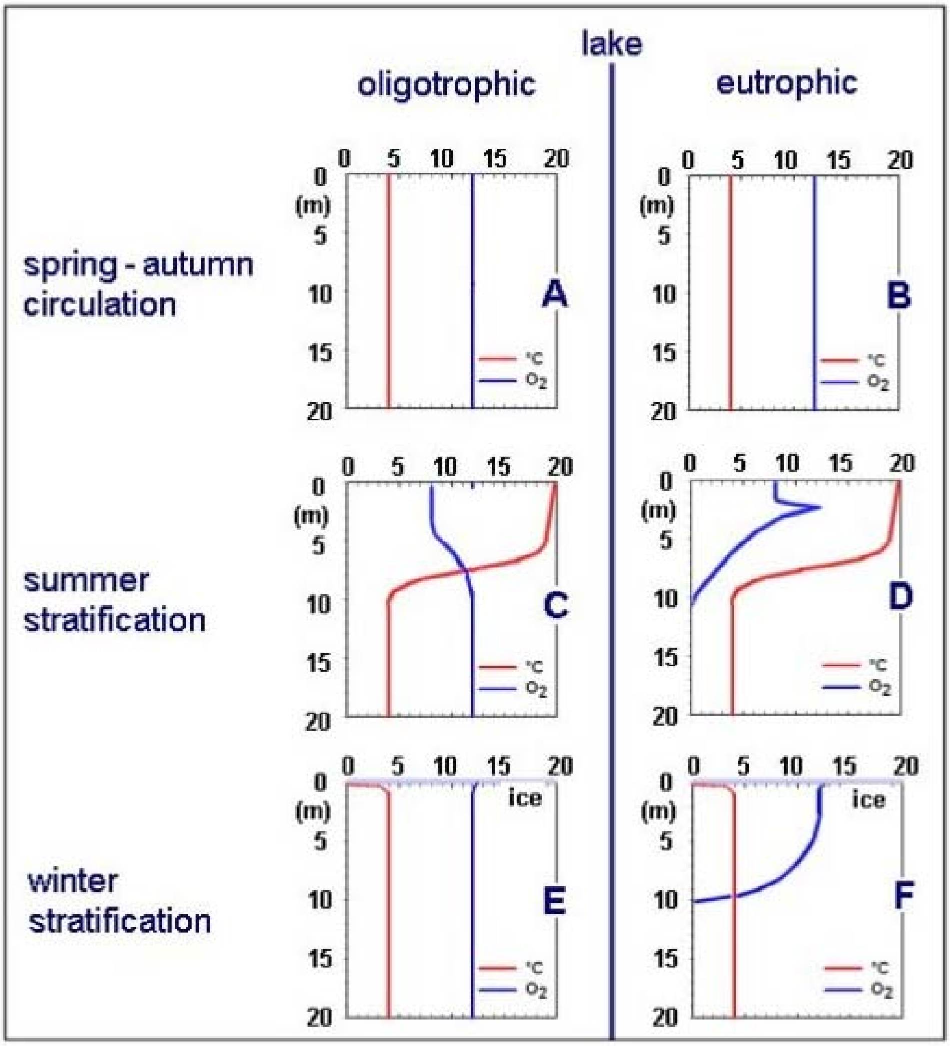


Figure 23. Vertical distribution with depth (m) of oxygen concentration (O: mg L^{-1}) and temperature (T: °C) in two ideal dimictic lakes, one oligotrophic and the other eutrophic.

Since most fishes can't live at oxygen concentrations below 2 mg L^{-1}, when summer or winter anoxia occurs a massive fish death is likely. The morphology of the basin influences the hypolimnetic anoxia phenomenon because, other things being equal, the hypolimnion of a shallow lake contains less water, and therefore less oxygen, with respect to a deep lake, thus becoming anoxic more easily and more quickly.

Nitrogen

Nitrogen is the most abundant gas in the atmosphere (almost 79%) and in waters. The maintenance of life requires large quantities of this element, essential component of proteins, nucleic acids and other cellular constituents. Nitrogen is not used directly by organisms since it is rather inert. To be used in animals and plants metabolism, nitrogen must be "fixed", that is combined with other elements to form more reactive compounds such as ammonium ion (NH_4^+) or nitrate (NO_3^-). Most of the nitrogen in these forms reaches lakes as a result of natural biological activity (nitrogen fixing bacteria and bacterial degradation of organic matter) or human activities taking place in the terrestrial ecosystem. In the aquatic environment the only organisms able to fix atmospheric nitrogen are anaerobic photosynthetic bacteria and cyanobacteria.

Carbon dioxide

Although the concentration of CO_2 in the atmosphere is low (0.033%), the CO_2 in water is relatively abundant. Photosynthesis requires the presence of carbon dioxide, and CO_2 is released during biological mineralization of organic matter. Carbon dioxide, unlike the other gases, is not only very

soluble in lake water but it also reacts with the solvent forming carbonic acid. This dissociates and raises the concentration of hydrogen ions lowering the pH.
The relative proportions of bicarbonate, carbonate, and free carbon dioxide depend upon the pH. At high values of pH, carbonate ions will predominate; at low values, free carbon dioxide and carbonic acid will predominate.
The various carbonates (of sodium, calcium, potassium, and magnesium) are important to the carbon dioxide equilibrium in waters. They originate by dissolution of carbonate rocks and reach water bodies through the hydrographic system. Increased pressure of carbon dioxide in the system increases the carbonate solubility. In some cases, photosynthetic activity results in the precipitation of certain carbonates. Biological activities producing or consuming CO_2 alter the equilibrium of inorganic carbon forms and therefore the pH. For example, the consumption of CO_2 for photosynthesis removes H^+ raising the pH. Conversely, the biological oxidation of organic matter produces CO_2 lowering the pH.
In not very acidic waters (pH much less than 7) nor very basic (pH much greater than 7 but less than 14), the carbon dioxide system behaves as a buffer, because, withincertain limits, a change in pH will cause a shift within the system that ultimately serves to offset the pH change. Most lakes have a pH between 6 and 8, but in nature also extremely acid volcanic lakes, with pH values below 4, as well as lakes with very high pH values (soda lakes) Occur.

4.6 Lake chemistry and element cycles

The carbon cycle
Since carbon is the basic element involved in matter and energy exchanges between living organisms, there is an incessant exchange of carbon between biotic and abiotic structures of the ecosystem, defined as the carbon cycle. This exchange involves the inorganic carbon forms as described above and the biological processes of synthesis and oxidation of organic carbon. The carbon cycle in water is shown in Figure 24. Using the light energy vegetable organisms (algae) convert CO_2, through photosynthesis, in carbohydrates, then used to synthesize more complex organic substances. The algae are consumed by animals and the organic matter of their cells is further processed. During their life vegetables and animals obtain energy from the consumption of organic matter (respiration). This process ends with the release of CO_2, which returns in the cycle as inorganic carbon still available for vegetables. When organisms the organic die matter of their bodies is decomposed by bacteria oxidizing it to CO_2.

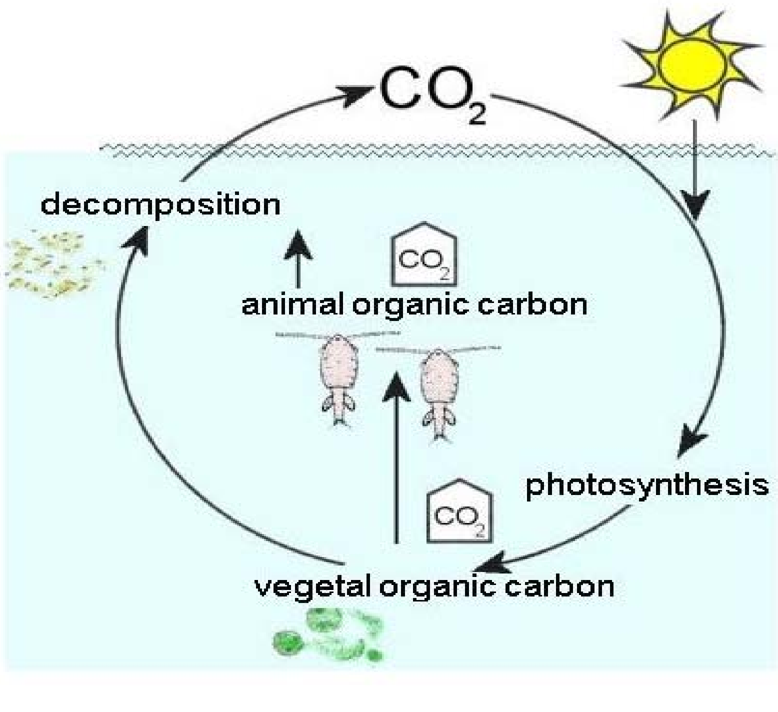


Figure 24. The carbon cycle in waters.

Elements occurring in lake water

The water acidity due to CO_2 dissolution causes the solubilization of soils and rocks of the catchment area. The ions transported by runoff determine the ionic spectrum of the elements present in lake water, closely dependent on the geology of the basin.

In addition, wastewater and meteoric water altered by human activities can significantly change the elements spectrum, for example by increasing the relative abundance of nitrates and phosphates, responsible for eutrophication.

The main elements contributing to the builting up of organic matter, i.e. nitrogen, phosphorus and sulfur, in waters are cycling from their ionic forms, mostly inorganic, to organic molecules and then back to inorganic status because of biological and, particularly, microbiological activities.

Phosphates, nitrates, and sulphates

The most important phosphorous compounds in lakes are orthophosphate and various organic phosphates. Phosphates and nitrates are consumed in large amounts in the upper layers of lakes during periods of high productivity of phytoplankton. High concentrations occur in deeper layers due to mineralization and regeneration from biological material in the sediments, especially during anoxic conditions (Figure 25). In many lakes, phosphorus and/or nitrogen are the limiting nutrients and therefore their abatement is necessary to reduce the eutrophication.

Nitrogen and its various compounds form another complex system in lakes, appearing as free nitrogen in solution, organic compounds, ammonia, nitrite, and nitrate. Sources of nitrogen compounds include influents of the lake (the most important source), fixation in the lake, and precipitation. Losses occur mainly through effluents but also by denitrification, sediment formation, and loss to the atmosphere (Figure 26).

Sulphur usually occurs as a sulphate ion in lake waters. If the bacterial oxidation of biological material at the lake bottom occurs under anaerobic conditions, sulphur from proteins is reduced to hydrogen sulphide. This is the normal condition of many meromictic lakes. The characteristic and unpleasant odour of this gas reveals the existence in a lake of conditions incompatible with eukaryote life.

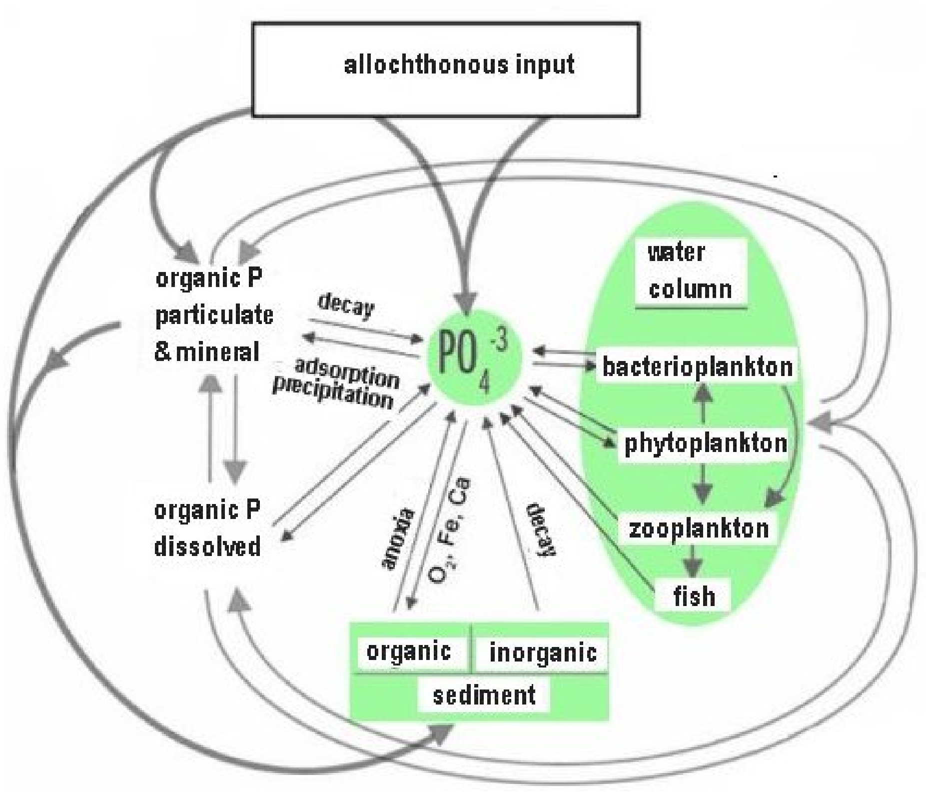


Figure 25. The phosphorus cycle in waters.

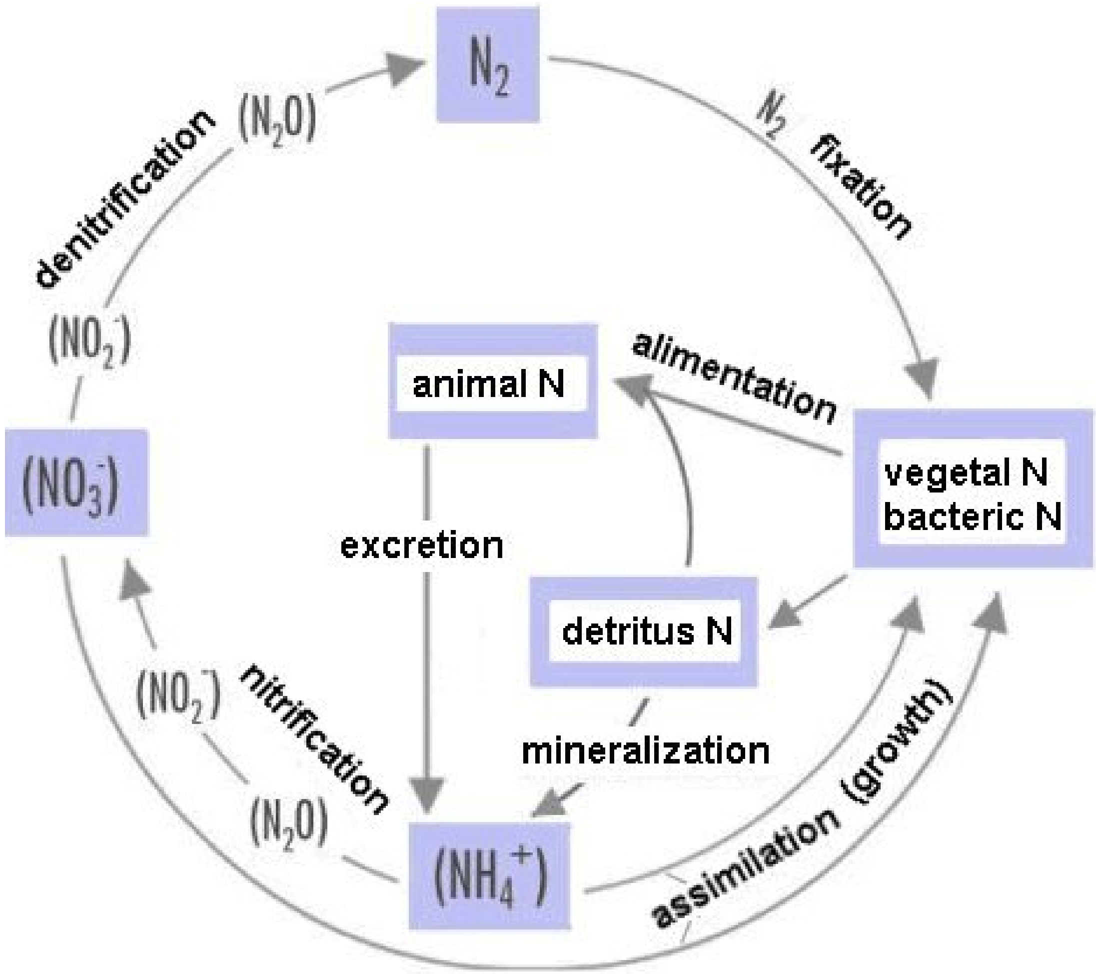


Figure 26. The nitrogen cycle. The cycle runs in five steps during which the following processes, mainly biological, take place: 1) production of organic N by algae and bacteria (from fixation of atmospheric N, from ammonia or nitrate); 2) assimilation of organic N by animals; 3) production of ammonia by animal excretion and by microbial mineralization of detritus; 4) oxidation of ammonia to nitrate (nitrification); 5) reduction of nitrates to N (denitrification).

A comprehensive text on issues related to freshwater chemistry is Stumm and Morgan (1995).

Organic matter

The lake water contains, in suspension and in true or colloidal solution, varying amounts of organic matter generated by in-lake biological activity (autochthonous substances) or drained by tributaries from catchment (allochthonous substances). The former comes from excretion and secretion by organisms, feces, intracellular matter released by dead cells. The allochthonous substances come from soil leaching and domestic and industrial waste. The terms describing the different organic matter fractions in lakes evolved according to analytical improvements. The organic matter is determined as CO_2 coming from its oxidation at high temperature so that the expression organic carbon is often used instead.

The boundary between particulate and dissolved fraction is set at 0.2 - 0.45 - 1 µm, according to the pore size of filters used for separation and the subsequent requirements for the filtrate analysis. The upper limit of particles, however, is arbitrarily placed around 100 µm, beyond which organic matter can be measured by weight (or biovolumes) selectively for different taxa. The size fractions of organic matter in lakes are summarized in table 4, also accompanied by the acronyms commonly used in limnology.

<table>
<tr><td></td><td colspan="2">density</td><td colspan="2">acronym</td><td>type</td><td rowspan="5">↑
^</td></tr>
<tr><td rowspan="9">Organic Matter</td><td rowspan="4">sedimenting</td><td rowspan="4">gravitoidal</td><td colspan="2"></td><td>mobile organisms > g</td></tr>
<tr><td colspan="3">---------- limit: ~ 100 µm</td></tr>
<tr><td rowspan="2">POM</td><td>live</td><td>microscopic organisms</td></tr>
<tr><td>dead</td><td>detritus</td></tr>
<tr><td rowspan="5">non sedimenting</td><td>colloidal</td><td>COM</td><td colspan="3">-----------limit: 1 – 0,45 – 0,2 µm</td></tr>
<tr><td rowspan="4">dissolved</td><td></td><td>RDOM</td><td>humic and fulvic acids</td><td rowspan="4">v
↓</td></tr>
<tr><td>DOM</td><td>ADOM</td><td>enzymes, hormones</td></tr>
<tr><td></td><td>LDOM</td><td>amino acids, shugars</td></tr>
<tr><td colspan="2">VOM</td><td>alcohols, aldehydes</td></tr>
</table>

Table 4. The organic matter in aquatic environments: classification by size and type of different organic matter fractions in waters.
Key acronyms:
OM: Organic Matter = Organic Matter;
(When expressed as carbon: OC = Organic Carbon);
V: volatile; D: dissolved C: colloidal P: particulate;
R: refractory = resistant to bacterial decomposition;
A: active = able to promote biochemical reactions;
L: labile = easily decomposable by bacteria.

The Volatile Organic Matter (VOM) is made up by both man-made and naturally occurring chemical compounds which have significant vapor pressures. The VOM has a tendency to evaporate at temperatures at which water is still liquid. The Dissolved Organic Matter (DOM) is the fraction smaller than 1 - 0.2 µm. It is mainly constituted by simple molecules such as sugars and amino acids and is defined labile since it is rapidly utilized by bacteria. Such molecules are released during photosynthesis and in this case they are also called EOC (Extracellular Organic Carbon). DOM encompasses also a fraction, defined "bioactive", including biochemically active molecules such as enzymes, vitamins and hormones. Furthermore, there are allochthonous substances coming from degradation products of lignin or of soil humus, such as fulvic and humic acids, extremely abundant in lakes of forested areas. They are also called "Colored Dissolved Organic Matter" (CDOM) since they give lakes a yellow-brown color. Some of them have very high molecular weight and are colloids (COM: Colloidal Organic Matter). Bacteria mineralize them with difficulty and very slowly and therefore they are defined Refractory Dissolved Organic Matter (RDOM).
Finally, the Particulate Organic Matter (POM) is the fraction made up by detritus (dead organisms and fragments of cells or organisms) and by the organisms (bacteria and protozoa) colonizing it. Algae as well may be part of these aggregates. The constituents of such assemblages are hardly isolated, so POM also includes a living component. The term *seston* is used to indicate the pool of small organic and inorganic particles, living and nonliving, suspended in water. The term *tripton* identifies, however, only the inorganic component of seston.
It should be stressed that particles and dissolved molecules occur in water in a dimensional continuum and, therefore, the identification of size fractions of organic matter in lakes only has an operational value. Since the autochthonous organic matter results from the production and decomposition budget of a lake, its abundance depends on the trophic status of the lake.

5 Lake food chain: autotrophy and heterotrophy in waters

The different chemical and physical characteristics of water and air (Table 5) expose aquatic and terrestrial organisms to very different environmental conditions.

	Water	Air
density (g L^{-1})	1000	1,19
viscosity (P)	0,009	0,0002
O_2 conc. (mg L^{-1})	8	250
CO_2 conc. (mg L^{-1})	0,3	250

Table 5. Comparison of key physical and chemical characteristics of water and air.

The consequences of such diversity can be summarized as follows:
- Due to the highest density of freshwater as opposed to the atmosphere, aquatic organisms do not require a supporting body apparatus as strong as that required by terrestrial organisms. Water has a density close to that of many organisms living in it.
- The viscosity of water, about 50 times higher than air, makes the moving energy cost for a comparable displacement higher for an aquatic than for a terrestrial organism;
- The oxygen concentration, much lower in water than in air, oblige the aquatic organisms to perform more work than the terrestrial ones to provide the same amount of oxygen to respiratory epithelium;
- The concentration of free carbon dioxide is higher in water than in the atmosphere. Aquatic vegetals, therefore, have more inorganic carbon available than the terrestrial ones, at least in the surface layers;
- Water autotrophs can access nutrients dissolved in water without the need of specific transporting structure. This, and the previous condition, favors the small size in aquatic plants and, accordingly, in the animals feeding on it.

From these considerations it emerges that, in the aquatic environment, animal life has to face more difficulties than plant life, also facilitated since for it a significant increase in body size is not necessary.

In spite of these differences, both in aquatic and in terrestrial ecosystems matter and energy flow through a chain of organisms transforming it and constituting the food chain (Figure 27). The energy flowing though the food chain progressively degrades to heat and matter is recycled, passing through stages of variable molecular complexity.

According to their role in the food chain aquatic organisms can be:

1. Primary producers. This category includes the autotrophic organisms able to synthesize organic matter using the energy of the sun and inorganic substances. The primary producers can be unicellular algae, often colonial, free floating (phytoplankton) or adhering to a substrate (periphyton) and aquatic plants (macrophytes) growing in the littoral zone. The category of autotrophic organisms also includes photosyntetic and chemosyntetic bacteria;
2. Consumers, including primary consumers (feeding on autotrophs), secondary (feeding on animals eating plants), tertiary (feeding on secondary consumers), and so on. The last link in the consumer chain is held by carnivorous fish, birds or fish-eating mammals. The consumers are heterotrophs because they use organic matter already produced, being unable to synthesize it from inorganic compounds;
3. Detritivores. They are organisms feeding on the remains of dead organisms and on the waste products of metabolism, progressively degrading it to less complex chemical structures;
4. Decomposers. They are mainly the heterotrophic bacteria, oxidizing (decomposing) the organic molecules till they are reduced to their inorganic constituents (mineraliziation). These are newly made available for the autotrophs and are thus re-cycled.

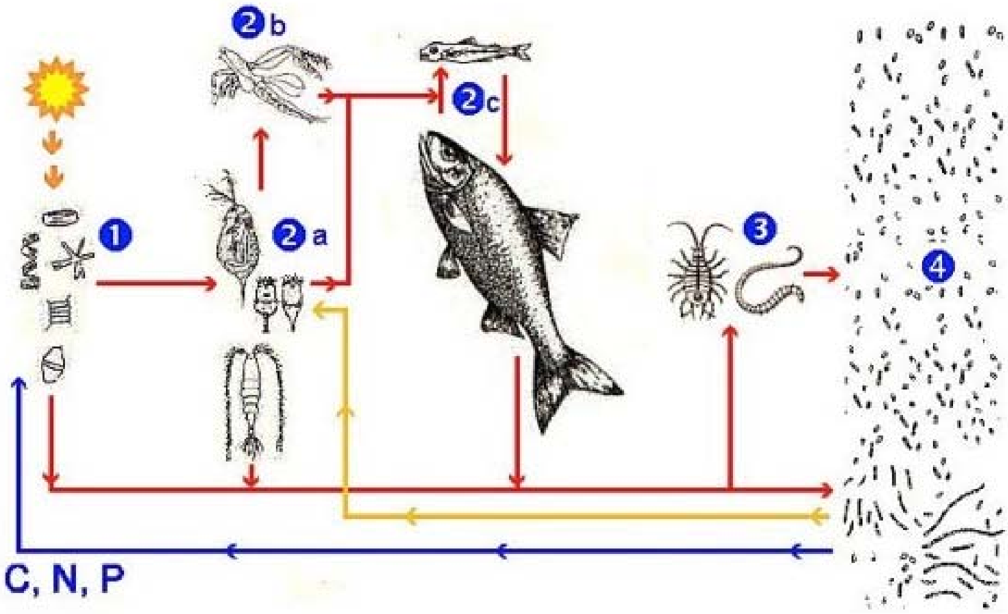


Figure 27. Scheme of the food chain. The solid line represents the transfer of the chemical energy (i.e. food) from primary producers (1) to primary consumers (2 a), to secondary (2 b) and to tertiary (2 c) up to detritivores (3). The chemical energy remaining after these steps is used by decomposers (4) recycling it, being themselves food for smaller plankton (dotted line) and mineralizing it, making the inorganic molecules again available to autotrophs (dotted line).

To complete the above classification of physiological activity in autotrophic and heterotrophic, mixotrophic activity must be added. It is frequent in aquatic environments and is performed by single-cell microorganisms able to photosynthesize organic substances and to feed on the organic substrate already present in waters. The category of mixotrophs is very adaptable since autotrophy and heterotrophy can be alternative or exclusive, depending on environmental conditions. A particular form of mixotrophy is performed by some species (protozoa and coelenterate) containing symbiotic algae in their protoplasm.

According to their typical habitat, aquatic organisms are also often classified as:
1. Plankton, consisting of animals (zooplankton), vegetals (phytoplankton), bacteria and archaea (bacterioplankton) and virus (virioplancton). Plankton occupies the littoral and the pelagic zone of lakes, but the presence of autotrophic phytoplankton and autotrophic bacterioplankton, both performing a light-dependent activity, is obviously limited to euphotic zone. The freshwater zooplankton community encompasses organisms mostly of microscopic size and belonging to different systematic groups, ranging from protozoa to crustaceans. Although some planktonic taxa have organs to move, the plankton is unable to oppose the current movement and is transported by the water mass hosting it. Hence the name plankton, which in Greek means "vagabond".
2. Benthos, the community living in the benthic zone (from the Greek *benthos* = abyss), at the surface or inside the bottom sediment. It is a very complex community, both from the taxonomical and the functional point of view. It includes mobile and sessile organisms and can vary greatly even within the same environment due to the physical differences (granulometry) of the sediment.
3. Nekton (from the Greek *néchein* = to swim) is the fish community, including littoral and pelagic species. It is therefore composed by organisms larger then plankton, able to transfer within the lake winning the current movements.
4. Neuston, which consists of microscopic organisms, protozoa and bacteria, living in the surface film at the water-air interface. This group also includes larger organisms (insects) able to move on the water surface because of surface tension.

5. Periphyton (or "Aufwuchs"), is the film of algae covering the submerged organic and inorganic substrates in the littoral zone. Protozoa, sponges, bryozoans and other animals live usually associated with the periphyton.
6. Psammon, is the animal community, including protozoa, rotifers, tardigrades, crustaceans, worms, larvae of some insects, living in interstitial water of sandy beaches.

5.1 The plankton

The ecophysiological or the taxonomic position inside the complex planktonic community is indicated with adequate prefixes. Plankton is also qualified on size basis, in agreement with some size ranges proposed over the years by different authors. Therefore the resulting classification does not reflect some real rigid boundaries, but rather the operational constraints, often imposed by the available separation technologies. It should be noted that often, when identifying a size class of plankton, an adjective is also used to specify the functional class, to distinguish, for example, between heterotrophic picoplankton (exclusively bacteria) and autotrophic picoplankton (mainly vegetal cells, prokaryotic and eukaryotic). The size, physiological, and taxonomic categories of freshwater plankton are illustrated in Figure 28.

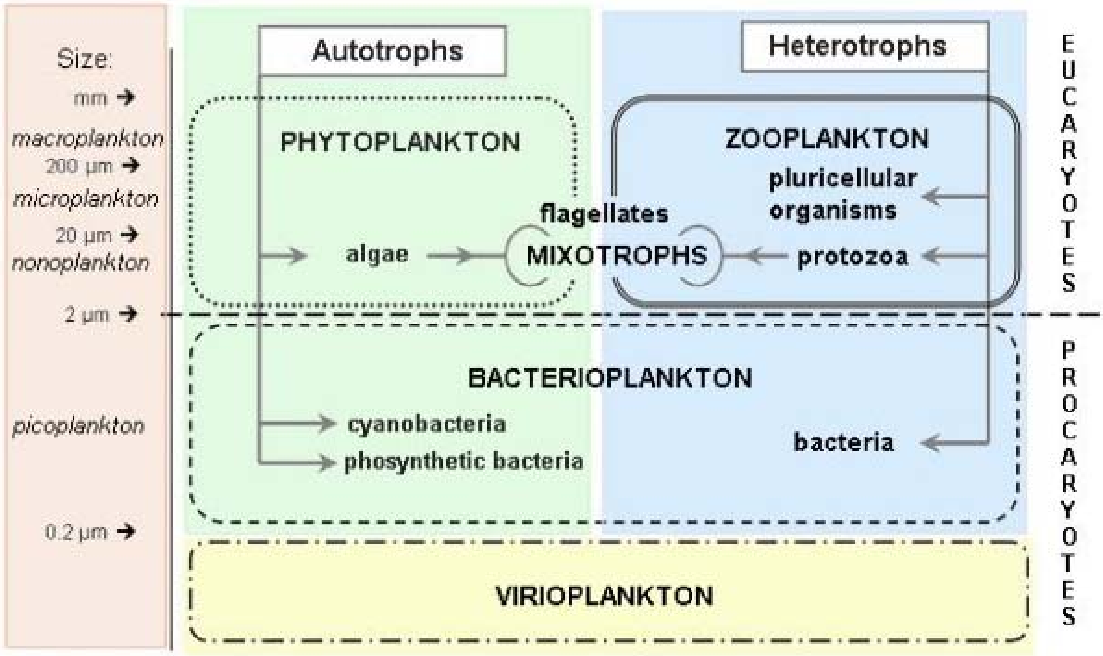


Figure 28. Diagram of size categories and of physiological and taxonomic groups making up the plankton.

5.2 Bacterioplankton and virioplankton

The virioplancton.
Although the presence of viruses in aquatic environments was ascertained early in the 1950's, their ecological role has been considered negligible till the 1990's, when their high abundance was recognized (10^4 to 10^8 viruses ml^{-1}) as was their ability to infect bacteria and algae (Weinbauer 2004). Viruses, therefore, can affect abundance, species composition and diversity of microbial communities and alter the flow of energy and nutrients in the microbial loop. Furthermore they can mediate the exchange of genetic material within and between species by transduction.
Viruses are the smallest organisms known and have a simple structure, consisting of nucleic acids, RNA or DNA, contained in a protein capsule, the capsid. Their size range is 20 - 200 nm and they can reproduce only within living cells of which are obligate parasites. A virus develops through an extracellular and an intracellular phase. In the first one the virus particle (virion), stable and resistant to denaturation, is freely floating in the waters. When a virion, during its passive diffusion, meets a host, it adsorbs to it, protruding protein structures that are receptors of the host's cell

surface. Then it begins the intracellular phase, as the virus itself, or the viral DNA, enters the host cell where it uses its biochemical structures to replicate. Eventually, the newly formed viral particles lyse the host cell, not necessarily destroying it, to be released into the environment. Besides this reproductive cycle, called lytic cycle, viral replication can occur through the lysogenic cycle, in which the viral genome becomes part of the host genome, integrated in it or as an autonomous plasmid. The viral genome remains in a dormant stage (prophage) ending when the changed environmental conditions (UV radiation, stress, chemicals, etc.) induce the lytic phase.

The examination by electron microscopy of viral particles found in aquatic environments has shown that viruses with capsids between 30 and 70 nm are the most abundant while larger viruses (> 80 nm) are rare. This indicates that most viruses of aquatic environments are bacteriophages. The viruses of eukaryotic algae have larger capsids of about 150 nm.

As the abundance of the virioplanktonic community depends on the abundance of the hosts, in highly productive lakes the viral explosions are more relevant than in less productive ones.

The abundance of the viral population can be assessed by epifluorescence microscope, counting the virus particles (Virus Like Particles: VLP) concentrated by differential filtration on 0.02 μm filters after staining with RNA and DNA fluorescent dyes (eg. SYBR-Green). From 1 to 9×10^7 VLP ml^{-1} have been found in lakes. The viral production can be assessed using a technique based on the measurement of the incorporation of radioactive fluorescent tracers (fluorescently-labeled virus tracers: FLV) or isolating the phages infecting bacteria or cyanobacteria. The viral production measured ranges from 0.1 to 7×10^6 viruses ml^{-1} h^{-1}.

The bacterioplankton

The organisms of bacterioplankton are prokaryotes, mostly between 0.2 and 2 μm in size, that is in the picoplankton size range. They can be autotrophs and heterotrophs. The first category includes cyanobacteria, which will be further illustrated in the phytoplankton section, and photosynthetic and chemosynthetic bacteria. Light harvesting in bacterial photosynthesis can't occur in the presence of oxygen and therefore the photosynthetic bacteria can develop only in anoxic environments. They may be very abundant in meromictic lakes where water layers reached by light but permanently segregated from the atmosphere can be found. Chemosynthetic bacteria are abundant only in environments of peculiar chemical features, and meet their energy requirement through the oxidation of minerals substrates.

Heterotrophic bacteria are numerically much more abundant then autotrophic bacteria and are the widest component of bacterioplankton. Archaea, discovered only in the late 1970's and as genetically different from bacteria as the mammals are, are also part of bacterioplankton. Once considered exclusive of extreme environments (hot springs, acidic water), now their abundance and role appear not negligible in lakes. Bacteria have a double role in the food chain (Figure 29):

1. demolition of the organic substance, first-hydrolyzed by the exoenzymes produced by bacteria and then mineralized, thus making their mineral constituents newly available;

2. recycling of dissolved organic matter, through the production of new bacterial cells usable by larger organizations, unable to use directly the dissolved organic matter.

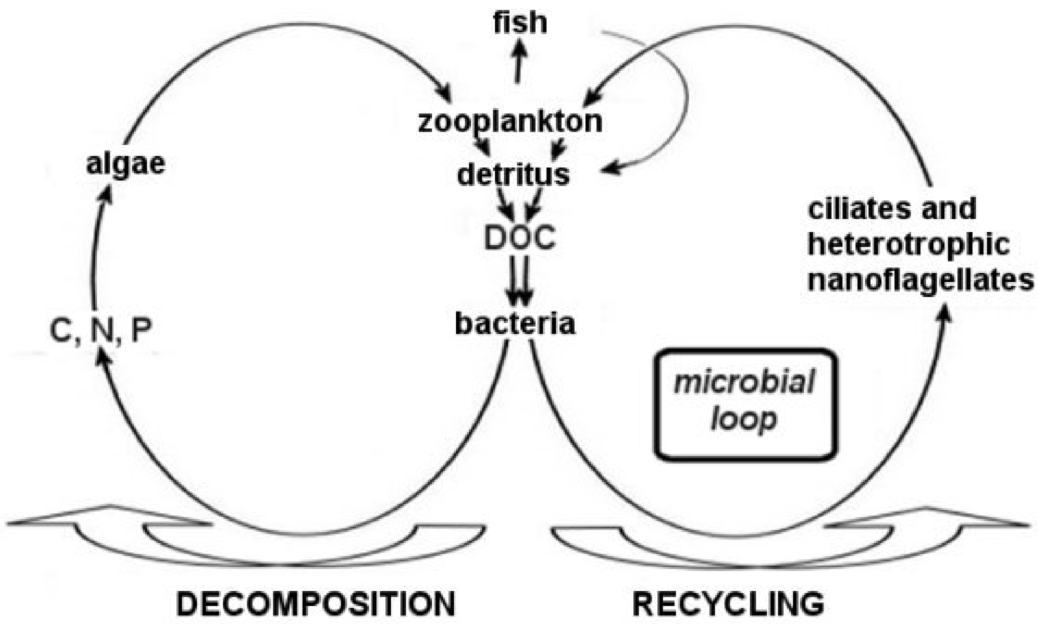


Figure 29. Role of bacteria in the food chain: decomposition and recycling of dissolved organic matter (DOC).

The recycling role, highlighted at the beginning of the 80's and defined as microbial loop (Azam, 1990), is of peculiar ecological importance because most of the organic matter in lakes is in dissolved form and the food chain would lose it if it wasn't transformed by bacteria in cell biomass, preyed upon by heterotrophic nanoplankton, in turn zooplankton prey. Although the bacterial cells abundance is quite large even in oligotrophic lakes (between 10^5 and 10^6 cell ml^{-1}), the measurement of bacterial number, biomass and activity still has a high associated error due to methodological problems raised by the high dilution.
The total number of bacteria in waters became routinely measurable with reasonable accuracy and precision in the mid 1970's, with the introduction of fluorescent staining of nucleic acids, of epifluorescence microscopy (Figures 30, 31). In those years membrane filters of adequate pore size to retain bacterial cells (0.2µm) and to be used with epifluorescence microscope also became available.

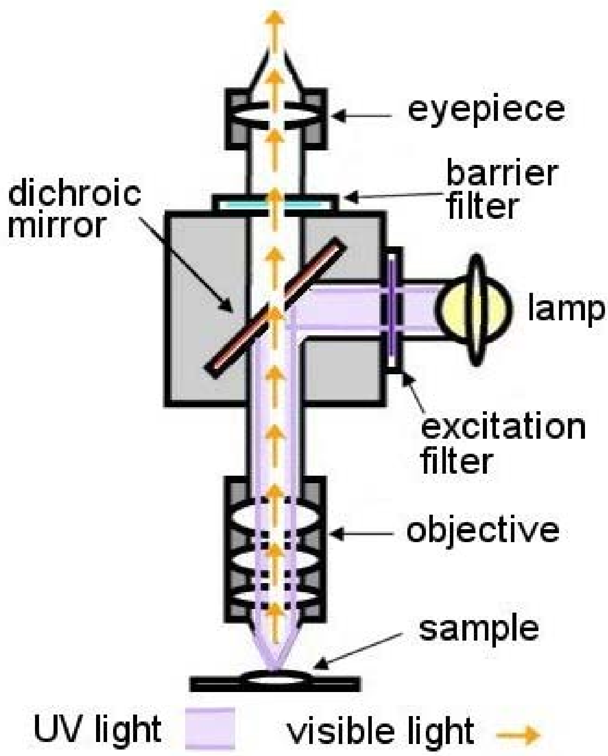


Figure 30. Section of an epifluorescence microscope. The light from a Hg vapor lamp is directed to the sample by a dichroic mirror and reaches the sample passing through an excitation filter selecting the wavelength (UV) exciting the fluorescence of the dye (Acridine Orange, DAPI or SYBR green). The fluorescence emitted by dye bound to bacterial DNA or RNA crosses the dichroic mirror and a barrier filter removing the residual excitation radiation, and finally reaches the observer through the eyepiece.

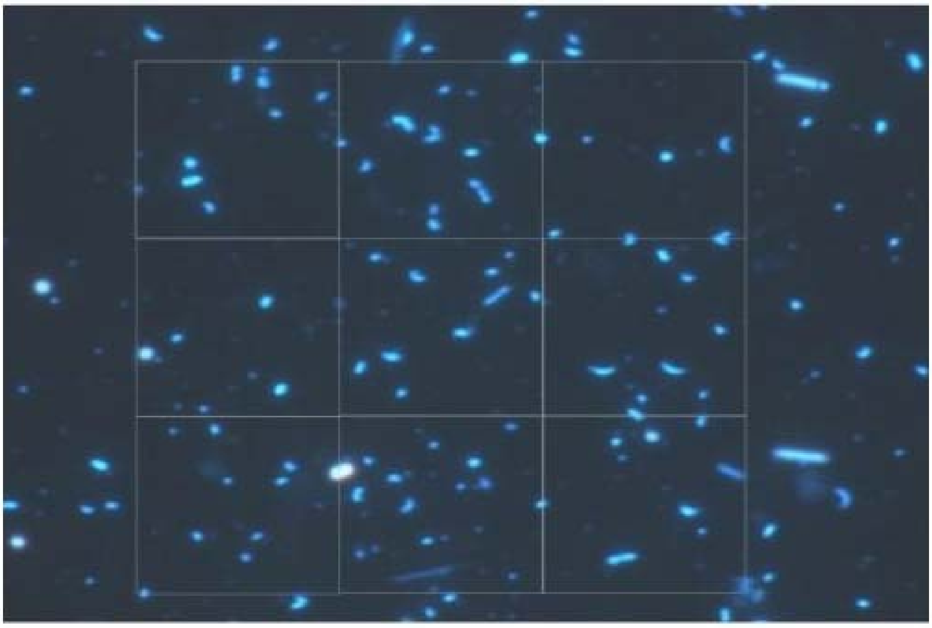


Figure 31. Bacterial cells stained with DAPI (blue fluorescence) observed in epifluorescence at 1250X. Each grid square is of 10 µm size.

The determination of the number and of some metabolic features of bacterial cells in waters is nowadays possible with speed and accuracy using flow cytometry. This technique allows for the counting and examination of microscopic cells, stained with appropriate fluorescent dyes, by suspending them in a stream of fluid. The fluid path is crossed by a laser beam of wavelength suitable to excite the fluorescence of the dye used. When a cell crosses the laser beam, it emits a characteristic fluorescence. By measuring the reflected laser light and fluorescence emitted is possible to estimate the number, size and fluorescence characteristics of cells passed through the laser beam.

The measurement of bacterial activity in waters suffers from methodological and theoretical difficulties. In fact, although the mass of organic carbon metabolized by bacteria in the whole lake is huge, in a water sample the variations in concentration of reagents and products of bacterial activity are very small, particularly in oligotrophic and mesotrophic lakes. It is therefore difficult to determine the bacterial consumption of dissolved organic matter from substrate concentration decrease or the bacterial respiration as O_2 consumption or CO_2 production. Also to measure the bacterial biomass production (BP: Bacterial Production) is not an easy task because the methods currently available, evaluating BP from the uptake of radiolabeled tracers, imply generalizations and assumptions adding uncertainty to the results (Simon and Azam 1989).
A better understanding of the role of bacteria in lakes is now developing thanks to the tools provided by the huge evolution of molecular biology in the last few decades. The use of molecular (i.e. genetic) techniques allows limnologists to study in much greater detail than it was possible ever before the issues of the type of bacteria involved in ecological interactions, studying the bacterial biodiversity changes and the coupled environmental changes. The knowledge of freshwater microbial food web in the last two decades has grown to deserve a specific text (Sigee, 2005).

5.3 Phytoplankton and zooplankton

5.3.1 The phytoplankton

The algal cells constituting the phytoplankton are at the beginning of the food chain because of their ability to synthesize the organic matter necessary to maintain the whole food chain working. The process ending with the production of organic compounds from inorganic substances and light is known as photosynthesis. The organic product of photosynthesis is glucose ($C_6H_{12}O_6$), the most common glucide on the planet. The carbon and the oxygen necessary to built up the organic matter are provided by atmospheric CO_2. The equation summarizing such process is:

$$6\ CO_2 + 6\ H_2O \rightarrow C_6H_{12}O_6 + 6\ O_2$$

Photosynthesis occurs in two phases. During the light dependent phase, light energy from the sun is harvested by special pigments, the most important of which is chlorophyll. The pigments are arranged in a structure named photosystem. In the light dependent reaction, an energy-rich electron of a chlorophyll molecule is passed along a chain of molecules known as the electron transfer system. The energy lost by the electron as it moves along the chain is used to make NADP, (Nicotinamide Adenine Dinucleotide Phosphate) and ATP (Adenosine Triphosphate), very energy-rich but relatively unstable molecules.
Then, in the dark phase, or Calvin cycle, ATP and NADP are used to produce energy-rich carbohydrate molecules which can be stored and used as a basis for all other forms of organic molecules.
The synthesis of new organic matter leads to an increase in cell size and subsequently to a division in two daughter cells. These can be completely separated or they can remain connected though their cell walls, thus forming a colony, showing in many species a characteristic morphology.
Freshwater phytoplankton communities are composed of prokaryotes, the Cyanobacteria, and of eukaryotes, including several taxonomic groups: Diatoms, Chrysophytes (or golden algae), Cryptophytes, Dynophytes, Euglenophytes and Chlorophytes (green algae). Autotrophic prokaryotes and eukaryotes have a different cellular structure. In prokaryotic cells the chromosomes are dispersed in the protoplasm and photosynthetic activity take place in invaginations of the cell membrane while in eukaryotic cells the chromosomes are contained in the nucleus and there are specific organelles, the chloroplasts, devoted to photosynthesis.

The Cyanobacteria, despite being considered as algae (Cyanophyta, or blue-green algae) are actually bacteria with the typical cell structure of prokaryotes. They differ from bacteria for the presence of chlorophyll *a*, the same photosynthetic pigment of eukaryotic algae, which has a different structure from bacteriochlorophyll, the photosynthetic pigment of phototrophic bacteria. The name blue-green algae comes from their color due to some accessory pigments as phycocyanin and allophycocyanin. Photosynthetic cyanobacteria were the first organisms on Earth performing photosynthesis using water as electron donor and releasing oxygen as reaction product. Their photosynthesis progressively enriched (over millions of years) in oxygen the Earth's atmosphere, allowing for the evolution of the life forms now present in the biosphere.
The single-cell cyanobacteria (1-2 µm cell size) may constitute, in oligotrophic lakes, most of the autotrophic picoplankton and account for up to 80% of total primary production. In eutrophic environments, however, the colonial cyanobacteria (genera *Anabaena, Microcystis, Planktothrix*) can have massive growths (cyanobacterial blooms) significantly affecting the lake water quality. Eventually, their excessive production of organic matter can lead to heavy oxygen consumption, even turning the lake anoxic. Moreover cyanobacteria blooms can make lake water unusable for bathing and drinking, as these organisms can produce toxins harmful to livestock and humans if swallowed or even by simple contact.

The Diatoms are one of the most important groups of algae. Their key feature is the presence of a siliceous cell wall, called frustule, composed of two valves: The upper valve is termed the epitheca and is slightly larger and overlaps the lower valve, the hypotheca. The diatoms have two distinct morphologies: the Centra-les, with a radial symmetry (*Cyclotella, Stephanodiscus*, etc.) and the Pennales, showing a bilateral symmetry (*Asterionella, Fragilaria, Navicula*, etc.).. The photosynthetic pigments are chlorophyll *a, c1, c2* and the other pigments are carotenoids which give to the cells their characteristic yellow-golden brown.

The Chrysophytes (Chrysophyceae) are typical of freshwater environments poor in calcium. They are mostly single cells. A peculiar feature is the presence of two flagella, parallel in some genera (*Synura, Mallomonas*, etc.), and opposite and perpendicular in others (*Ochromonas, Dinobryon, Uroglena,* etc.). Many species lack a true cell wall but often they have a layer of scales, the lorica, in which the cellulose can be accompanied by limestone, silica or iron oxides. Their main photosynthetic pigments are chlorophyll *a, c1, c2*.

The Cryptophytes (Cryptophyceae) are the only algae belonging to the division Cryptophyta. They have two flagella approximately as long as the cell. The outer portion of the cell or periplast is composed of a plasmatic membrane and a series of plates placed beneath. The number and shape of these plates are important taxonomic characters. The Cryptophytes contain chlorophyll *a* and *c2* and the phycobilins phycocyanin and phycoerythrin.

The Dynophytes (division Dynophyta) are important constituents of marine and freshwater phytoplankton. They are made by an upper part (the epicone) and a lower part (the hypocone) separated by a belt. They have a longitudinal groove perpendicular to the belt and longitudinal flagella. The main photosynthetic pigments are chlorophyll *a* and *c2*. Unlike other algae, the Dynophytes have an intermediate chromosomes organization between that of prokaryotes and eukaryotes and are thus defined mesokaryotes.

The Euglenophytes (division: Euglenophyta) as well share this intermediate chromosomal structure. These flagellates algae are present in mosly in eutrophic freshwater environments and are rarely found in oligotrophic lakes. The Euglenophytes have two basal bodies with one or two emerging flagella. Their chloroplast contains mainly chlorophyll *a* and *b*.

The Chlorophytes, or green algae, (division Chlorophyta) have morphological and physiological characteristics approaching those of higher plants. Chlorophyll *a* and *b* are present in their chloroplast, and they appear green because the chlorophyll is not masked by accessory pigments. A character making them different from other algal groups is the presence of 2 or more flagella similar in structure but differing in length.
Figure 32 presents the micrographs of some algal species. The phytoplankton taxonomy is a very complex issue; helpful though introductory information to approach the problem can be found in Streble and Krauter (1988).

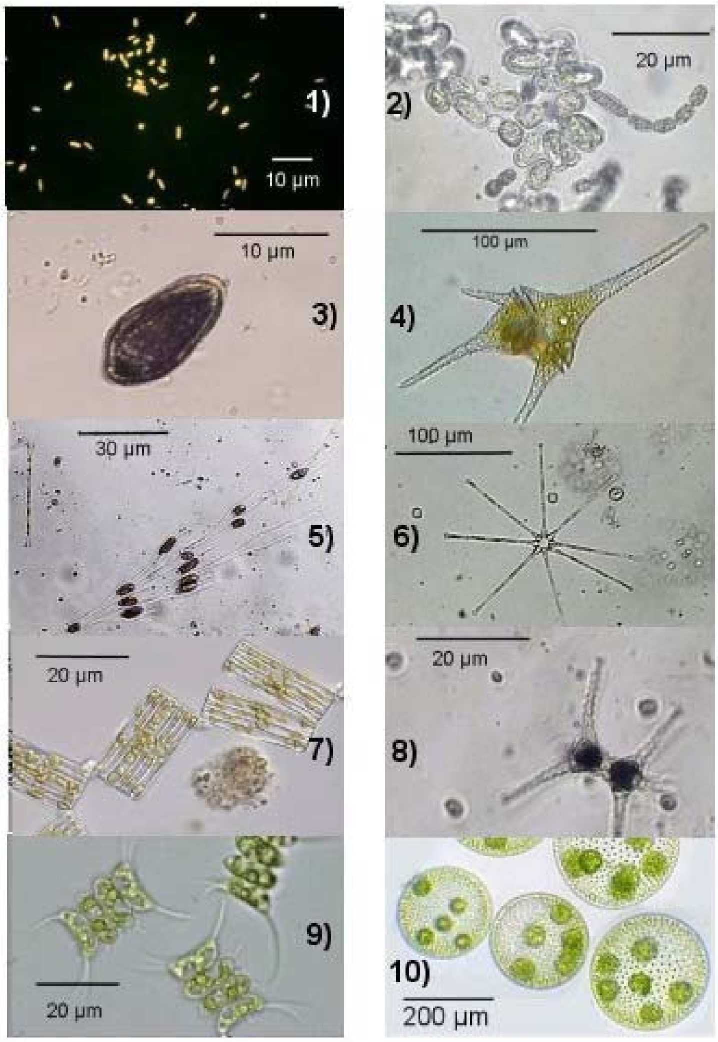


Figure 32. Examples of different morphologies and sizes of freshwater phytoplankton. **Cyanobacteria:** 1) *Synechococcus* sp., single cells; 2) *Anabaena* sp., colonial. **Cryptophytes:** 3) *Cryptomonas* sp. **Dynophytes:** *4) Ceratium* sp. **Chrysophytes:** 5) *Dinobryon* sp. **Diatoms:** 6) *Asterionella* sp.*; 7) Tabellaria* sp. **Chlorophytes:** 8) *Staurastrum* sp., 9) *Scenedesmus* sp., 10) *Volvox* sp.

The abundance and type of algae in lakes depends on many factors such as hydrological and the hydrochemical conditions (in particular the nutrients concentration), water temperature and turbulence, underwater light climate. Sometimes environmental conditions become particularly favorable for a specific algal species. This can then lead to trmendous developments of that species, causing the so called algal blooms. This phenomenon is common in, but not exclusive to, eutrophic environments.
The determination of abundance and species composition of algae populations provide, therefore, information on the trophic status of the lake and on its water quality.

The density and biomass of autotrophic picoplankton is evaluated with epifluorescence microscopy as described for bacterioplankton (chapter 5.2), but without using any fluorescent dye since the photosynthetic pigments are fluorescent when excited with appropriate wavelength (400 nm).
Also nano- and microplankton are sampled with closing bottles, while macroplancton is sampled using plankton nets of appropriate size and design. If the phytoplankton is sampled taking into account the water volume passing through the plankton net a quantitative sample is obtained. This can be then fixed with Lugol's liquid and stored till the counting. Normally, the phytoplankton must be concentrated before counting. Since most algal cells are destroyed by filtration, this is done pouring a know volume of sample (5 to 20 ml) in a small sedimentation chamber with a transparent bottom. Than the algal cells accumulated at the bottom of the chamber are identified, counted and measured using an inverted microscope, designed to host the sample holder table above the objective (Utermöhl microscope, Figure 33). To measure the algae size a calibrated ocular micrometer is used (Figure 34).

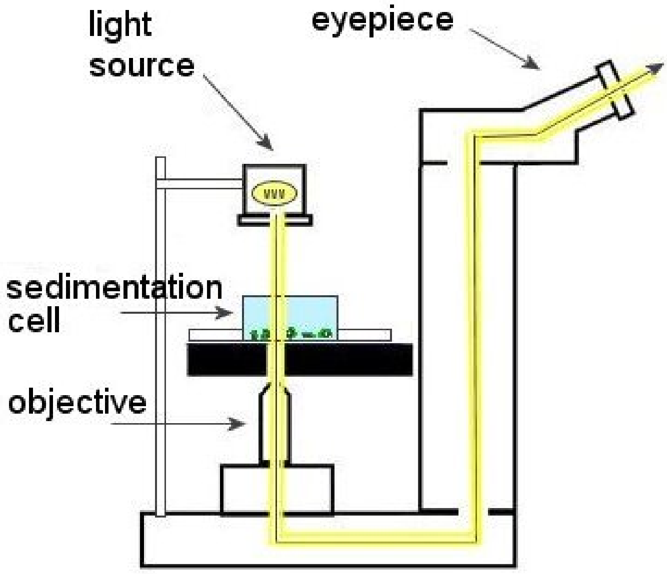


Figure 33. Schematic of inverted microscope with sedimentation cell for counting plankton.

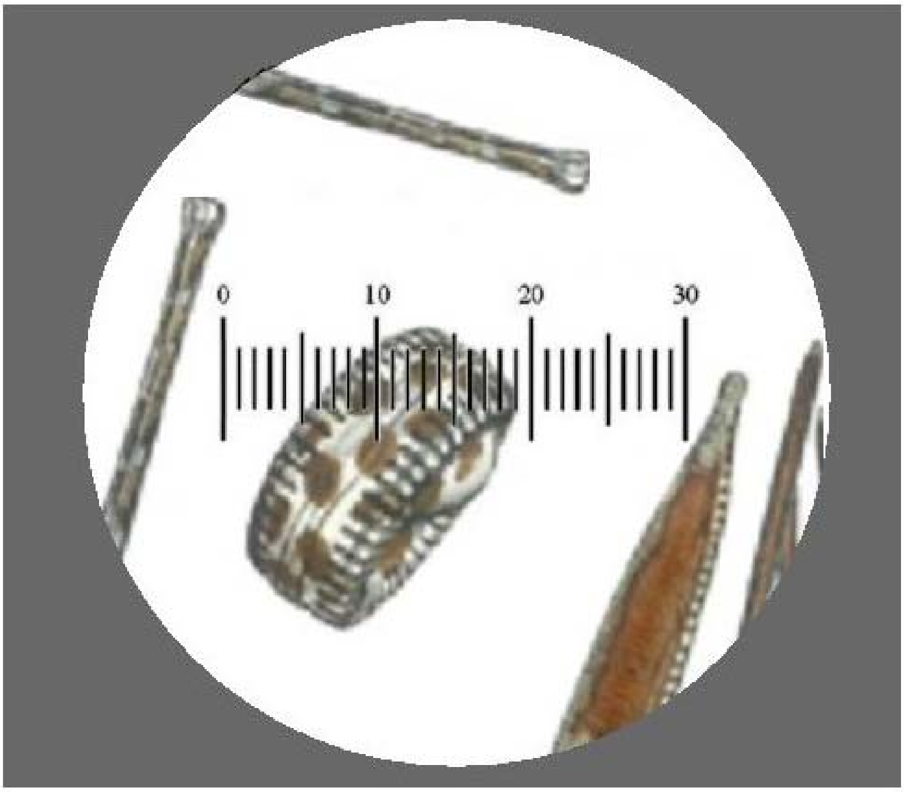


Figure 34. Diatoms observed through an ocular micrometer.

Taking into account the volume of sample placed in the sedimentation chamber, the cells number per liter or per m^3 of each algae genus / species is then computed. From a time series of samplings it is thus possible to assess the algal succession over the seasonal cycle and, with a pluriannual data set, the trophic evolution of a lake. The total phytoplankton biomass can than be calculated from the cells number, computing cells biovolume or using appropriate conversion factors.

Chlorophyll concentration is considered a proxy of algal biomass, although in natural samples its variability between species and between different growth conditions within the same species makes the chlorophyll-biomass relationship quite ambiguous. To measure the chlorophyll content of an algal population it is necessary:

1) to concentrate the phytoplankton through filtration of water sample by filters of appropriate pores size to retain the size fraction of interest;
2) to extract the chlorophyll with solvents (acetone, ethanol or methanol);
3) to determine the chlorophyll concentration in the extract with a spectrophotometer or a fluorometer;
4) to calculate the chlorophyll concentration in the sample, taking into account the filtered sample volume and the appropriate calibration curves obtained from chlorophyll standards.

There exist underwater probes allowing to measure the chlorophyll concentration directly *in vivo* (i.e. without extracting the pigment) and *in situ* using the fluorescence emission of chlorophyll excited by a radiation of appropriate wavelength.

To assess the state of an ecosystem besides the phytoplankton abundance and composition, it is essential to also know its productivity, measuring the phytoplankton primary production, ie the quantity of organic carbon synthesized by algae per unit of lake surface and per unit of time.
The methods for evaluating primary production are based on the measurement of the concentration change of a product or a reagent of photosynthesis reaction in lake water samples incubated for several hours in transparent and non-transparent bottles. In light and dark bottles algae are exposed to light or kept in the dark, thus making the photosynthetic activity possible and impossible, respectively.

Oxygen method: the O_2 concentration rise in light bottle corresponds to Net Primary Production (NPP) and is due to oxygen release by photosynthesis minus the O_2 consumed for autotrophic and heterotrophic respiration (R). This correspond to the O_2 decrease measured in dark bottles in absence of production. Thus:

$$6\ CO_2 + 6\ H_2O \rightarrow C_6H_{12}O_6 + 6\ O_2$$

Gross Primary Production (GPP) = Net Primary Production (NPP) + respiration (R).

This method is not applicable in oligotrophic and mesotrophic lakes, too unproductive to produce changes in O_2 concentration appreciable with the analytical methods nowadays available. In analogy with terrestrial ecosystems, primary production is often expressed per unit area, dividing the production per unit of volume measured at different depths for the thickness of the euphotic zone.

^{14}C method. Introduced early in the 1950s to overcome the sensitivity limits of the oxygen method, it is based on the addition of ^{14}C labeled inorganic carbon as bicabonate to lake water samples in light and dark bottles. The algae, during an incubation lasting some hours (usually 4), uptake the radioactive ^{14}C with the ^{12}C naturally present in the lake. Than the algal cells are concentrated trough filtration and incorporated ^{14}C is measured with a liquid scintillation counter. Knowing the amount of inorganic carbon originally present in the lake and the amount of ^{14}C incorporated by algae it is possible to calculate the total inorganic carbon taken up by algae (i.e. the NPP) from the equation:

$^{12}CO_2$ assimilated = ($^{14}CO_2$ incorporated/$^{14}CO_2$ added) x $^{12}CO_2$ concentration in lake

A comprehensive review of the ecology of freshwater phytoplankton was provided by Reynolds (1984).

5.3.2 The zooplankton

Before examining the ecological role of zooplankton, it is useful to summarize some taxonomic information on the main organisms constituting it (Figure 35). Because of the many classes involved, the identification of freshwater zootoplankton requires a wide taxonomical knowledge. The introductory text quoted above for the phytoplankton (Streble and Krauter 1988) also contains useful information for identification of zooplankton. An extensive literature exists on the plankton and its ecology. The following texts are possible starting points for addressing the topic: Kiørboe, 2008; Suthers and Rissik 2009; Likens 2010.

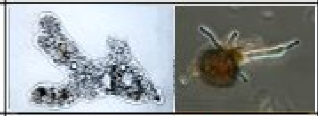
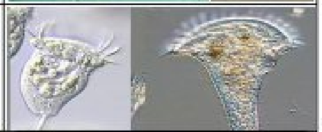
	class	Order - Sub-groups	
Protozoa	Rhizopoda (Amoebas)		
Protozoa	Zoomastigia (Flagellates)		
Protozoa	Ciliates	Olotrichs, Peritrichs, Spirotrichs (*Stentor, Vorticella)*	
Cnidaria	Hydrozoa	Limnohydrina (*Craspedacusta* sp.)	
Nemathelminthes	Rotatoria (Rotifers)	Monogononta (genera *Brachionus, Keratella, Kellikottia, Asplanchna, Polyarthra, Synchaeta, Filinia,* Fam. *Conochilidae*)	
Arthropoda	Crustacea – Subclass Phyllopoda	Cladocera, Famiglie *Sididae, Leptodoridae, Daphnidae, Bosminida, Polyphemidae*	
Arthropoda	Crustacea – Subclass Copepoda	Calanoida (*Diaptomus*), Cyclopoida (*Cyclops*), Harpacticoida	

Figure 35. Major zooplankton taxa present in lakes.

The **Protozoa** are unicellular organisms between tens and hundreds microns in size. They feed on bacteria or detritus particles which are incorporated in a vacuole where digestion occurs (phagocytosis). Planktonic protozoa move mostly by cilia. Feeding on bacteria, they have an important role in the food chain since they are a central step in the transformation of dissolved organic matter, directly used only by bacteria, in a food of size suitable for larger and more complex organisms.
The **Cnidarians** are actually a rare component of freshwater zooplankton. They are therefore more a curiosity than a major presence in the economy of the ecosystem, and it is not yet clear what the conditions sometime determining their massive growth in small lakes are.
The **Rotifera** are animals related to worms. They are not segmented and their length is between 100 μm and 1 mm. They take their name from a crown of cilia, always moving around their mouth to suck inside the food, consisting of algae, protozoa, bacteria and debris. Some genera (eg. *Asplanchna*) are carnivores. Some rotifers (eg. *Keratella*, *Kellicottia* and *Brachionus*) have a thick shell, sometime with thorns. Rotifers have a continuous growth and their generation time is of 3-6 days at about 15°C. They generally reproduce by parthenogenesis, ie without egg fertilization by males. A cyclic parthenogenesis is also possible, in which parthenogenetic generations alternate with sexual amphigonic reproduction.

The planktonic **crustaceans** are divided into two groups, **cladocerans** and **copepods**, which are the most important primary consumers of the lakes. The best known and most common cladoceran is *Daphnia*, commonly known as "water flea". Its body is made up of two valves enclosing the limbs, and circulatory, reproductive and digestive systems. The head and two pairs of antennae, the longest used for locomotion, protrude from the valves. These ventrally form a channel where *Daphnia* pipes, moving its limbs, the water with food particles (algae and detritus). *Daphnia,* as others cladocerans, are filter feeders because their limbs have filaments (setae) used to filter the water carrying food particles. The reproduction of Cladocera is generally parthenogenetic, ie without fertilization by males, appearing only in particular environmental conditions. The eggs are incubated in a dorsal space untill their development is completed, originating a new-born cladocera smaller but similar to adults. It will than increase in size through molting, as all crustaceans. Each female achieves the reproduction age in 7-8 days and can produce parthenogenetically up to 30-40 eggs at a time, making the Cladocera able to become quickly very numerous. The eggs originated from sexual reproduction are forms of resistance, called ephippia, which can last long time in the sediment to hatch when favorable conditions occur.
In addition to small phytophagous filter feeders, there are predator cladocerans (eg. *Leptodora*), which can reach 7-8 mm. Cladocerans develop in the warm period, increasing in number during spring for the concurrent development of algae on which they feed.
The Copepods are represented by Calanoids (*Diaptomus* sp.) and Cyclopoids (*Cyclops* sp.). The former are generally phytophagous during their whole life, while the latter are phytophagous in juvenile stages and predators when adult. As adults, they generally have a pear-shaped body divided into segments that carry arts and antennas, and these moves like oars to allow the animal to move. Sexual reproduction is the rule in copepods and their eggs are carried by females within ovigerous bags attached to the mother's body. Each egg originates an independent organism in larval stage, which will become adult after passing through eleven stages of larval development.

The synthesis of organic matter by autotrophs is defined as primary production and, by analogy, its transformation by heterotrophs is defined as secondary production. This transformation occurs following paths of complexity increasing with the complexity of the organisms in the food chain. The consumption of food particles, namely the assumption of organic matter, by protozoa and flagellates, can be assessed by measuring the amount of picoplanktonic cells they ingested in a defined time. The consumption of algae (grazing rate) by the larger zooplankton can be estimated by the decrease in the density of algal cells in unit of volume and time. Nevertheless, the assessment of zooplankton secondary production is commonly obtained from its population dynamics, measuring the growth rate and mortality of a population, as well as the effect of predation on it. Thus, the annual net secondary production of a zooplankton population is the sum of all biomass produced by the population itself during the year, taking into account the losses due to mortality, predation, emigration.

5.4 Benthos

Benthic organisms are those living in contact with the bottom sediment. The benthos includes fungi and bacteria as well as vegetals and animals of size from microns (algae, protozoa, rotifers, tardigrades) to centimeters (mollusks, worms, arthropods). In close relationship with the sediment as the benthos, but somehow away from it, are the aquatic macroalgae and macrophytes, that can account for a large portion of primary production, particularly in shallow lakes.

The **phytobenthos**, or periphyton, is the community of microscopic autotrophs living adherent to submerged inorganic (epilithic algae) and organic surfaces, including living plants (epiphytic algae). The vertical distribution of periphyton is, in lakes, limited to the depth reached by light.

The periphyton organisms are mainly filamentous algae, unicellular or colonial, belonging to the cyanobacteria, diatoms and chlorophytes.
In shallow lakes where the littoral zone is prevalent compared to the pelagic ones, the periphyton population can have a significant role in the overall ecosystem primary production. The examination of quality (species diversity) and quantity (abundance of organisms per unit area or pigment content) of periphyton is made removing with various techniques the algae film from natural substrates or exposing in situ artificial substrates (slides, ceramic plates, etc..) for a time sufficient to allow the surfaces colonization by periphyton, which is then removed and analyzed.

The **macrophytes**, or **hydrophytes**, are plants growing in aquatic environments or on substrates that are at least periodically submerged. The aquatic macrophytes may be emergent, floating or submerged. The emergent and submerged hydrophytes are always rooted in the substrate, the floating hydrophytes may be rooted in the substrate or freely floating.
Aquatic macrophytes are distributed in areas of transition between terrestrial and aquatic ecosystems. The emergent species live in shallow waters while the submerged ones occupy the deeper layers of littoral zone. In the intermediate position the rooted hydrophytes with floating leaves live, while the free floating hydrophytes, found in shallow eutrophic environments, are obviously independent from the depths (Figure 36).

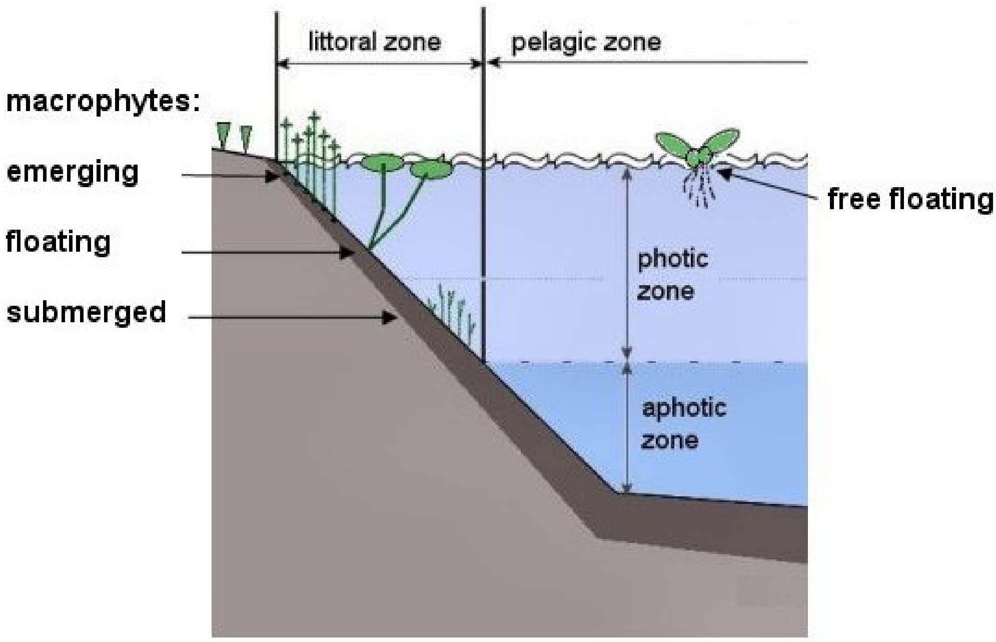


Figure 36. Section of the littoral zone of the lake with the different macrophytes types.

Emergent macrophytes are generally perennial, rooted in a substrate saturated with water or completely submerged. Common emergent hydrophytes are *Phragmites australis* (reeds), *Scirpus*, *Typha*, *Sagittaria* sp, *Carex*.
The floating hydrophytes have a root system anchored to the substrate and floating foliage, taking the atmospheric inorganic carbon, and flowers. Common representatives of this group are, for instance, *Nymphaea* sp., *Trapa natans* (water chestnut) and *Potamogeton* sp. In the free floating hydrophytes the root system is not anchored to any substrate and the nutrients are taken directly from the water. A very common example is *Lemna minor* and the non-indigenous *Elicornia crassipes,* introduced for phytoremediation purposes is also, at times, found in European waters. The shading effect of floating hydrophytes reduces the penetration of solar radiation, leading to a sharp reduction in phytoplankton populations.
The submerged hydrophytes grow till the light penetration depth, using the inorganic carbon present in water while the nutrients intake can occur also through the root system. Common representatives of this group are *Ceratophyllum* sp. and *Elodea* sp.

Some common macrophyte species is illustrate in Figure 37.

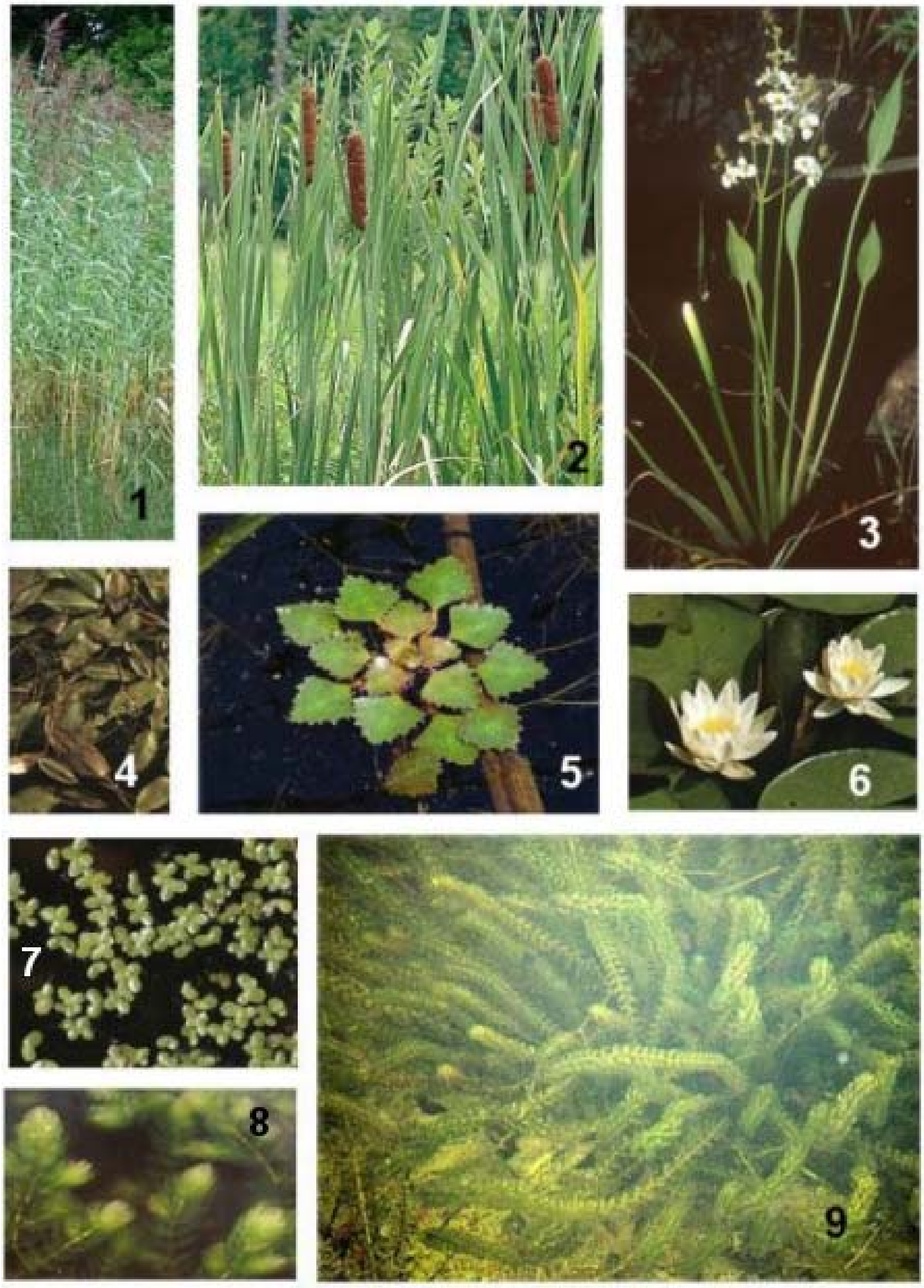


Figure 37. Emerging macrophytes: 1) *Scirpus* sp., 2) *Thyfa* sp., 3) *Sagittaria* sp. Floating macrophytes: 4) *Potamogeton* sp., 5) *Trapa natans*, 6) *Nymphaea alba*, 7) *Lemna minor*. Submerged macrophytes: 8) *Ceratophyllum demersum*, 9) *Elodea* sp .

The **benthic animals** are microinvertebrates (protozoa, rotifers, tardigrades), very abundant in freshwater bottom sediments. Furthermore, even in fresh water sponges (about 150 species), bryozoans (about 20 species) and sessile Cnidaria (Coelenterata) are present, but, while their contribution to ecosystem biodiversity is important, their ecological role seems modest. However, the most common benthic organisms are the macroinvertebrates, belonging to the group of insects, crustaceans and molluscs, oligochaetes, hirudineae (leeches) and flatworms. Since the various species occupy physically and chemically very different niches and they are often easily visible on the shores, benthic organisms are used as bioindicators of water quality in rivers. In lakes the value of benthic macrovertebrates as quality indicator is limited to the coastal area. A simple key for the classification of benthic macroinvertebrates is presented in Figure 38.

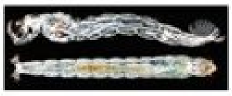
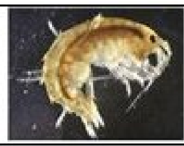
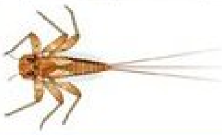
Macroinvertebrates:					**Phylum**, Class	
no legs	shell	single			**Mollusca** (mollusks), Gastropods	
no legs	shell	2 valves			**Mollusca** (mollusks), Bivalves	
no legs	no shell	non segmented body	flat		**Platyhelminthes,** Turbellaria (flatworms)	
no legs	no shell	non segmented body	cilindrical		**Nemathelminthes** Nematoda	
no legs	no shell	segmented body	no appendages	no sucker	**Anellida,** Oligochaeta	
no legs	no shell	segmented body	no appendages	sucker	**Anellida,** Hirudinea (leeches)	
no legs	no shell	segmented body	appendages		**Arthropoda,** Insecta (larvae)	
jointed legs	more than 6				**Arthropoda,** Malacostraca (Crustaceans)	
jointed legs	6				**Arthropoda,** Insecta,	
orders: Ephemeroptera (mayflies), Odonata (dragonflies and damselflies), Plecoptera (stoneflies), Hemiptera (true bugs), Trichoptera (caddisflies), Lepidoptera (butterflies and moths), Coleoptera (beetles), Megaloptera (alderflies, dobsonflies, fishflies), Neuroptera (spongillaflies), Diptera (two-winged or true flies)						

Figure 38. Key to the identification of macroinvertebrates.

The sediment type (muddy, sandy or rocky) is important in determining which species can thrive and in what abundance. Of course other factors such as availability of food and the physical and chemical properties of water may affect the density of benthic assemblages. The near-shore silty sediments are rich in organic detritus and host oligochaetes and the larvae of certain insects (mainly Chironomidae). In sandy sediments, subject to wave action, several species of mollusks (such as *Pisidium*, *Unio*, *Anodonta*) and gastropods, as *Viviparus* are found. The rocky bottoms are inhabited by a variety of organisms. Between the gravel or under the stones Gammarids, small (10-20 mm) omnivorous shrimp, and Asellidae (10-15 mm), small aquatic detritivorous isopods, live. The larvae of insects such as *Chironomus* and *Chaoborus* are common on the pebble surface.
Benthos living at depth in lakes with an extended pelagic zone faces an underwater climate characterized by lack of light, low temperature, and low oxygen concentration or even anoxia in

eutrophic lakes. For this reason, the density of benthic organisms in the sediment decreases rapidly with increasing depth but, while the deep zone of oligotrophic lakes can still have a relatively high number of species, in that of eutrophic lakes the benthic organisms are absent.
Among the main representatives of the deep fauna are the midges. These flies, which are generally detritivorous live in tubules made of sediment cemented by saliva, which serve as shelters and allow them to raise over the almost anoxic water-sediment interface.
However they have developed a physiological adaptation that allows them to live at low oxygen concentrations. At the end of the larval development, they reach the lake surface flying away as adults. Also *Chaoborus* occupies the sediment of deep lakes at the end of the larval stage. However, during the night the larvae of benthic *Chaoborus* migrate to surface waters to return then to the bottom sediments at dawn.
Also Oligochaeta (eg *Tubifex* sp.) are part of the profundal benthos. The oligochaetes and chironomids activity plays an important role in bioturbation of bottom sediments, promoting the replacement of interstitial water and accelerating nutrient recycling. Tubificids can remove up to 12.6 kg m^{-2} $year^{-1}$ of sediment. In addition, the ingestion of sediment particles and their subsequent expulsion from the digestive tract as small masses covered with mucus promote the bacterial mineralization, similarly to what happens in soil as a consequence of earthworm activity (Figure 39) (McCall and Tevesz 1982).

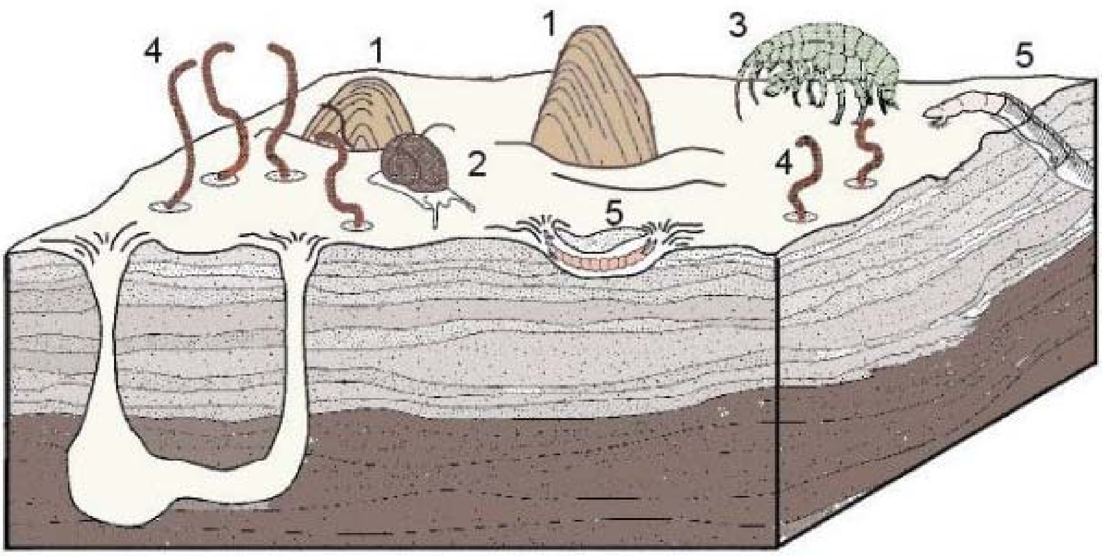


Figure 39. Macroinvertebrates digging the layered bottom sediments: mollusks (1), gastropods (2), amphipods (3), tubificid worms (4) and larvae of aquatic insects (5).

5.5 Nekton

The term nekton designates the aquatic animals able to move actively in the water, independently from the water masses movements. In the oceans the nekton includes fish, mollusks, reptiles and marine mammals. In freshwater only two species of aquatic mammals are known: *Phoca sibirica* (Lake Baikal, Siberia) and *Phoca hispida saimensis* (lake districts in northern Finland). There are also several different mammals adapted to life in inland waters, as the beaver and the otter, now rare in Europe, and the nutria, rodents of Central and South America now invading lakes and rivers of Southern Europe. In freshwater environments also reptiles and amphibians are present.

The fish population
Despite the undoubted interest of the above mentioned vertebrates, the fish population in lakes is by far the most important nekton component and it is normally considered the apex of the lake food chain. Nevertheless, many fish species are not really at the top of the food chain because, in

addition to the predators feeding on other fishes, there are carnivorous species feeding on zooplankton or benthos, and even herbivorous and detritivores species, which feed on plants or organic debris. Moreover, the diet of many species varies with age and food availability.
The species composition of the fish population depends on lake morphology, which influences the thermal regime, on lake chemistry (in particular on oxygen availability) and, finally, on the biological characteristics of the lake, which determines the quality and quantity of available food (Matthews, 1998).

Water temperature and fish species
The water temperature affects fishes very much because they do not have physiological mechanisms of body temperature regulation. They are, therefore, cold or warm stenotherms as they survive only within a narrow temperature range in acold or warm environment, respectively.
In the temperate zone there are cold-stenotherm species as Salmonids (trout, char, whitefish) and Gadidae (burbot) and warm-stenotherm species as Cyprinids (bream, roach, carp, tench), Percids (perch, largemouth bass) and Silurids (catfish), as shown in Figure 40.

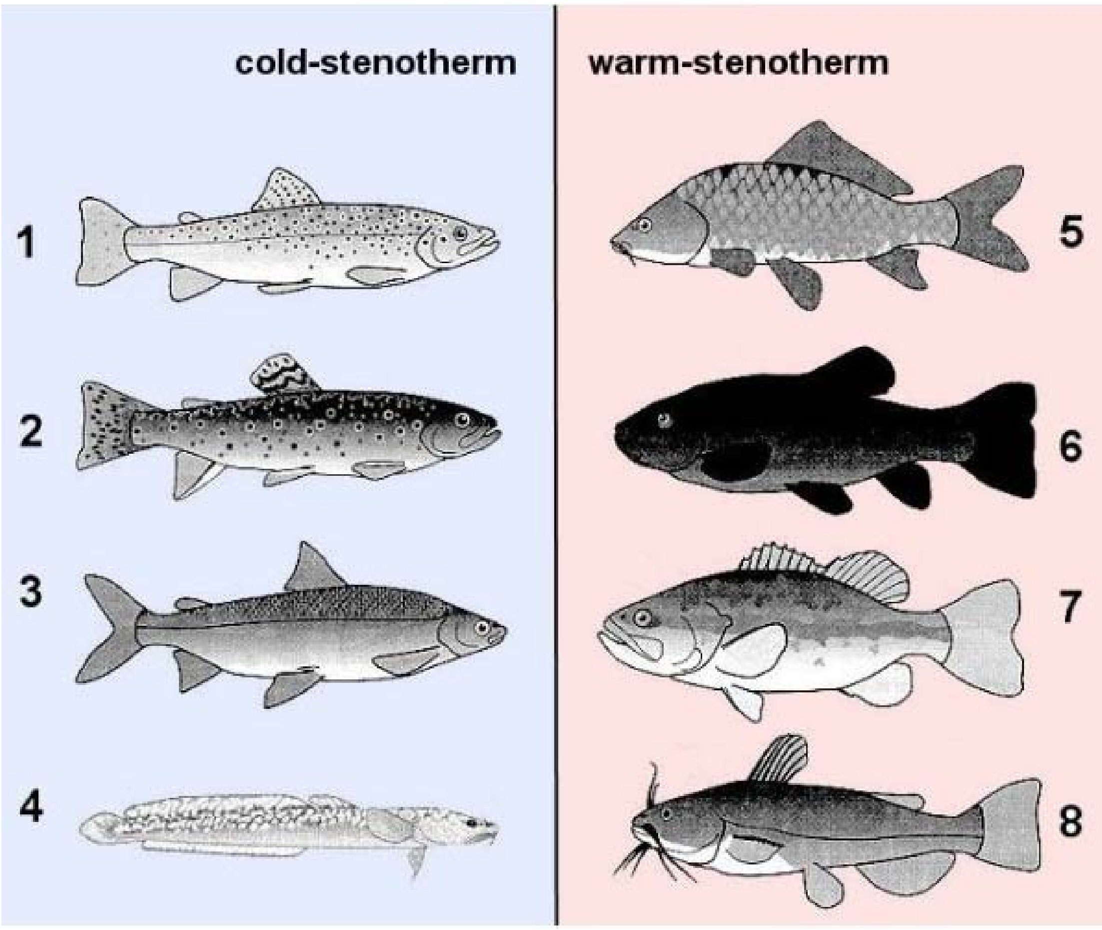


Figure 40. Optimum temperature of some fish species common in subaline lakes. 1: trout, 2: char, 3: whitefish, 4: burbot, 5: carp, 6: tench, 7: largemouth bass, 8: catfish.

Large subalpine deep lakes have a seasonal thermal evolution allowing these two groups to coexist because the epilimnion, where the temperature never drops below 6°C, can accommodate warm-stenotherm species and in the hypolimnion can live cold-stenotherm specie, as even in summer there are layers where the temperature never exceeds 15°C. In small, shallow lakes (depth less than 10-15 m), cold-stenotherm species can't live in summer as the temperatures are far beyond their tolerance limits. Since temperature affects fish nutrition, respiration, growth, reproduction, migration, each species searches for the optimum temperature for the vital activity prevailing at the time.

Concentration of dissolved oxygen and fish species

Freshwater fish species are adapted to tolerate a certain range of variation in the oxygen concentration necessary for normal breathing, and some can survive even at very low concentrations. Table 6 summarizes the oxygen requirements of some fish species common in temperate regions.

Table 6. Oxygen requirements of some fish species common in lakes of the temperate-zone.

The oxygen consumption by fish varies with age, activity, status, and living conditions (Table 7). In species adapted to live in low oxygen concentration, the activity reduction can occur to minimize oxygen consumption.

Species	**O_2 concentration (ml L^{-1})**	
	optimum	minimum acceptable
trout, minnow, loach	7–11	6
Grayling, Danube roach, barbel, burbot	5–7	5
roach, rudd, chub	5–6	4
carp, tench, catfish	5–6	1–2

Table 7. Examples of fish oxygen consumption.

Fish feeding

The fish larvae have a structure, the yolk sac, containing a nutrient reserve allowing it to survive for days or weeks after leaving the egg. When such reserve is exhausted, the small fish feed on planktonic organisms. This food source can be generalized to the fry of all fish species and continues at least throughout the first season of growth. After the first year of life, or the second or third in some cases, the diet can change drastically and the fish takes the typical eating habits of his species. According to their prevalent diet, fish can be:

- herbivores (or primary consumers) if they feed on aquatic plants and filamentous algae (e.g. *Chondrostoma soetta*);
- carnivores (or secondary consumers) if they feed on zooplankton or benthos (e.g. the whitefish *Coregonus* sp., the sunfish *Lepomis gibbosus*);
- predators (or tertiary consumers) if they feed on other fish or other vertebrates, such as pike (*Esox lucius*) and pikeperch (*Stizostedion lucioperca*).

This is not a strict classification since fish diet may change depending on the type of food available. For example, a predatory fish such as the trout may feed exclusively on plankton and benthos in mountain lakes, where other preys are absent. Many species, especially cyprinids, are actually omnivores because they adapt to different food types. There are also specific anatomical adaptations that improve, in some species, the efficiency attaining a specific food type. So the predators have big mouth and teeth, while the detritivores and herbivores have the mouth in ventral position and wattles with sensory function.

Corresponding anatomic adaptations exist also in the digestive system, with a stomach in carnivores lacking in herbivores and omnivores. The intestine is longer in predominantly herbivorous fish: in the grass carp is over 10 times the fish length, while in the pike is less than the fish length.

Types of fish and lake conditions

Mirroring the ecological zonation illustrated for rivers, also lakes host a different fish fauna according to different lake morphology and ecology. Nevertheless the fish population of a lake can also vary qualitatively and quantitatively for natural causes or for man activity (fishing, restocking practices, intentional or accidental introduction of new species, pollution).

In large deep lakes the fish fauna can be roughly divided into two main populations: the pelagic, consisting mainly of salmonids, and the littoral, consisting mainly of cyprinids, percids and centrarchids.
The presence of a well oxygenated hypolimnium with a temperature below 15-17°C also in summer allows the settlement of cold-stenotherm pelagic species (eg. salmonids). The pelagic species are almost exclusively zooplanktophagous or, as in the case of larger trouts (35-40 cm), ichthyophagous.
The littoral fish population is composed of cyprinids, such as bream (*Scardinius erythrophthalmus*), chub (*Leuciscus cephalus*) and roach (*Rutilus rubilio*). The bleak, considered a pelagic species, often makes seasonal migrations in the coastal area. In shallow waters with abundant aquatic vegetation, the carp (*Cyprinus carpio*) and the tench (*Tinca tinca)* live. In rocky shores the cyprinids pigo (*Rutilus pigus*) and savetta (*Chondrostoma soetta*) can be found and near the mouth of tributaries the barbel (*Barbus Barbus plebejus*) is present.
In coastal areas ichthyophagous predators such as pike (*Esox lucius*), perch (*Perca fluviatilis*) and largemouth bass (*Micropterus salmoides*), introduced in Europe from North America, are frequent.
In the sublittoral and littoral zone the Gadidae burbot (*Lota lota*), which inhabits the sublittoral rocky areas, the sunfish (*Lepomis gibbosus*), a small centrarchids introduced from North America, the anadromous eel (*Anguilala anguilla*), and the bullhead (*Cottus gobio*) are also present
The fish population of small lakes is similar to that found in the littoral zone of large lakes. Here the absence of a pelagic zone does not allow for the survival of salmonids, and other cold-stenotherm species. In addition, small shallow lakes are often very productive, with low oxygen concentration in deep layers, thus allowing only the presence of less demanding species, such as cyprinids.
The rudd, zooplanktophagic, is the dominant species but carp and tench are also present, well tolerating low oxygen concentrations and accepting wide food base (macroinvertebrates, plants, organic detritus, etc.). The ichthyophagous species (pike, perch and largemouth bass) are also present.

6. The fate of lakes

The life history of a lake may take place over just a few days or weeks, in the case of one formed by a small landslide, or it may cover geologic time periods, as for the largest lakes. A lake may come to its end physically through depletion of water inflows or through infilling by sediments. A lake is also exposed to a chemical-biological aging, which is not necessarily its death as a physical entity but may be its end as a water body usable by human beings.
Both physical and chemical-biological changes driving the lake to its end can be natural processes, slowly advancing in geological time periods. But often human activities induce or accelerate it, changing the hydrology of a region or introducing in the water bodies chemicals and pollutants altering the normal operation of the food web (Jorgensen et al. 2005).

6.1 Trophic state of the lake

The chemical-biological changes within a lake's history are the result of the ecological succession. In the early stages a lake has a reduced organic matter content and has a poorly developed littoral zone. Such conditions guarantee a plentiful oxygen content, and the lake is said to be **oligotrophic** (Figure 41). As the lake enrichment in organic material progress, it may become sufficiently productive to consume its oxygen content. The organic matter enrichment may be of allochthonous (domestic sewage and / or industrial wastes) or of autochthonous origin. In this case the excessive in-lake production of organic matter is the consequence of the excessive introduction of inorganic nutrients, nitrogen and phosphorus, fertilizing the lake. A lake in this condition is defined **eutrophic** (Figure 43) and it becomes often anoxic, particularly during summer stratification (see chapter 4.5). An intermediate stage in this course of events is called **mesotrophy** (Figure 42**).**
As eutrophic conditions develop, bottom sediments become enriched in organic material and the sediment layer thickens. As infilling proceeds, the macrophytes spread throughout the littoral zone and lakeward. Eventually the littoral zone progressively becomes a marsh, and the central part of

the lake diminishes to a pond. When the lake finally ceases to exist, the terrestrial vegetation becomes dominant and a terrestrial ecosystem takes the place of the former lake.

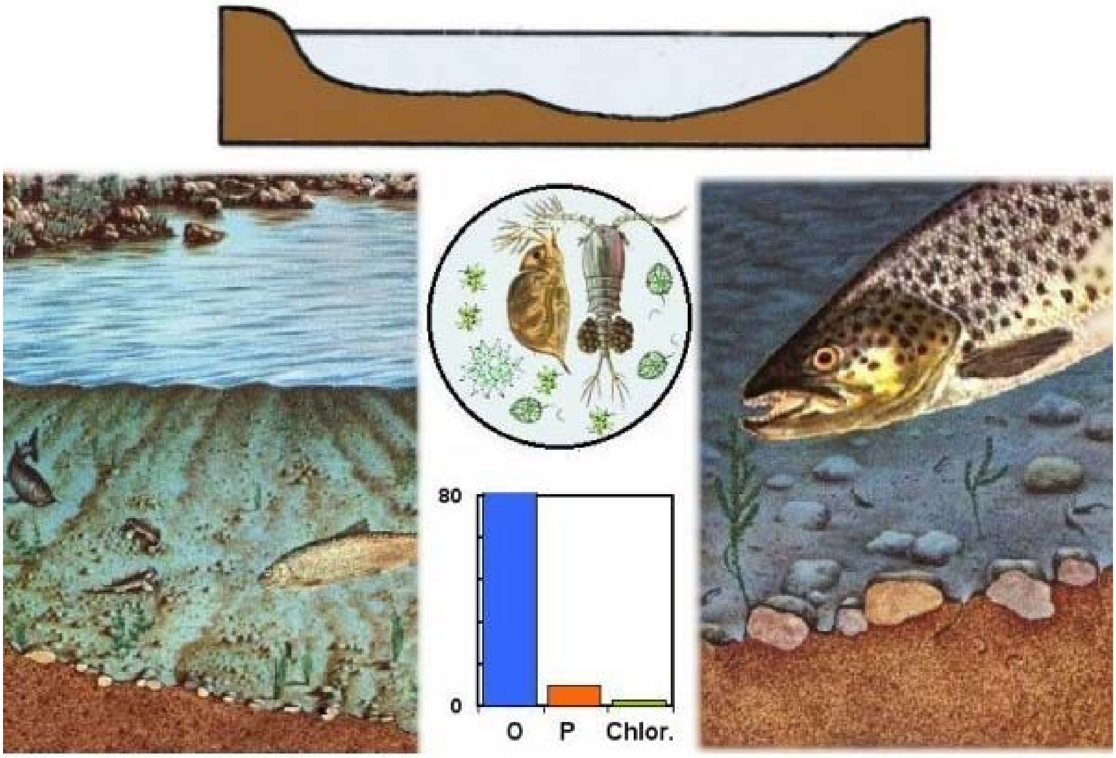


Figure 41. Oligotrophic lake.
Top, section of the lake: the sedimentary deposit on the bottom is small.
Center, microscopic field: view of the plankton, consisting of zooplankton and small phytoplankton.
Bar graph: bottom oxygen concentration (O: % saturation); phosphorus and Chlorophyll concentration (P and Chlor.: µg L^{-1}) in pelagic waters.
Left: the littoral zone, with good fish stocks and no hydrophytes.
Right: the lake bottom, where salmonids can live.

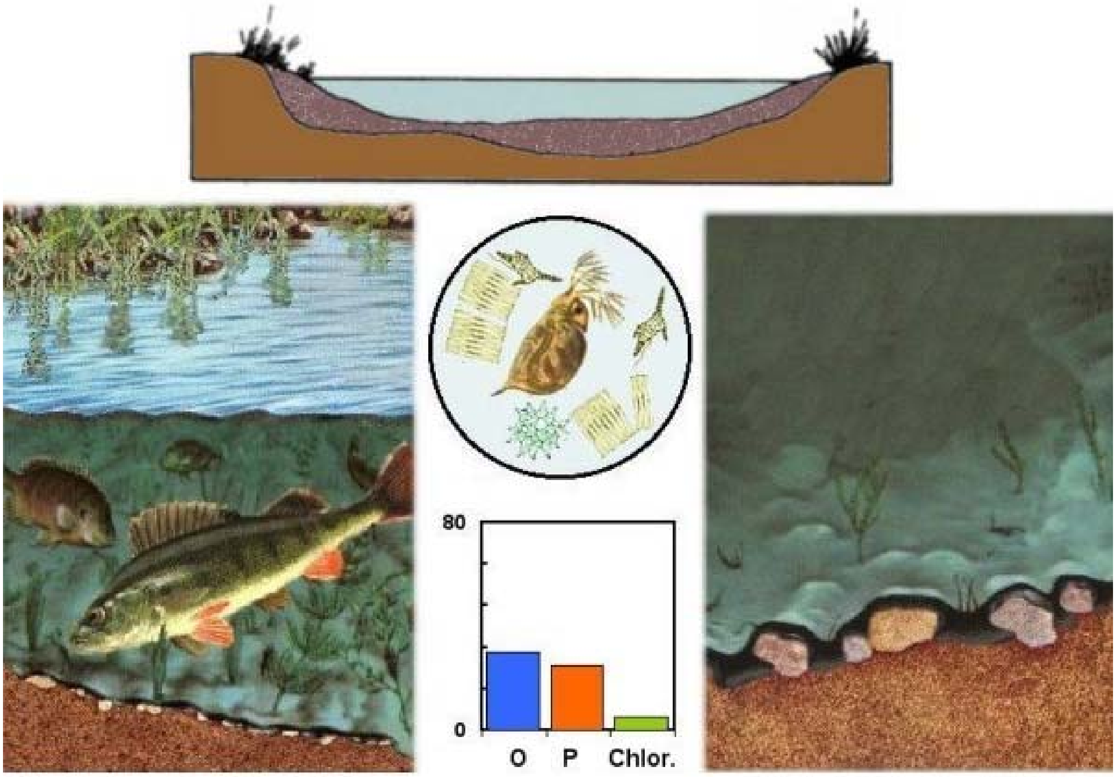


Figure 42. Mesotrophic lake.
Top, section of the lake: the sedimentary deposit on the bottom is important.
Center, microscopic field: view of the plankton, with increased abundance of algae.
Bar graph: bottom oxygen concentration (O: % saturation) is reduced and can reach 0 in summer. phosphorus and Chlorophyll concentration (P and Chlor.: µg L^{-1}) in pelagic waters is increased.
Left: the littoral zone, with a fish population of percids and cyprinids. The hydrophytes are abundant.
Right: the lake bottom, with an evident sediment cover and absence of fish at least during summer anoxia.

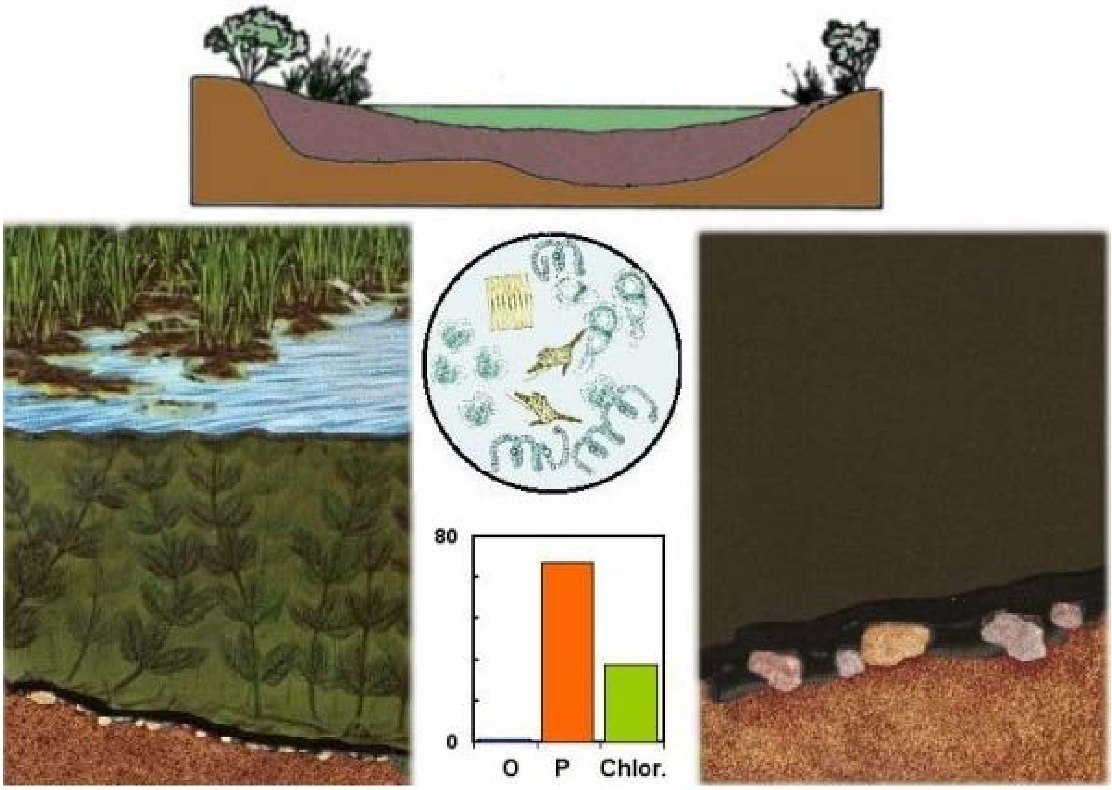


Figure 43. Eutrophic lake.
Top, section of the lake: the sedimentary deposit on the bottom has almost filled the lake and land vegetation now occupies the area previously occupied by water.
Center, microscopic field: view of the plankton, consisting mostly of phytoplankton and dominated by cyanobacteria.
Bar graph: bottom oxygen concentration (O: % saturation) is permanently near 0. Phosphorus and Chlorophyll concentration (P and Chlor.: µg L^{-1}) in pelagic waters is now very high.
Left: the littoral zone, with abundant presence of hydrophytes. The fish population is made of cyprinids, if there is enough oxygen.
Right: the lake bottom is covered by a thick layer of black anoxic sediment.

6.2 Inland waters and climate change

Lakes can be extremely sensitive to short- and long-term changes in the weather and so they are intrinsically sensitive to climate change either through a direct effect, or indirectly by affecting processes that take place in the catchment. Understanding the response of lakes to climate change is of great practical importance, since year-to-year changes in weather patterns can influence lake water quality, the ecological success of a particular species and the ecological status of a lake. In many cases palaeolimnological studies, reconstructing from sediment cores the paleoenvironments of inland waters and, especially, changes associated with such events as climatic change and human impacts, made it possible to get an idea of lakes pristine conditions assumed as reference condition to evaluate the lake evolution.

Many comprehensive surveys of temperature trends in major European lakes have shown that the largest lakes have warmed during the past 25 years in response to climate change, with small but significant increase of epilimnetic and particularly of hypolimnetic waters temperature (Ambrosetti and Barbanti, 1999; Dokulill et al. 2006). According to satellite observations, the warming trend was global, and the greatest increases were in the mid- to high-latitudes of the Northern Hemisphere.

The results have implications, yet not fully understood, for lake ecosystems, which can be adversely affected by even small water temperature changes (Thackeray et al. 2008; Elliott, 2006)..

For instance, even a small increase in water temperature can lead to the enhancement of primary production, possibly resulting in algal blooms that can make the lake water toxic to animals, can desynchronise life cycles and cause physiological problems for cold-adapted species, facilitating the success of non-native invasive species that change the lake's natural ecosystem.
Climate change influence on rivers comes through its effects in modifying the hydrological regime of a region. Increasing precipitation and evaporation obviously change the river discharge, not only altering the water amount but also modifying the seasonal timing of precipitation events, increasing the risk of flooding and drought.
Although the future scenarios of climate change influence on inland waters are still controversial and uncertain, no doubt exists that temperatures of lakes increased in the past 20-30 years (George et al. 1995, 2004). A more realistic evaluation of the effects of such increase requirea a further effort in environmental research.

7. Conclusions

In today's societies, requirements of freshwater, much of which is derived from lakes and rivers, include its use for drinking, for irrigation, for fishing, for power generation, for cooling purposes, and for recreation. Furthermore, the economic importance of waterways as communication links is enormous. Obviously, these requirements vary considerably among regions, climates and lakes and rivers morphology.
Such uses can be conflicting and in many case the overexploitation of water resources for a single use ended up with the loss of the resource itself.
For instance, Lake Aral was reduced in 50 years to 10% of its former size because its water supply had been diverted for irrigation purposes. Although such catastrophic results are not that frequent, it must be stressed that also minor lake level fluctuations can greatly affect the lake food chain, exposing the littoral zone and the flora and fauna living there to drought, reducing the spawning area for fishes, etc. The existence of an increasing number of conflicting freshwater uses is a consequence of the increased human pressure on freshwater environments. This requires, even more than before, a "fine tuning" in rivers and lakes management. The necessary prerequisite is an increased research effort to improve the knowledge of freshwater ecosystems.

Glossary

Abiotic: not alive; non-biological;
Algae: single-celled, colonial, or multi-celled, aquatic vegetals. Aquatic algae are mainly microscopic plants containing chlorophyll and performing photosynthesis. They uptake inorganic nutrients from the water to convert it to organic matter. Thus are at the base of the food web in lakes. Freely suspended forms are called phytoplankton; forms attached to rocks, stems, twigs, and bottom sediments are called periphyton.
Anaerobic: it means "without air" and refers to microorganisms living without oxygen.
Anoxia: condition of being without dissolved oxygen (O_2).
Anoxic: completely lacking in oxygen.
Anthropogenic: caused by human beings.
Aquatic respiration: use of oxygen in an aquatic system by bacteria for the decomposition of organic matter and for their metabolism by fish, algae, zooplankton, aquatic and macrophytes.
Autochthonous: originated inside the lake/river.
Allochthonous: coming from outside the lake/river.

Basin: area of land draining into a lake or river; also referred to as drainage basin or watershed.
Benthic: refers to being on the bottom of a lake.
Benthic zone: lake zone close to the bottom sediment.
Bioavailable: able to be utilized by organisms.
Biomass: weight of a living organism or of population.
Biotic: referring to a live organism; opposite to abiotic.

Carbon Cycle: the circulation of carbon atoms through the abiotic and biotic compartments of the ecosystem.
Carnivores: organisms that eat other organisms ("meat" eaters).
Chemocline: in a meromictic lake, the boundary separating an upper layer of less-saline water that can mix completely at least once a year (mixolimnion) from a deeper, more dense (saline) layer (monimolimnion) never mixing with the overlying layer; sharp gradient in chemical concentration.
Consumers: organisms that must eat other organisms to get the energy for their metabolism; organisms that cannot produce new organic matter by photosynthesis or chemosynthesis (as producers).
Convection currents: water movement caused by changes in density or temperature gradients.
Cyanobacteria: bluegreen algae; prokaryotes organisms lacking a cell nucleus as bacteria but performing photosynthesis as plants.

Decomposition: the breakdown or mineralization of organic matter by bacteria and fungi.
Denitrification: anaerobic bacterial process in which nitrate is used instead of oxygen during the oxidation of organic carbon compounds to yield energy (respiration). The process oxidizes organic carbon reducing nitrate to nitrogen gas or to nitrous oxide.
Density: The mass of a substance or organism per unit volume (kg/cubic meter; grams/liter).
Density stratification: formation in a water body of layers of different density; the process is controlled by temperature, solutes and particle concentration.
Detritus: dead or decaying organic matter; often called organic detritus to distinguish it from the mineral detritus.
Diatom: group of algae characterized by silica cell wall.
Diffusion: the movement of a substance from an area of high concentration to an area of low concentration. Turbulent diffusion, or mixing, is promoted by atmospheric motions (wind) diffusing water, heat, and other chemicals by exchanging parcels (eddies) between regions of the water body.
Dimictic: having two mixing periods, typically in spring and fall.

DOC: Dissolved Organic Carbon.

Ecological pyramid: conceptual model whereby the amount of biomass or energy at each level of the food chain decreases moving from primary producers through the different levels of consumers.
Ecosystem: all of the interacting organisms in a defined space in association with their interrelated physical and chemical environment.
Epilimnion: the upper layer of a thermally stratified lake, where wind mixing made possible the gas exchange with the atmosphere.
Euphotic zone: layer of water where sun radiation is sufficient for photosynthesis to occur.
Eutrophic : lake very biologically productive because of the high nutrient input.
Eutrophication: process by which lakes and streams are enriched by nutrients (usually phosphorus and nitrogen) which leads to an excessive growth of algae .

Fetch: distance the wind blows over a lake surface without appreciable change in direction; it affects the intensity of turbulent mixing.
Flow rate: rate at which water moves by a given point.
Food chain: transfer of food energy from plants through herbivores to carnivores.
Food web: a net of food chains hooked together into a complex interconnected web.

Grazers: herbivores; zooplankton in the open water zone.

Heat: energy that is transferred from one body to another because of a difference in temperature.
Heat budget: amount of heat energy required annually to raise the temperature of a water body from its winter minimum to its summer maximum.
Herbivores: plant eaters.
Heterogeneous: not uniform; patchy.
Holomictic: a lake that mixes completely throughout the water column at least once a year.
Homeothermia: condition of a lake with the same temperature throughout the water column
Hypolimnetic oxygen depletion: condition of a lake where the dissolved oxygen in the bottom layer (hypolimnion) is gradually consumed during summer stratification through respiration and decomposition before it can be replaced by water circulation.
Hypolimnion: the bottom layer of a stratified lake. It is isolated from wind mixing and often too dark for much plant photosynthesis to occur.

Inflow: water flowing into a lake.
Isothermal: constant in temperature.

Limnetic zone: open water zone, pelagic zone
Littoral: nearshore out from shore to the depth of the euphotic zone where it is too dark on the bottom for macrophytes to grow.

Macrophytes: aquatic higher plants, rooted and with differentiated tissues.
Meromictic: lake that never mix completely (see chemocline)
Mesotrophic: moderately productive lake.
Mean depth: the average depth of a water body; determined by dividing lake volume by the lake surface (called z mean).
Metabolism: chemical and physical processes continually going on in living cells and organisms.
Metalimnion: transition zone between the mixed epilimnion and the colder hypolimnion layers in a stratified lake. This layer contains the thermocline (see thermocline).
Mixolimnion: the upper layer of less dense water that can mix completely at least once a year in a meromictic lake (see chemocline).

Monimolimnion: Bottom layer of stagnant water in a meromictic lake that never is completely mixed (see chemocline).
Morphometry: shape of a lake basin; includes parameters needed to describe the shape of the lake such as volume, surface area, mean depth, maximum depth, maximum length and width, shoreline length, shoreline development (length of the perimeter).

Neuston: minute or microscopic organisms inhabiting the surface layer of a water body.
Nitrogen fixation: conversion of elemental nitrogen of the atmosphere to a form that can be used as a nitrogen source by organisms. Biological nitrogen fixation in lakes is mostly carried out by certain species of cyanobacteria.
Nutrient load: nutrients discharged from the watershed (basin) into a receiving water body.

Oligotrophic: unproductive lake, with low nutrients concentration and low algae biomass, usually very transparent with abundant hypolimnetic oxygen if stratified.
Omnivorous: capable of eating plants, animals and detritus.
Outflow: water flowing out of a lake.

Paleolimnology: study of the history of lakes though the analysis of sediment cores taken from the lake bottom.
PAR: Photosynthetically Active Radiation.
Pelagic: offshore zone of a lake, above the depth to which light penetration is less than 1% of surface light irradiance.
Periphyton: algae attached to underwater vegetation and rock surfaces.
Phosphorus: key nutrient influencing and often limiting the plant growth in lakes.
Photosynthesis: process by which green plants convert carbon dioxide dissolved in water to sugars and oxygen using sunlight for energy.
Photosynthesizers: organisms that produce their energy through phtosynthesis.
Phytoplankton: microscopic floating plants, mainly algae, living suspended in water bodies and drifting about transported by currents.
Planktivores: animals eating plankton; usually refers to fish that feed on zooplankton.
POC: Particulate Organic Carbon.
Polymictic: lake that mixes completely intermittently.
Primary consumers: first level of consumers according to the ecological pyramid concept; organisms eating herbivorous grazers.
Primary producers: organisms converting inorganic carbon to biomass. They are mostly photosynthesizers, but also includes the chemosynthetic bacteria using chemical instead of light energy.
Primary production: the yield of new biomass (plant) growth during a specified time period.

Respiration: metabolic process by which organic carbon molecules are oxidized to carbon dioxide and water with a net release of energy. Aerobic respiration consumes molecular oxygen.

Secondary consumers: consumers such as predator zooplankton eating other zooplankton. or fish feeding on plankton.
Sedimentation: accumulation of organic and inorganic matter on the lake or river bottom. Sediment includes decaying algae and weeds, and soil and organic matter eroded from the lake's watershed.
Shoreline: zone where lake and land meet.
Spring circulation (or overturn): period of complete vertical mixing in the spring after ice-out and prior to thermal stratification.
Stratification: formation of distinct horizontal layers in a lake due to difference in density or temperature.

Stratified: separated into distinct layers.
Substrate: attachment surface or bottom material in which organisms can attach or live-within, such as rock, sand, woody debris or living macrophytes.

Temperate: lakes located in a climate where the summers are warm and the winters moderately cold. The Temperate Zone is between the Tropic of Cancer and the Arctic Circle.
Temperature profile: a graph of temperature versus depth, where the depth is on the y axis and temperature is on the x axis.
Tertiary consumers: larger consumers like fish feeding on other fish, birds and humans eating fish.
Thermal stratification: formation of a turbulently mixed layer of warm water (epilimnion) overlying a colder mass of relatively stagnant water (hypolimnion) in a water body due to density difference between warm and cold (denser) water.
Thermocline: thin but distinct layer in a large water body in which temperature changes more rapidly with depth than it does in the layers above or below. By definition to have a thermocline the temperature gradient must be at least 1°C per meter of depth.
TOC: Total Organic Carbon.
Tributary: Feeder stream.
Trophic state: the eutrophication is the process by which lakes are enriched with nutrients, increasing the algal production. The extent of this process is reflected in a lake's trophic classification or state: oligotrophic (nutrient poor), mesotrophic (moderately productive), and eutrophic (very productive).
Trophic webs: Conceptual model of the interconnections of species of organisms according to their different feeding groups.

Watershed: all land and water areas that drain toward a river or lake; also called drainage basin.
Weathering: mechanical and chemical breakdown and dissolution of rocks of a watershed..

Zooplankton: animal organisms freely floating in open water, eating bacteria, algae, detritus and sometimes other zooplankton; they are in turn eaten by planktivorous fish.

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Biographical Sketch

Roberto Bertoni is Senior Scientist at CNR-ISE (National Research Council - Institute for the Study of Ecosystems) Verbania Pallanza, formerly "Istituto Italiano di Idrobologia".
He obtained the Degree in Biological Sciences at the University of Milan in 1971. Its field of interest is Aquatic Microbial Ecology and, in particular, the spatial-temporal trend of particulate and dissolved organic matter and of microbial assemblages. His activity is also addressed towards the development of innovative tools to solve specific sampling problems (two patents) and to the application of image analysis techniques to quantify the microorganisms. The ultimate objective of his research is the study of the role of autotrophic and heterotrophic microorganisms in modifying the flow of energy and of organic matter in lakes. His research is developed through numerous international contacts which enabled him to study pristine environments (North Patagonian Andean

lakes). He was responsible for the EU project MICOR, for the evaluation of UVB radiation effects on microbial communities. He collaborated in research activities in extreme environments in the Program EV-K2 and in the EU project MOLAR. He participated in the EU EMERGE project and collaborated in the EU project Euro-limpacs. He is currently involved in life plus project EnvEurope. He is engaged in student training and is support teacher in the PhD cycles of the University of Parma, where he was external Professor of Limnology (2004-2005).
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