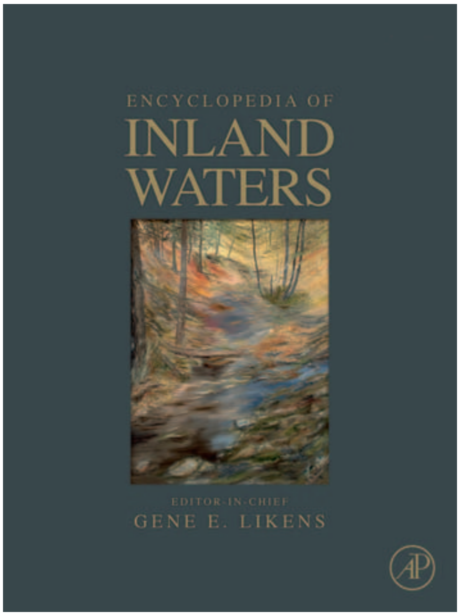

Lewis W M. (2009) Ecological Zonation in Lakes. In: Gene E. Likens, (Editor) Encyclopedia of Inland Waters. volume 1, pp. 416-422 Oxford: Elsevier.

Ecological Zonation in Lakes

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Introduction

Lakes show many kinds of spatial variation in both vertical and horizontal dimensions. Variation can be chemical, physical, or biotic, and is important to the understanding of ecosystem functions. Although some types of variation are unique to specific classes of lakes, others are common to most lakes, and correspond to an obvious spatial organization of the biota in lakes. The existence of certain common types of spatial organization in lakes has led to the naming of specific zones that have distinctive ecological characteristics.

A complete list of all zones that have been named by limnologists would be lengthy and complex (Wetzel, 2001). Complex nomenclatures have been abandoned by modern limnologists, however. Modern limnology focuses on simple zonation systems that are easily applied by limnologists and others interested in lakes. Table 1 gives a summary of zonation systems that are currently in broad use.

Horizontal Zonation: Littoral and Pelagic

The nearshore area of a lake (littoral zone) differs from the offshore shore area (pelagic zone). The only group of autotrophs in the pelagic zone is the phytoplankton, which consists of very small algae that are suspended in the water column. The littoral zone also has phytoplankton (which move freely between littoral zone and pelagic zone), but also has two other categories of autotrophs (Figure 1): aquatic vascular plants (aquatic macrophytes), and films of attached algae (periphyton). Periphyton grow on the leaves of macrophytes and on other solid surfaces such as mud, sand, rocks, or wood.

The outer margin of the littoral zone, beyond which is the pelagic zone, is the point at which significant growth of macrophytes and periphyton becomes impossible because of darkness. This boundary corresponds approximately to the location at which the amount of solar irradiance reaching the bottom of the lake is <1% of surface irradiance. At bottom irradiances <1%, there is little or no net photosynthesis, which prevents growth of the attached autotrophs (macrophytes and periphyton) that are typical of the littoral zone.

For a lake of a given size and shape, the width of the littoral zone depends on transparency of the water as well as shoreline slope (Figure 2). In oligotrophic lakes, which have low nutrient concentrations and therefore develop very small amounts of the phytoplankton biomass that could shade the lower water column of lakes, the littoral zone extends to depths of 4–20 m or even more, depending on transparency of the water. In the eutrophic category, the depth of 1% irradiance ranges between 0.1 and about 2 m, and the mesotrophic category spans ~2–4 m. In the most extreme cases of eutrophication (lakes highly enriched with nutrients), where the depth of 1% light corresponds to only a few centimeters, the littoral zone as defined by light is virtually absent, and the littoral zone may be defined instead by the zone of influence for traveling waves and corresponding disturbance of the bottom (0.5–1.5 m). In general, small lakes have a higher percentage of surface area in the littoral zone than do large lakes (Figure 2), although some large, shallow lakes have large littoral zones (e.g., Lake Okeechobee, Florida).

Although littoral zones are most easily defined on the basis of macrophytes and attached algae, a littoral zone can also be distinguished from a pelagic zone by its distinctive heterotrophic communities and by its food-web structure. Because littoral zones provide shelter, whereas pelagic zones do not, littoral zones often support dense populations of organisms that thrive when protected from predation. Larval and juvenile fish, for example, seek shelter within the littoral zone from predation by larger fish. Large invertebrates, such as dragonfly larvae or crayfish, typically are most abundant in littoral zones, where they are least likely to be consumed by fish. The littoral zone also has invertebrate communities that specialize in the consumption of attached algae by nipping or scraping the algal coatings on macrophytes or other solid surfaces. In the pelagic zone, there is no food source comparable to the periphyton of a littoral zone. In general, the communities of a littoral zone are more diverse than those of the pelagic zone, and the key species of the two zones differ.

In the pelagic zone of a lake, the autotroph community is composed of phytoplankton (Figure 1), which are adapted for life in an environment that is free of solid surfaces. Consumers, such as zooplankton, living and reproducing in the pelagic zone must escape predators by avoiding the upper, illuminated part of the water column during the day, or must be agile or so small as to be impractical as a food for many predators.

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Vertical Zonation: Water Column, Sediments, and the Benthic Interface

Lakes have a vertical zonation consisting of the water column, underlying lacustrine sediments (lake sediments), and the benthic zone, which occupies a few centimeters above and below the sediment–water interface (Figure 3). The water column extends across both the pelagic and littoral zones. The water column of the pelagic zone is driven by wind-generated currents into the littoral zone where water is displaced from the littoral zone into the pelagic zone. Thus, water-column constituents such as dissolved gases, dissolved solids, suspended solids, and suspended organisms are constantly exchanged between the pelagic zone and the littoral zone whenever there are currents in the top few meters of a lake. Chemical differences between the top few meters of the pelagic zone and the littoral zone may develop under the influence of biological processes, however, when currents are weak.

Although the water column is shared by the pelagic zone and the littoral zone, lacustrine sediments always underlie the pelagic zone but may or may not cover all of the littoral zone. Sediments are produced by the settling of mineral and organic matter that is derived from the watershed of a lake, and from organic matter consisting of fecal pellets, organic debris (detritus), and skeletal fragments of organisms derived from the lake itself. A constant sedimentation of this fine mixed solid material occurs over the entire lake. Disturbance of sediments by moving water occurs primarily in shallow water, where most of the energy of wind-generated currents and traveling waves are expended against the bottom of the littoral

Table 1 Summary of the four major zonation systems for lakes.

Zonation	*Temporal variability*	*Description*
Horizontal	Stable	
Pelagic zone		Offshore (bottom irradiance <1%)
Littoral zone		Nearshore (bottom irradiance ≥1%)
Vertical	Stable	
Water column		Water extending from lake surface to bottom
Lacustrine sediments		Lake-generated solids below the water column
Benthic zone		Interface of water column and lake bottom
Vertical	Seasonal	
Epilimnion (mixed layer)		Uppermost density layer (warm)
Metalimnion		Middle density layer (transition)
Hypolimnion		Bottom density layer (cool)
Vertical	Dynamic	
Euphotic zone		Portions of a lake with ≥1% light (photosynthesis)
Aphotic zone		Portions of a lake with <1% light (no photosynthesis)

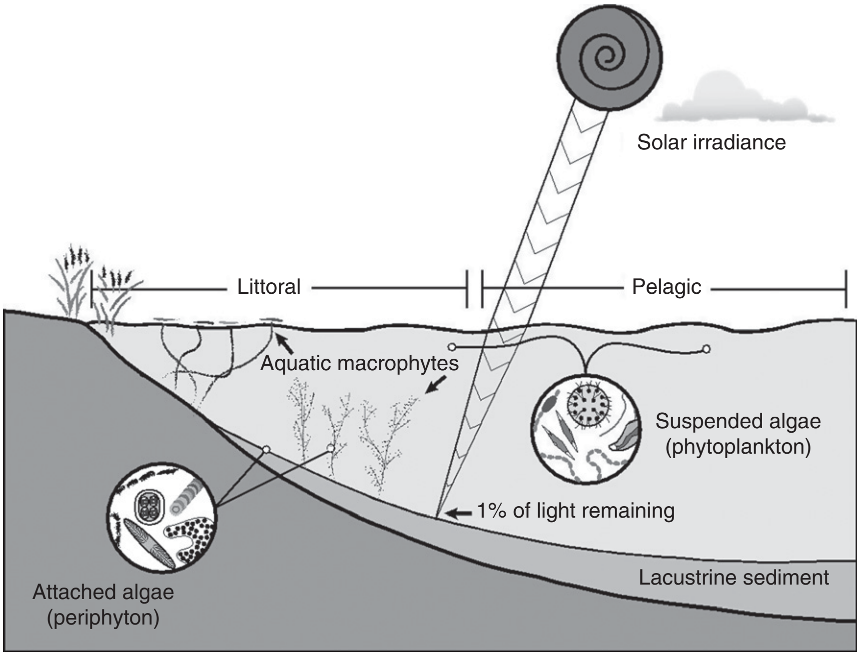

Figure 1 Depiction of the littoral and pelagic zones of a lake. The littoral zone extends outward from the shoreline to approximately the location at which the solar irradiance at the bottom of the lake corresponds to about 1% of the solar irradiance at the top of the water column. Within the littoral zone, growth of aquatic macrophytes and attached algae (periphyton) is possible. The pelagic zone begins at the outer margin of the littoral zone. Phytoplankton are exchanged freely between the littoral and pelagic zones as well.

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zone. Thus, energy near the shore may cause fine sediments, such as those that are characteristic of lakes, to be swept to deeper water. For this reason, lacustrine sediments may not accumulate in all parts of a littoral zone. Alternatively, in lakes that are small or strongly sheltered from wind, and thus not subjected to extremes of wind-generated disturbance, lacustrine sediments may occupy most or all of the littoral zone.

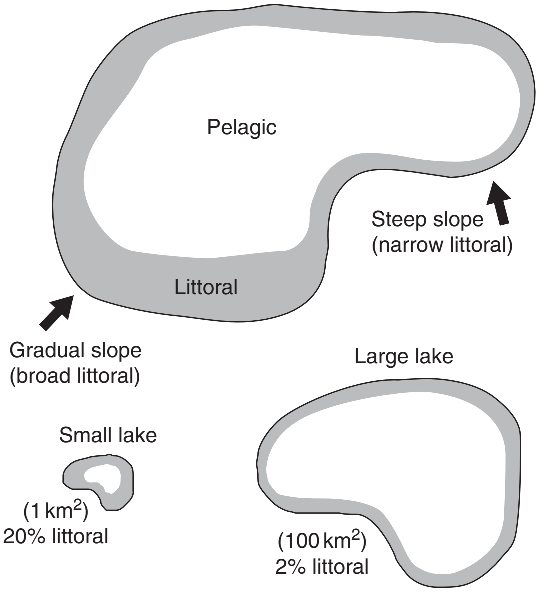

Figure 2 A plan view of the littoral and pelagic zones of lakes, illustrating variation in the width of the littoral zone associated with changes in slope along the margin of any given lake, and the tendency of smaller lakes to have a higher percent areal coverage of littoral zone for the total lake area.

Lacustrine sediments are capable of supporting eukaryotic organisms (algae, protozoans, invertebrates, vertebrates) only when they are oxic. When the hypolimnion is oxic, the top few millimeters of sediment often (but not always) will be oxic. Below the top few millimeters, there typically is a decline in oxygen because microbial respiration supported by organic matter in the sediments leads to the depletion of oxygen, but some oxygen (e.g., 50%) may persist because invertebrates in the sediment pump oxygen through small tunnels into the sediment to as much as 10–20 cm within the sediments. Almost all of the deeper sediments (>10–20 cm) in lakes, which may be many meters thick, are anoxic and can support only microbes that are capable of anaerobic metabolism. When the water of the hypolimnion is anoxic, the entire sediment profile is anoxic, and can support only anaerobic microbes. There are many such microbes, and anoxic sediments show strong evidence of their metabolism, including accumulation of reduced substances such as ferrous iron, sulfide, and methane. At progressively greater depths in sediments, however, the metabolism of microbial anaerobes slows because the easily used portions of organic matter are exhausted or because oxidizing agents such as sulfate or nitrate may be depleted. Thus, there is a decline in microbial metabolic rate from the upper sediments to the deepest sediments, which are almost inert biologically.

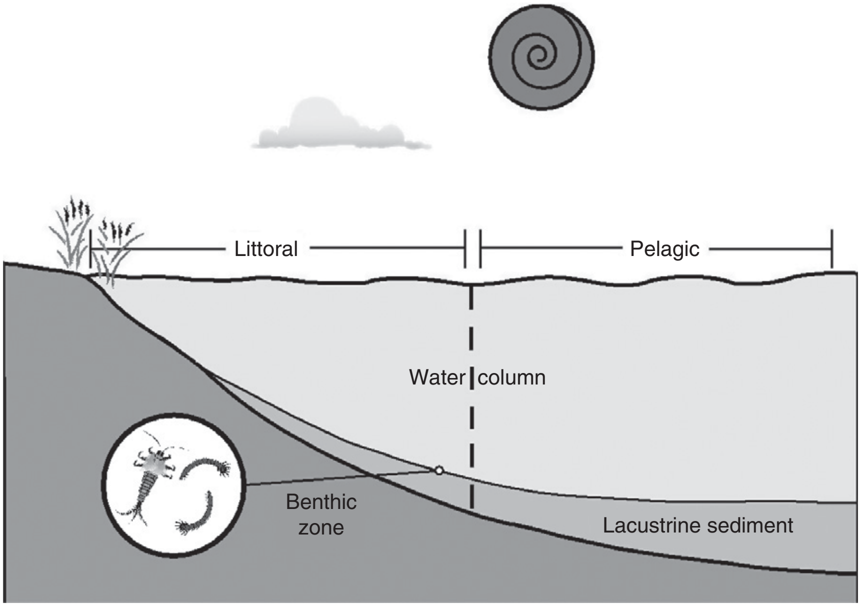

Figure 3 Illustration of the division of a lake into three vertical components: water column, lacustrine sediments, and the boundary between the water column and sediments (benthic zone).

The interface between the water column and the lacustrine sediments carries its own name (‘benthic zone’) because it is exceptionally important from the ecosystem perspective, despite its narrow dimensions. Organisms that live on the sediment surface or just below it (down to about 20 cm) carry the name ‘benthos’. In sediments below the pelagic zone, the benthos does not include autotrophs because there is no light reaching these sediments. The benthic zone is rich in invertebrates, provided that it is oxic at the surface, which is not always the case. Oxic benthic zones often support a number of important invertebrates, most of which are embedded within the sediment, as necessary to avoid predation. Examples include midge larvae and the larvae of other insects (Figure 3). Certain fish species (e.g., catfish) may be associated closely with the benthic zone, in that they are adapted to find and consume the embedded invertebrates by chemosensory means, without using vision. Oxic benthic zones also support protozoans and bacteria conducting oxic metabolism, including especially the oxic breakdown of organic matter. Anoxic benthic zones only support anaerobic bacteria and a few specialized protozoans.

The benthic zone extends not only across the bottom of the pelagic zone but also across the bottom of the littoral zone (Figure 3). The benthic component of the littoral zone includes not only the interface between lacustrine sediments and the water column but also between the water column and any parts of the littoral zone that happen to be swept free of lacustrine sediments. Thus, the entire solid surface at the bottom of a lake lies within the benthic zone.

Seasonal Zonation: Vertical Layering Based on Density

Because the temperature of water affects its density, it is common for lakes to develop layers of different density corresponding to temperature differences across the layers. At temperate latitudes, all but the shallowest lakes develop a density stratification during spring that typically persists until late fall. Similar seasonal stratification is also common in subtropical and tropical lakes, but the duration of stratification is longer and the nonstratified period (mixing period) does not contain an interval of ice cover, as it often does at temperate latitudes.

Density stratification causes an ecologically important vertical zonation of lakes (Figure 4). An upper layer, which contains the air–water interface, is the epilimnion of a stratified lake; it may also be referred to as the ‘mixed layer’. The epilimnion is the warmest and least dense of the three layers. Its thickness is strongly influenced by the size of the lake, in that larger lakes show a higher transfer of wind energy to water currents, which thickens the mixed layer during its period of formation. In sheltered water bodies, mixed layers may be as thin as two meters, but in larger ($>10\,\text{km}^2$), windswept water bodies, they may be as thick as 15–20 m. In addition, the thickness of a mixed layer in a given lake increases over the fall cooling period, during which the bottom of the mixed layer erodes the layer below.

The mixed layer often shows sufficient irradiance throughout its full thickness to support photosynthesis. Even in lakes that have very low transparency,

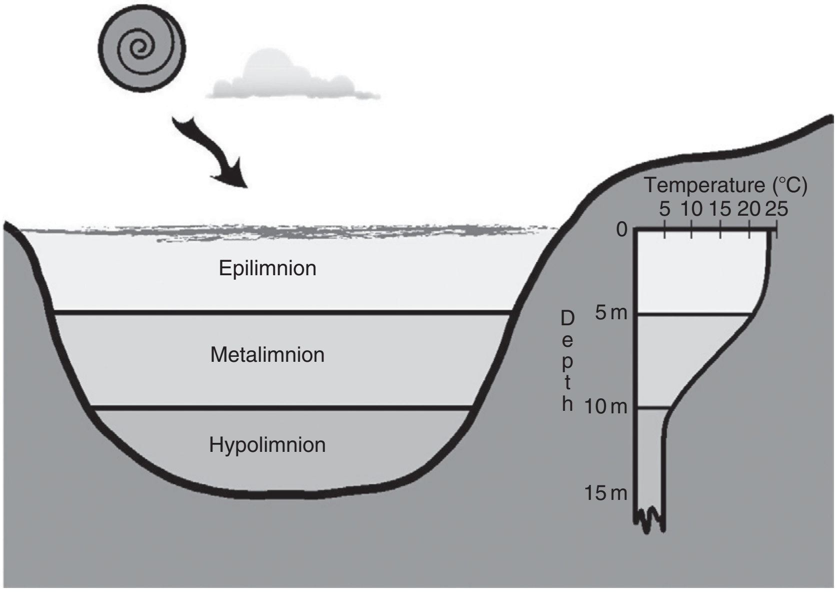

Figure 4 Illustration of the three density (temperature) layers determined by seasonal stratification of a water column.

the uppermost portion of the mixed layer is well illuminated.

The mixed layer extends continuously across the pelagic zone and littoral zone. Only in highly transparent lakes does the littoral zone extend below the mixed layer. Within the pelagic portion of the mixed layer, zooplankton herbivores feed vigorously on phytoplankton, but may move downward out of the mixed layer during the day in order to avoid predation. Other small invertebrates often migrate out of the mixed layer during daylight hours as well. Most of the energy of wind transferred to water is dissipated within the mixed layer; this energy contributes to the high degree of uniformity in the mixed layer at small to intermediate distance scales (up to 10 km or more), except during extended calm weather.

Below the mixed layer of a stratified lake is a thermal gradient, corresponding to a density gradient. The gradient makes a transition in temperature and density between the mixed layer and the coolest layer, which lies in contact with the bottom of the lake. The thermal transition is referred to as the thermocline, but the layer within which the thermocline lies is best referred to as the metalimnion (Figure 4). The metalimnion may or may not receive sufficient irradiance to support photosynthesis. In lakes that are quite transparent, phytoplankton often grows in the metalimnion, whereas lakes of low transparency seldom show growth of autotrophs in the metalimnion. In the pelagic zone, phytoplankton growing in the metalimnion of a transparent lake may be of different species composition than phytoplankton growing in the mixed layer. Some mass transfer occurs between the epilimnion and the metalimnion, the amount of which is dependent on the amount of turbulence at the interface of the two layers. The thickness of the metalimnion varies a great deal among lakes. It is seldom thinner than 2 m, and may be as thick as the mixed layer or even thicker.

The deepest seasonal layer in lakes is the hypolimnion. The temperature and density of the hypolimnion typically reflect conditions that occur when seasonal stratification becomes established. It is common for stratified lakes at temperate latitudes to have hypolimnetic waters that are near 4 °C, the temperature at which water is most dense, or slightly above 4 °C, reflecting the prevailing water temperature at the time of spring stratification. At lower latitudes, the minimum temperature increases, until it reaches approximately 24 °C within 10° latitude of the equator. Thus, a stratified lake might have a hypolimnion of 4 °C in Wisconsin and 24 °C in Venezuela.

The hypolimnion, in contrast to the mixed layer, has a very low degree of turbulence, is too dark for photosynthesis, and is isolated from the surface. Also, except at low latitudes, it is much cooler than the mixed layer (Figure 4).

Because of its physical isolation from photosynthesis and from atmospheric oxygen, the hypolimnion typically loses oxygen during the period of stratification. The loss of oxygen depends on the size of the hypolimnion, its temperature, the duration of stratification, and the amount of organic matter coming down to it from above, which is a byproduct of the trophic status of the lake. In lakes that are just deep enough to support stable stratification (e.g., 10–20 m), the hypolimnion may be absent, as the metalimnion reaches the bottom of the lake. In deeper lakes, the hypolimnion may equal the volume of the epilimnion, and in very deep lakes (e.g., >100 m), the hypolimnion may be much larger than the epilimnion. Lakes with a very large hypolimnion often maintain hypolimnetic oxygen throughout the stratification season, especially at temperate latitudes where the hypolimnion is cool. Lakes with a very small hypolimnion typically lose most or all of their oxygen, even if they have low productivity, because the sediments of a lake contain enough organic matter to demand most or all the oxygen from a small hypolimnion. Oxygen concentration in lakes with a hypolimnion of intermediate size is quite sensitive to trophic state. Eutrophic lakes typically lose most or all of their hypolimnetic oxygen, thus producing an anoxic benthic zone, whereas lakes of lower productivity may retain an oxic hypolimnion overlying a benthic zone that has an oxidized surface.

Loss of oxygen is of great importance to the metabolism of a lake because eukaryotes (most protozoa, invertebrates, fish, algae) cannot live in anoxic waters. Thus, loss of hypolimnetic oxygen excludes nonmicrobial components of the biota from the deep waters of a lake.

Zones with Dynamic Dimensions: Euphotic and Aphotic

Photosynthesis in the water column of lake is dependent on the availability of photosynthetically available radiation (PAR, wavelengths 350–700 nm). PAR, which corresponds closely to the spectrum of human vision, is removed exponentially as it travels through a water column. The availability of PAR is high during daylight hours at or near the surface of the water column. If nutrients are present, rates of photosynthesis are likely to be high near the surface. A progressive decline in PAR with depth is paraleled by a decline in rates of photosynthesis with depth. At a depth corresponding to ~1% of the surface irradiance, net photosynthesis reaches zero, which is a threshold beyond which accumulation of plant biomass is not possible. At depths below the 1% level, photosynthetic organisms (e.g., phytoplankton) lose mass and either die or become dormant unless they are returned to the surface by water currents, which commonly occurs in the mixed layer but not in the metalimnion or hypolimnion.

The depth between the water surface and the depth of 1% irradiance is referred to as the euphotic zone (Figure 5). Below the depth of 1% irradiance is the aphotic zone. The euphotic zone may not occupy the entire epilimnion of a lake, or may extend to the full thickness of the epilimnion. In some cases, the euphotic zone may extend into the metalimnion, but its extension into the hypolimnion of a lake is unlikely.

The thickness of the euphotic zone is dependent on transparency of the water, which in turn is influenced by dissolved color (colored organic acids from soils), inorganic suspended matter (silt and clay), and living organisms, and especially those that contain chlorophyll, an efficient absorber of light. Because the concentrations of each of these constituents can vary on relatively short time scales (e.g., weekly), the thickness of the euphotic and aphotic zones is dynamic; it is subject to both seasonal and irregular change over time.

The thickness of the euphotic zone may be small at times of high runoff, when suspended inorganic material and colored organic compounds enter lakes in the largest quantities. Other times when the euphotic zone may be thin it coincides with algal blooms, which can produce sufficient chlorophyll to reduce the transparency of the water column substantially. Conversely, the euphotic zone may thicken substantially when nutrients are exhausted because phytoplankton biomass is likely to decline, thus increasing transparency of the water. Also, strong grazing by zooplankton may thicken the euphotic zone by removing phytoplankton biomass.

The euphotic zone extends across an entire lake, including both pelagic and littoral zones. In fact, the mean thickness of the euphotic zone determines the outer boundary of the littoral zone because of its effect on the attached vegetation that is characteristic of littoral zones.

Overview

The four sets of zones shown in Table 1 define distinctive habitats within lakes that are associated with specific categories of organisms and biogeochemical or metabolic processes. The zones reflect some of the most important physical and chemical factors that control biotically driven processes and biotic community structure. Zonation, although generally a qualitative rather a quantitative concept, reflects accumulation of experience and measurements across lakes of many kinds. Therefore, knowledge of zonal

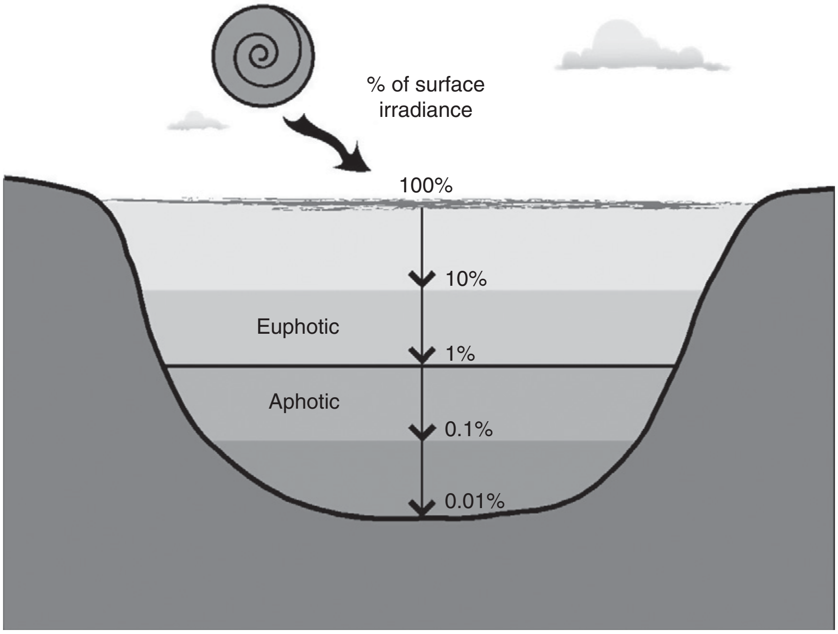

Figure 5 Illustration of the division of a lake into euphotic and aphotic zones. The euphotic zone, which is the lake volume within which positive net photosynthesis can occur, corresponds approximately to the depth at which ≥1% of incoming irradiance is found. Portions of the lake below this boundary have negative net photosynthesis or negligible total photosynthesis.

boundaries in a lake allows some general predictions to be made about the kinds of organisms and rates of biogeochemical processes that will occur in a given lake, and the spatial distribution of these organisms and processes.

Glossary

Aphotic – Without light, generally interpreted limnologically as receiving less than 1% of solar irradiance reaching a lake surface.

Epilimnion – The uppermost and warmest layer (also called the mixed layer) of a lake that experiences density stratification induced by seasonal warming at the lake surface.

Euphotic – That portion of a lake receiving sufficient solar irradiance to support photosynthesis (typically more than 1% of full solar irradiance).

Hypolimnion – The most dense, deepest, and coolest layer of a thermally stratified lake. The hypolimnion does not support photosynthesis, because it lacks solar irradiance, and in many cases shows partial or complete depletion of dissolved oxygen.

Littoral – Near the shore of a waterbody, where irradiance reaching the bottom is above 1% of solar irradiance at the water surface.

Metalimnion – A layer of transitional density and temperature that connects the epilimnion to the hypolimnion.

Pelagic – Beyond the littoral zone of a lake.

Benthic – The zone of a lake extending a few centimeters above and below the bottom of the lake.

See also: Density Stratification and Stability; Geomorphology of Lake Basins; Optical Properties of Water; Photosynthetic Periphyton and Surfaces.

Further Reading

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