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Understanding: Lake Ecology Primer

There are a total of 21 web pages in this on-line limnology primer. Use the navigation bar located on the top left side of each page, or use the links provided at the bottom of each page to move forward or backward in the primer. Throughout these pages, you will find terms that are linked to their respective definitions. Move the mouse over the link to see a pop-up window with the definition. Move your mouse away from the term, and the pop-up window will go away. Click on the link to open the full glossary, and find more defined terms. Here is an example, **Water on the Web**.

A pdf version of the Limnology primer is available to download or print -- **limnology.pdf (892 Kb)**. You'll need **Acrobat Reader** installed to view this.

Overview

The following overview is taken from LAKE ECOLOGY OVERVIEW (Chapter 1, Horne, A.J. and C.R. Goldman. 1994. Limnology. 2nd edition. McGraw-Hill Co., New York, New York, USA.)

Limnology is the study of fresh or saline waters contained within continental boundaries. Limnology and the closely related science of oceanography together cover all aquatic **ecosystems**. Although many limnologists are freshwater ecologists, physical, chemical, and engineering limnologists all participate in this branch of science. Limnology covers lakes, ponds, reservoirs, streams, rivers, wetlands, and estuaries, while oceanography covers the open sea. Limnology evolved into a distinct science only in the past two centuries, when improvements in microscopes, the invention of the silk plankton net, and improvements in the thermometer combined to show that lakes are complex ecological systems with distinct structures.

Today, limnology plays a major role in water use and distribution as well as in wildlife habitat protection. Limnologists work on lake and reservoir management, water pollution control, and stream and river protection, artificial wetland construction, and fish and wildlife enhancement. An important goal of education in limnology is to increase the number of people who, although not full-time limnologists, can understand and apply its general concepts to a broad range of related disciplines.

A primary goal of Water on the Web is to use these beautiful aquatic ecosystems to assist in the teaching of core physical, chemical, biological, and mathematical principles, as well as modern computer technology, while also improving our students' general understanding of water - the most fundamental substance necessary for sustaining life on our planet.

Acknowledgements

The Lake Ecology section is intended to provide a general background to Water on the Web by introducing the basic concepts necessary to understand how lake ecosystems function. The reader is later referred to a list of texts and journals for more in-depth coverage of the science of freshwater ecosystems. Much of the text, formatting, and figures are based on the four documents listed below, although extensive modifications have been made to include the original lecture notes of Co-principal Investigator Richard Axler. Additional citations have been included to provide appropriate credit.

Moore, M.L. 1989. NALMS management guide for lakes and reservoirs. **North American Lake Management Society**, P.O. Box 5443, Madison, WI, 53705-5443, USA.

NALMS. 1990. Lake and reservoir restoration guidance manual. Second edition (note - a revised manual is currently in preparation). **North American Lake Management Society**, P.O. Box 5443, Madison, WI, 53705-5443, USA.

Michaud, J.P. 1991. A citizen's guide to understanding and monitoring lakes and streams. Publ. #94-149. Washington State Department of Ecology, Publications Office, Olympia, WA, USA 360-407-7472.

Monson, B. 1992. A primer on limnology, second edition. **Water Resources Center**, University of

Minnesota, 1500 Cleveland Avenue, St. Paul, MN 55108, USA.

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Lake Variability

People often visualize a lake as a uniform mass of water, almost like a full bathtub that is evenly mixed from top to bottom, side to side and front to back. In fact, lakes are extremely **heterogeneous**, or patchy. The physical, chemical, and biological characteristics of lakes are extremely variable. Lakes vary physically in terms of light levels, temperature, and water currents. Lakes vary chemically in terms of nutrients, major ions, and contaminants. Lakes vary biologically in terms of structure and function as well as static versus dynamic variables, such as **biomass**, population numbers, and growth rates. There is a great deal of spatial heterogeneity in all these variables, as well as temporal variability on the scales of minutes, hours, **diel** (day/night), seasons, decades, and geological time. Though lakes vary in many dimensions they are actually highly structured, similar to a forest **ecosystem** where, for example, a variety of physical variables (light, temperature, moisture) vary from the soil up through the canopy.

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Physical Structure and Geological Characteristics

Formation of Lakes

Knowledge of the formation and history of a lake is important to understanding its structure. The current chemical and biological condition of a lake depends on many factors, including:

- how it was formed
- size and shape of the lake **basin**
- size, **topography**, and chemistry of its **watershed**
- regional climate
- local biological communities
- activities of humans during the past century

There are four major areas in the US with an abundance of natural lakes:

- limestone solution lakes of Florida
- mountain lakes of the Pacific Northwest
- the heavily glaciated Great Lakes region
- the glaciated Adirondacks region of the Northeast

The focus of Water on the Web, and this Lake Ecology section, is on lakes in the glaciated landscapes of the Great Lakes region. In Minnesota, there are 12,034 lakes larger than 4 hectares (10 acres). The glaciers that covered much of the state until about 12,000 years ago created most Minnesota lakes. Glaciers formed lake **basins** by gouging holes in loose soil or soft bedrock, depositing material across stream beds, or leaving buried chunks of ice that later melted to leave lake basins (Figure 1). When these natural depressions or impoundments filled with water, they became lakes.

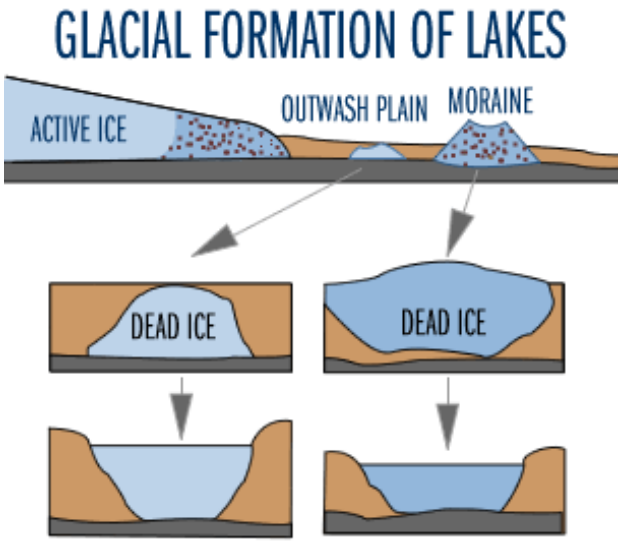

Figure 1

After the glaciers retreated, sediments accumulated in the deeper parts of the lake. These sediments entered the lakes from tributaries and from decomposed **organic** material derived from both the watershed and aquatic from plants and **algae**. An average Minnesota lake contains 9-12 meters of such sediment in its deeper parts.

Lake sediment deposits provide a record of a lake's history. **Paleolimnology** is the study of lake sediments. Paleolimnologists collect lake sediments using special coring devices to study a lake's physical, chemical and biological history. Lake sediments are often dated using the **radioisotopes** lead-210 and carbon-14. The age of a given sediment sample is based on the radioactive decay of the isotope. Other dating methods are based on identifying sharp increases of pollen in the core from ragweed and other plants indicative of agricultural soil disturbances or deforestation. **Stratigraphic** analyses of sediments have been used increasingly to assess the history of lakes, especially with regard to human impact. Lake **acidity**, water **clarity**, and algal **productivity** have been inferred by analyzing **diatom** abundance and composition, as well as plant pigments. Soil erosion can be inferred by the proportion of **inorganic** and organic matter and by chemical analyses for metals. Recently in Minnesota, these sediment dating, coring, and analysis techniques have been used to estimate spatial and temporal patterns in the mercury (Hg) content of lake sediments. These data were used to infer trends and sources of Hg in the state.

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Light

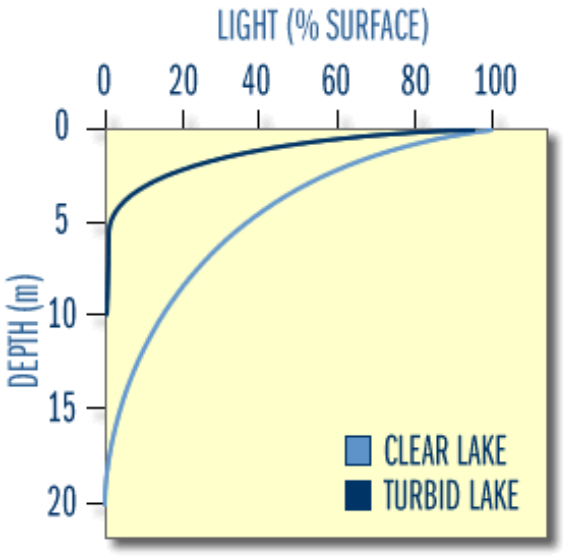
Perhaps the most fundamental set of properties of lakes relates to the interactions of light, temperature and wind mixing. The absorption and **attenuation** of light by the **water column** are major factors controlling temperature and potential **photosynthesis**. **Photosynthesis** provides the food that supports much of the **food web**. It also provides much of the **dissolved oxygen** in the water. Solar **radiation** is the major source of **heat** to the water column and is a major factor determining wind patterns in the lake **basin** and water movements.

Light intensity at the lake surface varies seasonally and with cloud cover and decreases with depth down the water column. The deeper into the water column that light can penetrate, the deeper photosynthesis can occur. Photosynthetic organisms include **algae** suspended in the water (**phytoplankton**), algae attached to surfaces (**periphyton**), and vascular aquatic plants (**macrophytes**).

The rate at which light decreases with depth depends upon the amount of light-absorbing dissolved substances (mostly **organic** carbon compounds washed in from decomposing vegetation in the watershed) and the amount of absorption and scattering caused by suspended materials (soil particles from the watershed, algae and **detritus**).

The percentage of the surface light absorbed or scattered in a 1 meter long vertical column of water, is called the **vertical extinction coefficient**. This **parameter** is symbolized by "**k**".

In lakes with low k-values, light penetrates deeper than in those with high k-values. Figure 2 shows the light **attenuation profiles** from two lakes with attenuation coefficients of 0.2/m and 0.9/m.



LIGHT VERSUS DEPTH PROFILES FOR A CLEAR LAKE ($k=0.2\ M^{-1}$) AND A TURBID LAKE ($k=0.9\ M^{-1}$).

Figure 2

The maximum depth at which algae and macrophytes can grow is determined by light levels. Limnologists estimate this depth to be the point at which the amount of light available is reduced to 0.5%–1% of the amount of light available at the lake surface. This is called the **euphotic zone**. A general rule of thumb is that this depth is about 2 to 3 times the limit of visibility as estimated using a **Secchi disk**. Light may be measured in a variety of ways for a number of different characteristics. The reader is referred to the reference texts for more information. Since photosynthesis depends fundamentally on light, significant

changes in light penetration in a lake will produce a variety of direct and indirect biological and chemical effects. Significant changes in lake transparency are most often the result of human activities, usually in association with **landuse** activities in the watershed.

Also see "**What is Light?**" for an excellent primer on light.

Table 1. Estimated ranges of water transparency values for various lakes.
"Clear" water refers to the lack of bog-staining color. WOW lakes in bold face.
Vertical extinction coefficient, **k**, defined previously. Secchi depths in meters.

LAKE	k (m^{-1})	Secchi Depth (m)	Euphotic Zone (m)	Description
Crater Lake (OR)	0.06—0.12	25— 45	>120	Clear, sky blue ultra-oligotrophic lake
Lake Tahoe (CA/ NV)	0.12	40	90—136	As above but decreasing **clarity** since1960s due to watershed overdevelopment **http://trg.ucdavis.edu/**
Lake Superior				
Lake Superior (Blue water)	0.13	15— 20	46—60	Ultra-oligotrophic; most oligotrophic of the Laurentian Great Lakes
Lake Superior (Green water near Duluth)	0.3	5— 12	20—30	Western arm near Duluth and St. Louis River and harbor inputs
St. Louis River (Duluth-Superior Harbor)	4.21	0.7	>5	Brown (bog) stained from river plus high **suspended sediments**
Lake Michigan	0.19—0.24	?	19—31	Meso-oligotrophic
Lake Huron	0.1 — 0.5	?	25—31	Meso-oligotrophic
Lake Erie	0.2 — 1.2	2—10 (1970—1990) >10 (1993—1995)	12—26	Eutrophic (clarity improving recently due to zebra mussels)
Lake Ontario	0.15 — 1.2	?	12—29	Mesotrophic
Lake Baikal, Siberia	0.2	5— 40	15—75	Oligotrophic
Grindstone Lake (Pine County, MN)	0.82	3— 6	8—20	Mesotrophic, water is fairly stained or colored
Ice Lake (Itasca County, MN)	0.83	2— 5	6—15	Mesotrophic
Lake Minnetonka (Hennepin County, MN)				
West Upper	0.78	1.4	3—5	Mesotrophic
Halsted Bay	2.9	0.5	<2	Eutrophic

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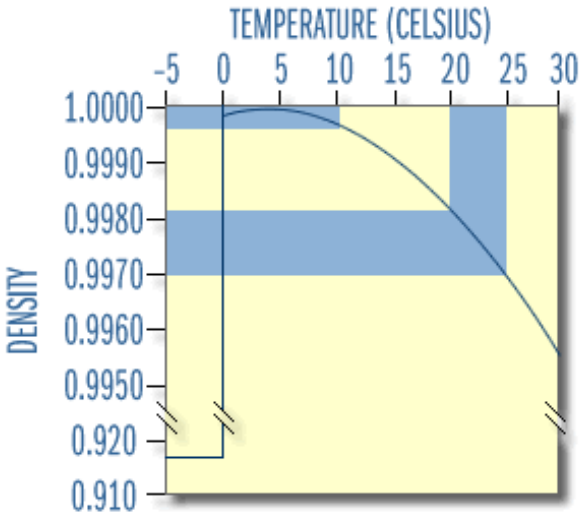
Density Stratification

In the spring, immediately after **ice-out** in **temperate** climates, the **water column** is cold and nearly **isothermal** with depth. The intense sunlight of spring is absorbed in the water column, which also **heats** up as the average daily temperature of the air increases. In the absence of wind, a **temperature profile** with depth might be expected to resemble Figure 2 (see the **Light section**), decreasing exponentially with depth. However, **density**, another physical characteristic of water, plays an important role in modifying this pattern.

Water differs from most other compounds because it is less dense as a solid than as a liquid. Consequently ice floats, while water at temperatures just above freezing sinks. As most compounds change from a liquid to a solid, the molecules become more tightly packed and consequently the compound is denser as a solid than as a liquid. Water, in contrast, is most dense at 4°C and becomes less dense at both higher and lower temperatures. The density/temperature relationship of fresh water is shown in Figure 3. Because of this density-temperature relationship, many lakes in temperate climates tend to stratify, that is, they separate into distinct layers.



DENSITY/TEMPERATURE RELATIONSHIP FOR DISTILLED WATER. SHADED AREAS SHOW RELATIVE DIFFERENCE IN DENSITY FOR 5°C TEMPERATURE CHANGES.

Figure 3.

Spring

In lakes of the upper Midwest and at higher elevations, the water near a lake's bottom will usually be at 4° C just before the lake´s ice cover melts in the spring. Water above that layer will be cooler, approaching 0° C just under the ice. As the weather warms, the ice melts. The surface water heats up and therefore it decreases in density. When the temperature (density) of the surface water equals the bottom water, very little wind energy is needed to mix the lake completely. This is called **turnover**. After this **spring turnover**, the surface water continues to absorb heat and warms. As the temperature rises, the water becomes lighter than the water below. For a while winds may still mix the lake from bottom to top, but eventually the upper water becomes too warm and too buoyant to mix completely with the denser deeper water. As Figure 3 suggests, the relatively large differences in density at higher temperatures are very effective at preventing mixing. It simply takes too much energy to mix the water any deeper.

It is useful to visualize a more extreme example of **density stratification**. Imagine a bottle of salad dressing containing vegetable oil and vinegar. The oil is lighter (more buoyant) than the vinegar which is mostly water. When you shake it up you are supplying the energy to overcome the buoyant force, so the two fluids can be uniformly mixed together. However, if allowed to stand undisturbed, the more buoyant (less dense) oil will float to the top and a two-layer system will develop.

In some cases, such as happened at Ice Lake in April, 1998 and 1999, the surface water may warm up rapidly immediately after ice-out, causing the lake to stratify thermally without completely mixing. This prevents atmospheric oxygen from reaching the bottom waters. As a consequence, the entire water column never reaches 100% oxygen **saturation**. This can be observed for Ice Lake by comparing temperature and oxygen profiles from March 5, 1998 (still frozen), April 18, 1998 (the lake was completely ice-free on April 11, 1998), and April 30, 1998.

Summer

As summer progresses, the temperature (and density) differences between upper and lower water layers become more distinct. Deep lakes generally become physically **stratified** into three identifiable layers, known as the **epilimnion**, **metalimnion**, and **hypolimnion** (Figure 4). The epilimnion is the upper, warm layer, and is typically well mixed. Below the epilimnion is the metalimnion or **thermocline** region, a layer of water in which the temperature declines rapidly with depth. The hypolimnion is the bottom layer of colder water, isolated from the epilimnion by the metalimnion. The density change at the metalimnion acts as a physical barrier that prevents mixing of the upper and lower layers for several months during the summer.

The depth of mixing depends in part on the exposure of the lake to wind (its **fetch**), but is most closely related to the lake's size. Smaller to moderately-sized lakes (50 to 1000 acres) reasonably may be expected to stratify and be well mixed to a depth of 3–7 meters in north temperate climates. Larger lakes may be well mixed to a depth of 10–15 meters in summer (e.g., Western Lake Superior near Duluth, MN).

Note that although "thermocline" is a term often used synonymously with metalimnion, it is actually the plane or surface of maximum rate of decrease of temperature with respect to depth. Thus, the thermocline is the point of maximum temperature change within the metalimnion.

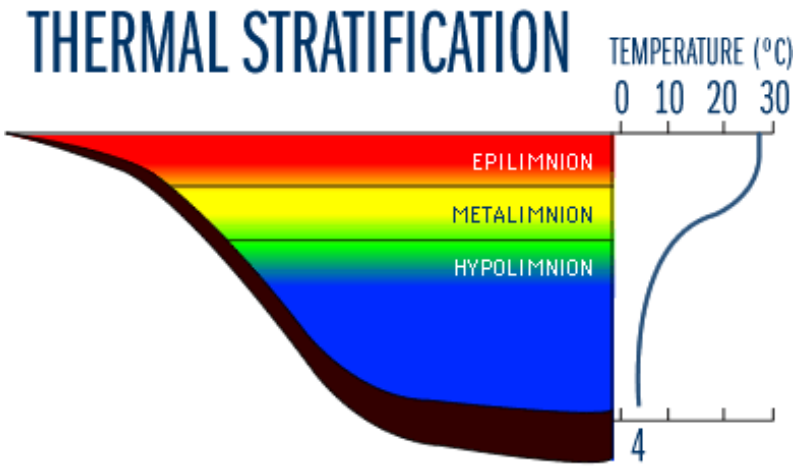


Figure 4.

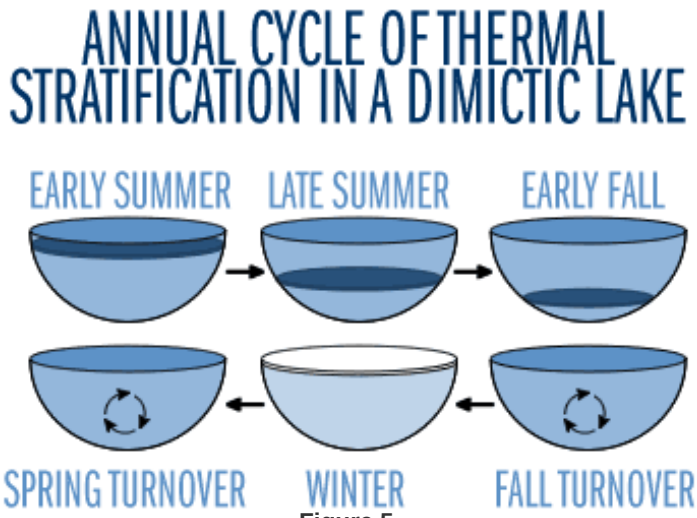


Figure 5.

Autumn

As the weather cools during autumn, the **epilimnion** cools too, reducing the density difference between it and the **hypolimnion** (Figure 5). As time passes, winds mix the lake to greater depths, and the **thermocline** gradually deepens. When surface and bottom waters approach the same temperature and density, autumn winds can mix the entire lake; the lake is said to "turn over." As the atmosphere cools, the surface water continues to cool until it freezes. A less distinct density stratification than that seen in summer develops under the ice during winter. Most of the water column is isothermal at a temperature of 4°C, which is denser than the colder, lighter water just below the ice. In this case the **stratification** is much less stable, because the density difference between 0°C and 4°C water is quite small. However, the water column is isolated from wind-induced turbulence by its cap of ice. Therefore, the layering persists throughout the winter.

Here are some movies that demonstrate density stratification. You will need the **Quicktime Plug-in** from Apple to view these movies. These movie files are large (2 - 5 Mb), so you should have a fast Internet connection. In the near future we hope to redo the movies to improve their quality and reduce their size.

- **Movie 1** - Here's what happens when warmer water (green) enters the surface of a lake in winter. The second addition shows that the warm water is buoyant (less dense) than the cold water and therefore rises.
- **Movie 2** - Here's what happens when colder water enters a summer-stratified lake.
- **Movie 3** - Same as movie 2 without the dyed green epilimnion.
- **Movie 4** - See what happens to the epilimnion (mixed layer) and thermocline during a storm. Did the lake mix?
- **Movie 5** - Same as movie 4, but with increased turbulence. See what starts to happen when the class 5 tornado hits.
- **Movie 6** - Shows how stream sediment entering a lake or reservoir deposits its load. Why does some material stay in the upper layer and some crash to the bottom?

- **Movie 7** - An estuary is a 2-layer system with freshwater overlying salt water. Here we see how freshwater behaves when added to each layer.

- **Movie 8** - Same as movie 7, but here we introduce water that is saltier than the upper freshwater layer. Example: Hurricanes can "throw" huge amounts of saltwater into coastal lakes. What happens to this water and what might its impact be?

Overview

This pattern (spring turnover — summer stratification — fall turnover — winter stratification) is typical for **temperate** lakes. Lakes with this pattern of two mixing periods are referred to as **dimictic**. Many shallow lakes, however, do not stratify in the summer, or stratify for short periods only, throughout the summer. Lakes that stratify and destratify numerous times within a summer are known as **polymictic** lakes. Both polymictic and dimictic lakes are common in Minnesota.

Since installing the RUSS unit in Ice Lake we have made an interesting observation. Spring turnover is incomplete. There was not enough mixing in spring, 1998 or 1999 to completely re-aerate the entire water column to 100% saturation. On the other hand, Lake Independence, a lake of comparable depth (15-18 meters) but much larger in size (more fetch) and less sheltered from the wind, mixed completely. We suspect that most aquatic scientists would not have expected to see Ice Lake's bottom water, nearly saturated with **oxygen** in fall, 1998, to be **anoxic** by mid-winter and then persist in this state until the following fall. Once stratified thermally in summer, even the barrage of severe thunderstorms that occurred near Ice Lake in summer, 1999, lacked the energy to dramatically decrease the thermocline or increase the oxygen content of the hypolimnion. **Heat and Oxygen budget section of Ice Lake**.

It was cold and windy enough during fall, 1998 for Ice Lake to mix thoroughly, bringing oxygen to the bottom waters (to about 100% saturation). This is likely typical for Ice Lake during most autumns, although it is possible for a cold, calm period to allow the lake surface to freeze before the water column has been fully exposed to the atmosphere and re-charged with oxygen.

Visit the data files under **each lake page** or review the entire data set using the **Profile Plotter** tools.

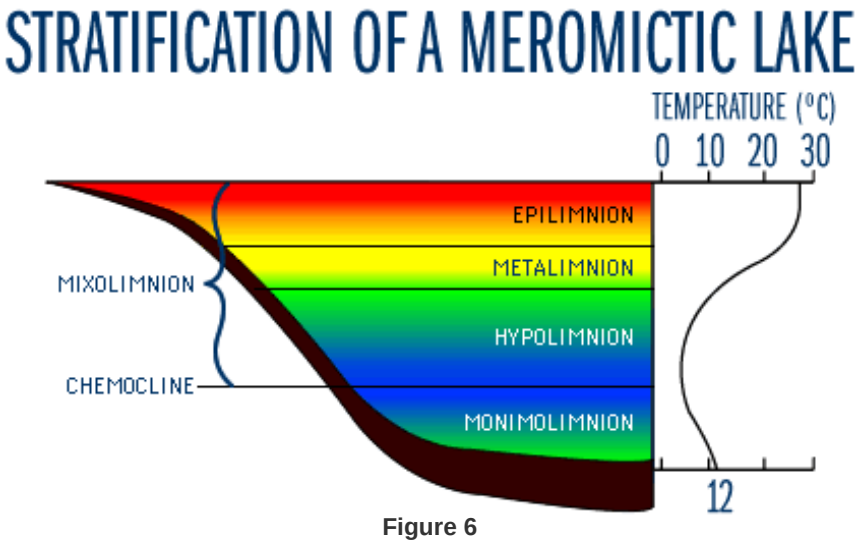


Figure 6

The West Upper Lake Station of Lake Minnetonka, Lake Independence and thousands of other Upper Midwestern lakes that are relatively deep (>10 meters) and reasonably large (>100-200 acres or 40-80 ha) are probably dimictic, leading to complete re-oxygenation of the water column for at least some period of time. Ice Lake, though small (41 acres or 16.6ha), is sheltered and deep (16 m) for its size. Lakes that have formed in former open pit mines in Northeastern Minnesota are unusually deep for their size. Lakes with these characteristics probably only mix completely once a year in the fall for a brief period before freezing. Some of the deeper mine pit lakes (>75 meters deep) probably never mix completely to the bottom, although data are sparse.

Much less common are lakes that circulate incompletely resulting in a layer of bottom water that remains stagnant. To distinguish them from the **holomictic** (mixing from top to bottom) lakes, these partially mixing lakes are referred to as **meromictic**. They mix partially, in the sense that they may have extensive mixing periods which go quite deeply into the hypolimnion, but they do not turn over completely, and a layer of bottom water remains stagnant and anoxic for years at a time. The non-mixing bottom layer is known as the **monimolimnion** and is separated from the **mixolimnion** (the zone that mixes completely at least once a year) by the **chemocline** (Figure 6). The stagnant, and typically **anaerobic**, monimolimnion has a high concentration of dissolved solids compared to the mixolimnion. In general, meromictic lakes have large **relative depths**. These lakes are typically small and sheltered from the wind by the morphology of their **basin**. In this case, the density differences caused by temperature are smaller than density differences due to the high dissolved solids (salts) concentration of the monimolimnion. Large lakes that rarely freeze over are also typically monomictic, mixing throughout the fall, winter and spring and stratifying in the summer.

To visualize this effect, try dissolving several tablespoons of table salt (NaCl) in hot water. Add a few drops of food coloring and then fill a mayonnaise jar half-full. Now, very gently add cool tap water with a small measuring cup to fill the glass. Set up a second jar half full with clear, cool water and then add the colored hot water to fill the glass - but don't add the salt. Compare the stability of the density stratification in the two systems by gently shaking or stirring the water columns.

Table 2.

MIXING REGIME	LAKES	MAX DEPTH (m)	AREA (acres/hectares)
DIMICTIC (2mixes/yr)	**Lake Minnetonka** (Minneapolis, MN)	34	14,004 acres (5,670 ha)
	Grindstone Lake (Sandstone, MN)	46	500 acres (200 ha)
	Lake Independence (Minneapolis, MN)	18	850 acres (344 ha)

	Pike Lake (Duluth, MN)	18	500 acres (200 ha)
MONOMICTIC (1mix/yr – mixed all winter and spring)	**Lake Erie**	70	6.4 x 106 acres (2.6 x 106 ha)
	Lake Huron	228	14.8 x 106 acres (6.0 x 106 ha)
	Ice Lake* (Grand Rapids, MN)	16	41 acres (16.6 ha)
	Lake Michigan	281	14.4 x 106 acres (5.8 x 106 ha)
	Lake Ontario	244	4.9 x 106 acres (2.0 x 106 ha)
	Lake Superior	300	20.3 x 10^6 acres (8.2 x10^6 ha)
	Lake Tahoe (CA/NV)	499	123,253 acres (49,900 ha)
	Lake Mead (NV – largest US reservoir)	180	163,320 acres (66,096 ha)
POLYMICTIC (many mixes/yr)	Shallow lakes & ponds	< 4	wide range
	Mille Lacs Lake, MN	13	132,510 acres (53,648 ha)
	St. Louis River and Duluth-Superior Harbor	1-8	11,993 acres (4,856 ha)
MEROMICTIC (never totally mixed because of stagnant bottom layer)	**Miners Pit Lake** (Ely, MN)	48	138 acres (56 ha)
	Pennington Pit Lake, (Crosby, MN)	79	57 acres (23 ha)
	Brownie Lake (Minneapolis, MN)	15	18 acres (7.3 ha)
	Deming Lake (Itasca State Park, MN)	14	12.3 acres (5.0 ha)
	Big Soda Lake (Fallon, NV)	60	400 acres (160 ha)
* variable from year to year			

For additional information, Learn about ARCHIMEDES's principle at **EXPLORATORIUM** and a shockwave demonstration of **density and water displacement**.

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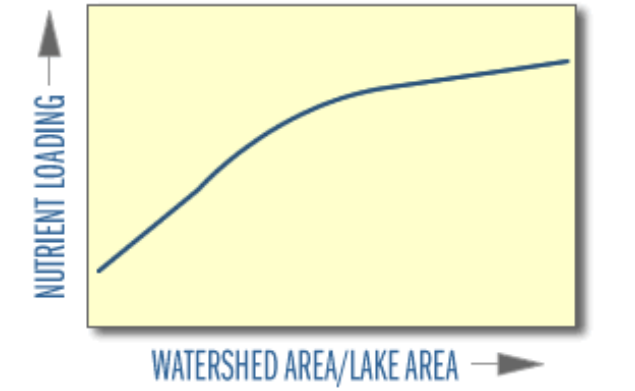
The Watershed

The **watershed**, also called the drainage **basin**, is all of the land and water areas that drain toward a particular river or lake. Thus, a watershed is defined in terms of the selected lake (or river). There can be subwatersheds within watersheds. For example, a **tributary** to a lake has its own watershed, which is part of the larger total drainage area to the lake.

A lake is a reflection of its watershed. More specifically, a lake reflects the watershed's size, **topography**, geology, **landuse**, soil fertility and erodibility, and vegetation. The impact of the watershed is evident in the relation of **nutrient loading** to the watershed:lake surface area ratio (Figure 7). See also the section on **conductivity**.



GENERAL PATTERN OF NUTRIENT LOADING ASSOCIATED WITH INCREASING WATERSHED SIZE RELATIVE TO LAKE AREA.

Figure 7.

Typically, water quality decreases with an increasing ratio of **watershed area** to lake area. This is obvious when one considers that as the watershed to lake area increases there are additional sources (and volumes) of runoff to the lake. In larger watersheds, there is also a greater opportunity for water from precipitation to contact the soil and **leach** minerals before discharging into the lake. Lakes with very small watersheds that are maintained primarily by groundwater flow are known as **seepage lakes**. In contrast, lakes fed primarily by inflowing streams or rivers are known as **drainage lakes**. In keeping with the watershed:lake area relationship, seepage lakes tend to have good water quality compared with drainage lakes. However, lakes are often more susceptible to acidification from **acid rain** because of their low **buffering capacity**.

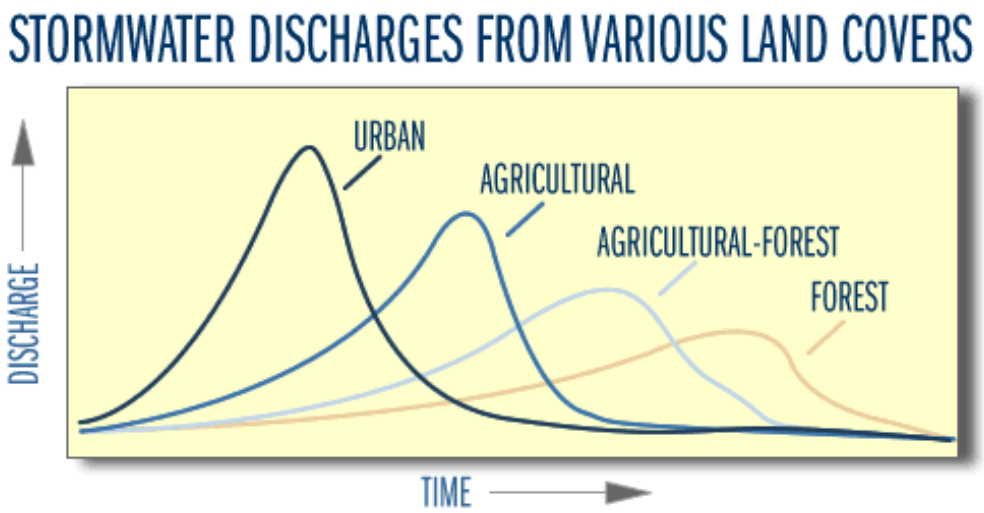


Figure 8.

Landuse has an important impact on the quality and quantity of water entering a lake. As Figure 8 shows, the **stormwater discharge** to a lake differs greatly among landuses. In urban areas, the high proportion of **impervious surfaces** prevents absorbance of rainwater into the soil and increases the rate of surface water flow to the lake. The high **flushing rates** from urban areas can increase erosion of stream banks and provide sufficient force to carry large particles (i.e., soil) to the lake. Thus, water quantity affects water quality.

Additionally, as water flows over roads, parking lots and rooftops, it accumulates nutrients and contaminants in both dissolved and particulate form.

Table 3. Phosphorus export coefficients (from Reckhow and Simpson, 1980).

	Phosphorus (kg/km^{2}yr)		
	HIGH	**MID**	**LOW**
Urban	500	80-300	50
Rural/Agriculture	300	40-170	10
Forest	45	14-30	2
Precipitation	60	20-50	15

Table 3 gives representative values of **export rates** of **phosphorus** from various landuses and other sources. Phosphorus is particularly important because its availability often controls the amount of algae and the overall **productivity** of a lake. These values are in units of kg/km^2/yr (mass of phosphorus per unit area per year). Not included here, but also important, is the influence of soil type and slope. Finer particles and steeper slopes mean higher **export rates**.

To clarify the relative landuse impacts, we can compare annual loads from 10 hectare (24 acre) plots of the selected landuses using the high export coefficients in Table 3.

Forest	4.5 kg phosphorus
Rural/Agriculture	30.0 kg phosphorus
Urban	50.0 kg phosphorus

One can see that, all other things being equal, converting a forest into a city can increase the phosphorus export to a lake more than ten times. Another way to look at these numbers is that almost seven years of **phosphorus** loading from a forested area can be deposited within one year by mixed agriculture areas and almost eleven years of phosphorus loading from a forested area can be deposited within a year from urbanized areas. A greater **loading rate** puts a greater strain on the system to assimilate the nutrients.

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Chemical

General Lake Chemistry

In the absence of any living organisms, a lake contains a wide array of molecules and ions from the **weathering** of soils in the **watershed**, the atmosphere, and the lake bottom. Therefore, the chemical composition of a lake is fundamentally a function of its climate (which affects its **hydrology**) and its **basin** geology. Each lake has an **ion** balance of the three major **anions** and four major **cations** (see Table 4).

Table 4. ION BALANCE FOR TYPICAL FRESH WATER

Anions	Percent	Cations	Percent
HCO_3^-	73%	Ca^{+2}	63%
SO_4^{-2}	16%	Mg^{+2}	17%
Cl^-	10%	Na^+	15%
		K^+	4%
other	< 1%	other	< 1%

Ion balance means the sum of the negative ions equals the sum of the positive cations when expressed as equivalents. These ions are usually present at concentrations expressed as mg/L (parts per million, or **ppm**) whereas other ions such as the nutrients phosphate, nitrate, and ammonium are present at µg/L (parts per billion, or **ppb**) levels.

Humans can have profound influences on lake chemistry. Excessive landscape disturbance causes higher rates of **leaching** and erosion by removing vegetative cover, exposing soil, and increasing water runoff velocity. Lawn fertilizers, wastewater and urban stormwater inputs all add **micronutrients** such as nitrogen and **phosphorus**, major ions such as chloride and potassium, and, in the case of highway and parking lot runoff, oils and heavy metals. Emissions from motorized vehicles, fossil fuel-burning electric utilities and industry, and other sources produce a variety of compounds that affect lake chemistry.

Perhaps the best understood ions are H^+ (**hydrogen ion**, which indicates **acidity**), SO_4^{-2} (sulfate) and NO_3^- (nitrate) which are associated with **acid rains**. Mercury (Hg) is another significant air pollutant affecting aquatic **ecosystems** and can **bioaccumulate** in aquatic **food webs**, contaminating fish and causing a threat to human and wildlife health (see also the **Minnesota Pollution Control Agency**'s section on Hg).

Lakes with high concentrations of the ions calcium (Ca^{+2}) and magnesium (Mg^{+2}) are called **hardwater lakes**, while those with low concentrations of these ions are called **softwater lakes**. Concentrations of other ions, especially **bicarbonate**, are highly correlated with the concentrations of the hardness ions, especially Ca^{+2}. The ionic concentrations influence the lake´s ability to assimilate pollutants and maintain nutrients in **solution**. For example, calcium carbonate ($CaCO_3$) in the form known as **marl** can precipitate phosphate from the water and thereby remove this important nutrient from the water.

The total amount of ions in the water is called the **TDS** (total dissolved salt, or total **dissolved solids concentration**). Both the concentration of TDS and the relative amounts or ratios of different ions influence the species of organisms that can best survive in the lake, in addition to affecting many important chemical reactions that occur in the water. One example of particular interest in the Great Lakes region involves the calcium requirement of the exotic zebra mussel that is causing profound changes in Lake Erie (see **National Aquatic Nuisance Species Clearinghouse** or **Sea Grant Nonindigenous**

Species Site). Lake Superior appears to be relatively immune to infestation by this invader because of low calcium concentration. Its bays, however, such as the lower St. Louis River and Duluth-Superior Harbor, may not be immune to zebra mussel infestation.

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Dissloved Oxygen

Biological activity peaks during the spring and summer when photosynthetic activity is driven by high solar **radiation**. Furthermore, during the summer most lakes in **temperate** climates are **stratified**. The combination of **thermal stratification** and biological activity causes characteristic patterns in water chemistry. Figure 9 shows the typical seasonal changes in **dissolved oxygen** (DO) and temperature. The top scale in each graph is **oxygen** levels in mg O_2/L. The bottom scale is temperature in °C. In the spring and fall, both **oligotrophic** and **eutrophic** lakes tend to have uniform, well-mixed conditions throughout the **water column**. During summer **stratification**, the conditions in each layer diverge.

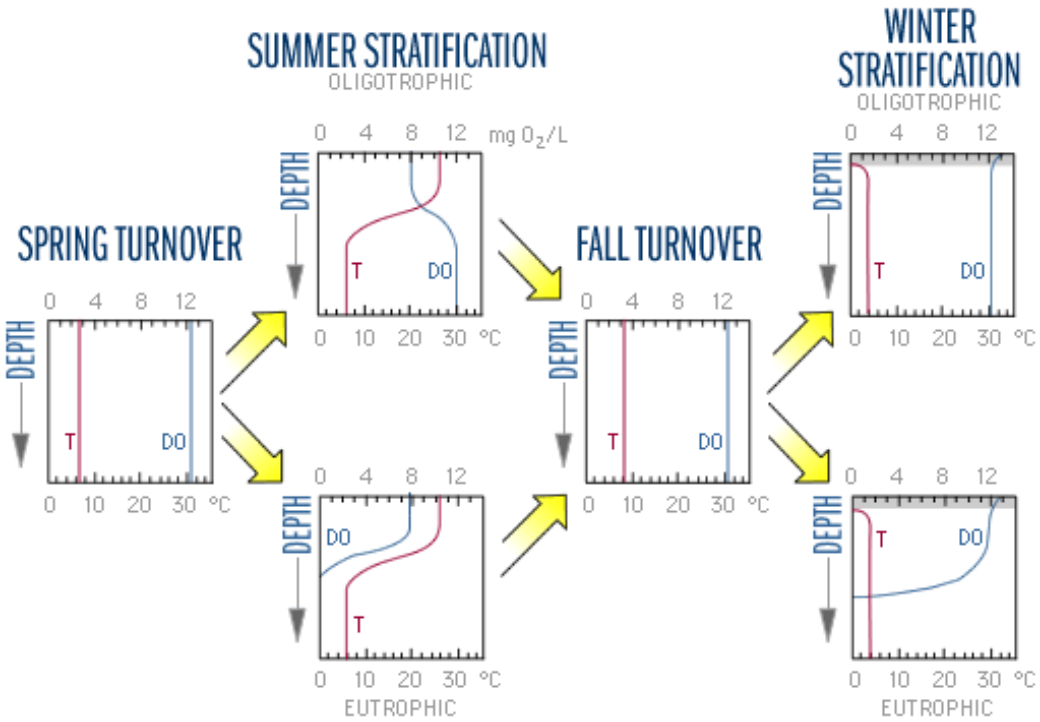

Figure 9. (adapted from Figure 8-1 in Wetzel, R.G. 1975. Limnology. W.B.Saunders Company)

The **DO** concentration in the **epilimnion** remains high throughout the summer because of **photosynthesis** and **diffusion** from the atmosphere. However, conditions in the **hypolimnion** vary with **trophic** status. In eutrophic (more productive) lakes, hypolimnetic DO declines during the summer because it is cut-off from all sources of oxygen, while organisms continue to respire and consume oxygen. The bottom layer of the lake and even the entire hypolimnion may eventually become **anoxic**, that is, totally devoid of **oxygen**. In oligotrophic lakes, low algal **biomass** allows deeper light penetration and less **decomposition**. Algae are able to grow relatively deeper in the **water column** and less oxygen is consumed by decomposition. The DO concentrations may therefore increase with depth below the **thermocline** where colder water is "carrying" higher DO leftover from spring mixing (recall that oxygen is more soluble in colder water). In extremely deep, unproductive lakes such as Crater Lake, OR, Lake Tahoe, CA/NV, and Lake Superior, DO may persist at high concentrations, near 100% saturation, throughout the water column all year. These differences between eutrophic and oligotrophic lakes tend to disappear with fall **turnover** (Figure 9).

In the winter, oligotrophic lakes generally have uniform conditions. Ice-covered eutrophic lakes, however, may develop a winter stratification of dissolved oxygen. If there is little or no snow cover to block sunlight, **phytoplankton** and some **macrophytes** may continue to photosynthesize, resulting in a small increase in

DO just below the ice. But as microorganisms continue to decompose material in the lower water column and in the sediments, they consume oxygen, and the DO is depleted. No oxygen input from the air occurs because of the ice cover, and, if snow covers the ice, it becomes too dark for photosynthesis. This condition can cause high fish mortality during the winter, known as "winter kill." Low DO in the water overlying the sediments can exacerbate water quality deterioration, because when the DO level drops below 1 mg O_2/L chemical processes at the sediment-water interface frequently cause release of **phosphorus** from the sediments into the water. When a lake mixes in the spring, this new phosphorus and ammonium that has built up in the bottom water fuels increased algal growth.

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Nutrients

Aquatic organisms influence (and are influenced by) the chemistry of the surrounding environment. For example, **phytoplankton** extract nutrients from the water and **zooplankton** feed on phytoplankton. Nutrients are redistributed from the upper water to the lake bottom as the dead plankton gradually sink to lower depths and decompose. The redistribution is partially offset by the active vertical migration of the plankton.

In contrast to DO, essential nutrients such as the **bioavailable** forms of **phosphorus** and nitrogen (dissolved phosphate, nitrate, and ammonium) typically increase in the spring from snowmelt runoff and from the mixing of accumulated nutrients from the bottom during **spring turnover**. Concentrations typically decrease in the **epilimnion** during summer **stratification** as nutrients are taken up by algae and eventually transported to the **hypolimnion** when the algae die and settle out. During this period, any "new" input of nutrients into the upper water may trigger a "bloom" of algae. Such inputs may be from upstream tributaries after rainstorms, from die-offs of aquatic plants, from pulses of urban stormwater, direct runoff of lawn fertilizer, or from leaky lakeshore septic systems. In the absence of rain or snowmelt, an injection of nutrients may occur simply from high winds that mix a portion of the nutrient-enriched upper waters of the hypolimnion into the epilimnion. In less productive systems, such as those in Northeastern Minnesota, significant amounts of available nitrogen may be deposited during rainfall or snowfall events (**wet deposition**) and during the less obvious deposition of aerosols and dust particles (**dry deposition**). For instance, Lake Superior has been enriched by as much as 300 µg/L during this century, presumably due to air pollution. Nitrogen and phosphorus in dry fallout and wet precipitation may also come from dust, fine soil particles, and fertilizer from agricultural fields.

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Biological

Lake Zones

A typical lake has distinct zones of biological communities linked to the physical structure of the lake (Figure 10). The **littoral** zone is the near shore area where sunlight penetrates all the way to the sediment and allows aquatic plants (**macrophytes**) to grow. Light levels of about 1% or less of surface values usually define this depth. The 1% light level also defines the **euphotic zone** of the lake, which is the layer from the surface down to the depth where light levels become too low for **photosynthesizers**. In most lakes, the sunlit euphotic zone occurs within the **epilimnion**.

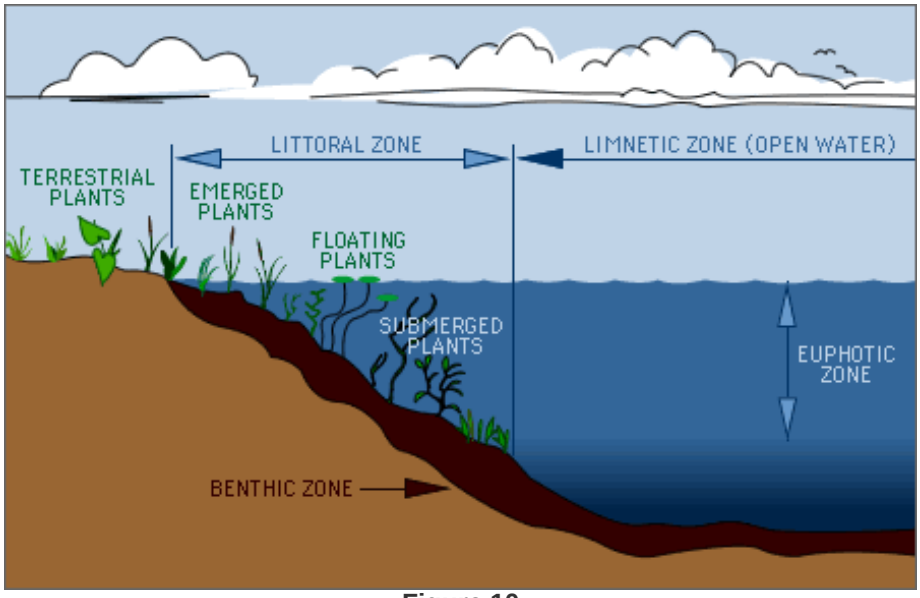

Figure 10

However, in unusually transparent lakes, **photosynthesis** may occur well below the **thermocline** into the perennially cold **hypolimnion**. For example, in western Lake Superior near Duluth, MN, summertime algal photosynthesis and growth can persist to depths of at least 25 meters, while the mixed layer, or **epilimnion**, only extends down to about 10 meters. Ultra-**oligotrophic** Lake Tahoe, CA/NV, is so transparent that algal growth historically extended to over 100 meters, though its mixed layer only extends to about 10 meters in summer. Unfortunately, inadequate management of the Lake Tahoe **basin** since about 1960 has led to a significant loss of transparency due to increased algal growth and increased sediment inputs from stream and **shoreline** erosion.

The higher plants in the littoral zone, in addition to being a food source and a **substrate** for algae and invertebrates, provide a habitat for fish and other organisms that is very different from the open water environment.

The **limnetic zone** is the open water area where light does not generally penetrate all the way to the bottom. The bottom sediment, known as the **benthic zone**, has a surface layer abundant with organisms. This upper layer of sediments may be mixed by the activity of the **benthic** organisms that live there, often to a depth of 2-5 cm (several inches) in rich **organic** sediments. Most of the organisms in the **benthic zone** are invertebrates, such as **Dipteran** insect larvae (midges, mosquitoes, black flies, etc.) or small crustaceans. The **productivity** of this zone largely depends upon the organic content of the sediment, the amount of physical structure, and in some cases upon the rate of fish predation. Sandy substrates contain relatively little organic matter (food) for organisms and poor protection from predatory fish. Higher plant growth is typically sparse in sandy sediment, because the sand is unstable and nutrient deficient. A rocky bottom has a high diversity of potential habitats offering protection (refuge) from predators, substrate for

attached **algae** (**periphyton** on rocks), and pockets of organic "ooze" (food). A flat mucky bottom offers abundant food for benthic organisms but is less protected and may have a lower diversity of structural habitats, unless it is colonized by higher plants.

Lake Organisms

THOSE THAT GO WHERE THEY CHOOSE

FISH	AMPHIBIANS TURTLES	LARGER ZOOPLANKTON AND INSECTS

THOSE THAT GO WHERE THE WATER TAKES THEM

LIVING THINGS = PLANKTON
- animals - zooplankton
- algae - phytoplankton
- bacteria - bacterioplankton

DEAD STUFF = DETRITUS
- internal - produced within lake
- external - washed in from watershed

THOSE THAT LIVE ON THE LAKE BOTTOM

BENTHOS = ANIMALS
- aquatic insects
- molluscs - clams, snails
- other invertebrates - worms, crayfish

PLANTS
- higher plants - macrophytes
- attached algae - periphyton

BACTERIA & FUNGI
- **sewage sludge**
- **aufwuchs** - mixture of algae, fungi and bacteria

Figure 11

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The Food Web

The biological communities within lakes may be organized conceptually into **food chains** and **food webs** to help us understand how the **ecosystem** functions (Figures 12 and 13). The simplest illustration of the organization of the organisms within an ecosystem is the **ecological pyramid** (Figure 14). The broad base of **primary producers** supports overlying levels of **herbivores** (**zooplankton**), **planktivores** and much smaller numbers of **carnivores** (predators). These individual **trophic** levels may be idealized as a food chain, but in fact many organisms are **omnivorous** and not necessarily characterized by a particular level. Further, **consumers** in particular often shift levels throughout their life cycle. For example, a larval fish may initially eat fine particulate material that includes **algae**, bacteria and detritus. Then it may switch and graze on larger zooplankton and ultimately end up feeding on so called "forage fish" or even young game fish (i.e., top predators) when it reaches maturity (Figure 13).

TYPICAL FOOD CHAIN

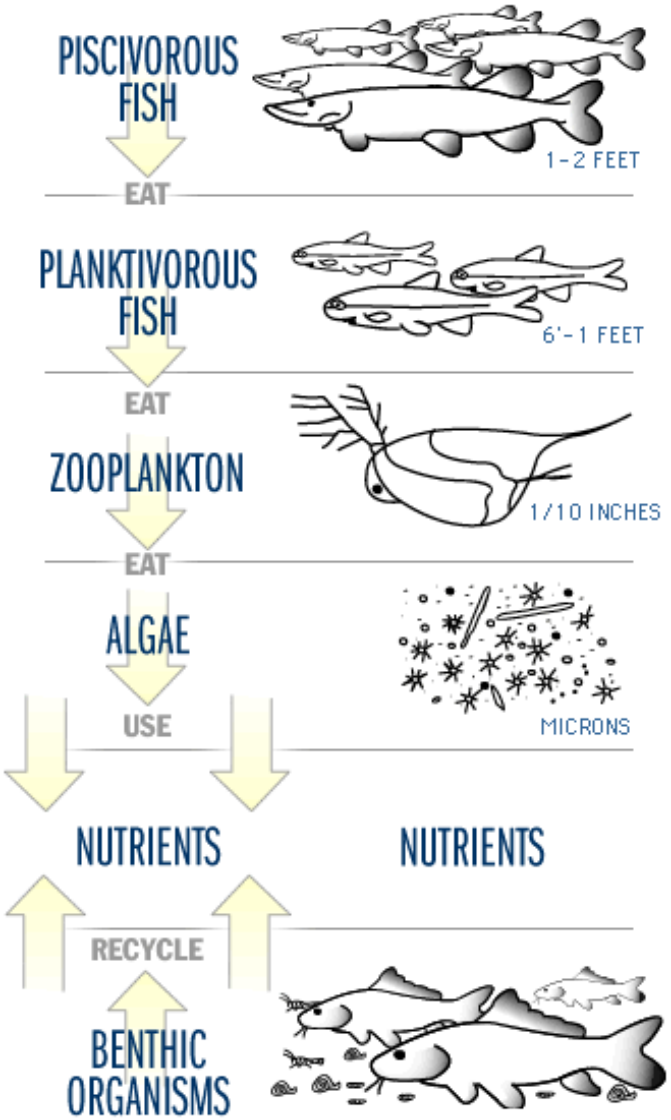

Figure 12.
FOOD WEB FOR LAKE MEAD, NV

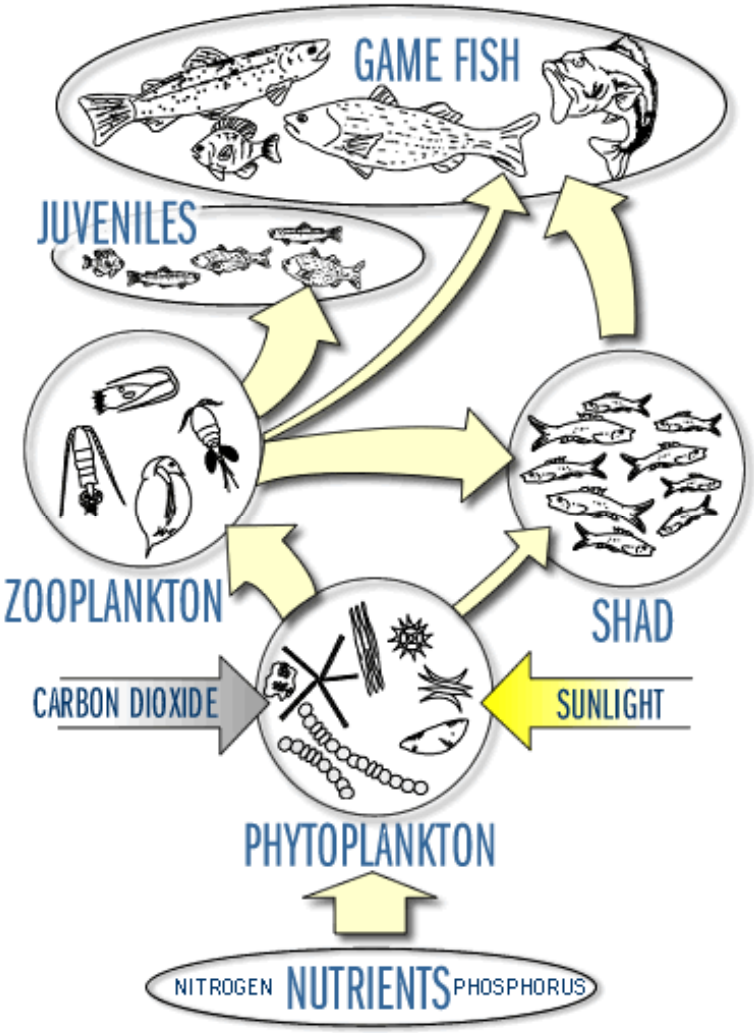

Figure 13.

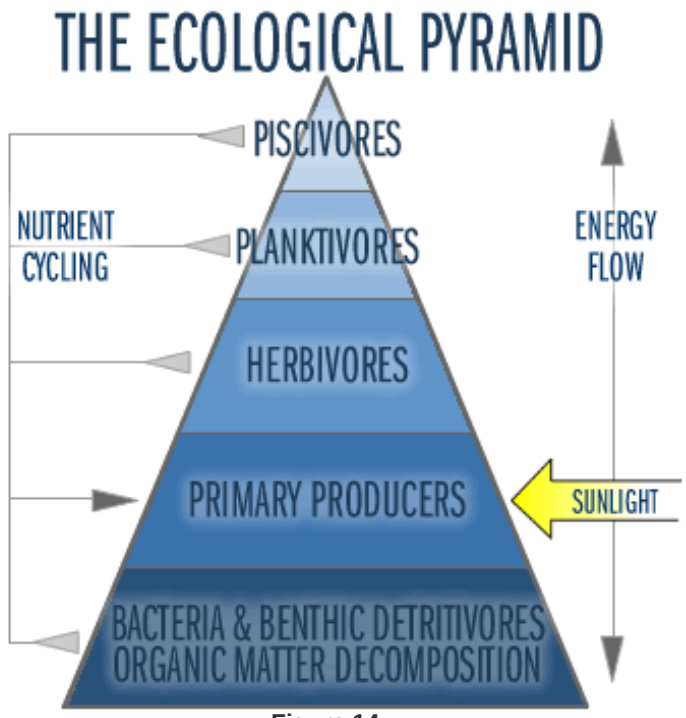

Figure 14.

Food webs may be described in terms of both energy and nutrient (carbon, nitrogen or **phosphorus**) flows (Figure 15). Although the process typically begins with sunlight-driven **photosynthesis** by algae and plants, balanced nutrition is also required to sustain life. For example, we cannot live strictly on sugar, despite its high caloric content, irrespective of what our kids may argue.

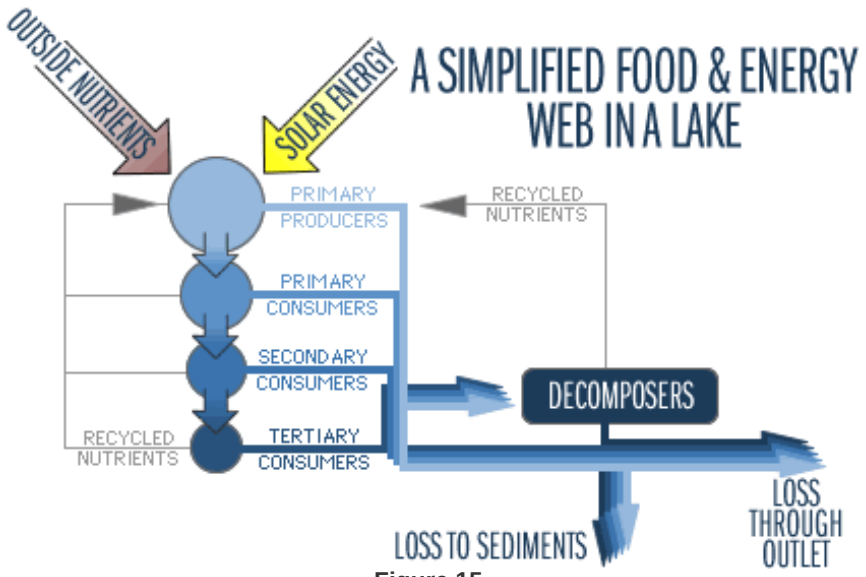

Figure 15.

There are two basic life-sustaining processes in lakes, just as on land; **photosynthesis** and **respiration**. Green plants capture energy from sunlight to convert nonliving, **inorganic** chemicals (**carbon dioxide**, water, and mineral compounds) into living, **organic** plant tissue. Lake **photosynthesizers** include algae and **macrophytes**. Together, they are the primary producers, because they create the organic material required by most other organisms for nutrients and energy. Oxygen, the waste product of photosynthesis, adds to the **oxygen** supplied to the lake by the atmosphere. In water layers where photosynthetic rates are very high, such as during an algal bloom, the water may become supersaturated. That is, the oxygen content may exceed 100% of **saturation** with respect to the amount the water could hold if it was allowed to equilibrate with the atmosphere. This saturation value, in turn, depends on the temperature of the water. Colder water can hold more O_2 than warmer water. During periods of **stratification**, the only potential source of O_2 to the deeper zones of the lake is photosynthesis. This occurs only if light penetrates below the **thermocline**. In lakes where light does not penetrate below the **thermocline**, there is no internal source of oxygen to the deeper waters.

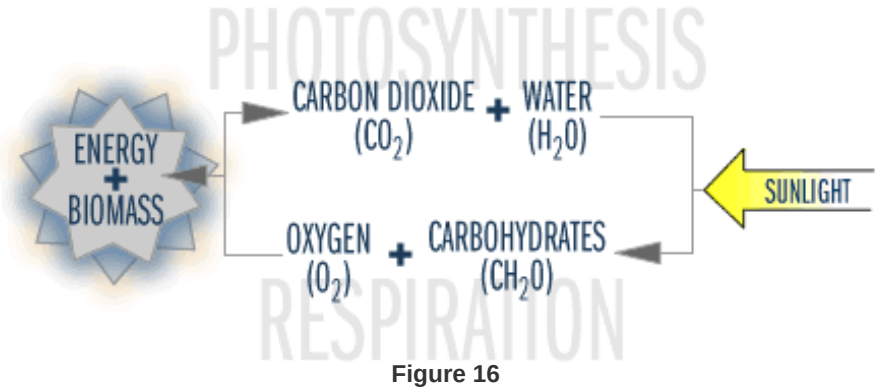

Figure 16

Besides light, algae and higher plants need oxygen, **carbon dioxide** (CO_2), and mineral nutrients to survive and grow. Except for a very few species of blue green algae, most are unable to survive in **anoxic** (no O_2) water. CO_2 is virtually always available and comes from the **weathering** of carbonate rocks, such as limestone, in the watershed, **diffusion** from the atmosphere (very important in **softwater**, **acid rain** sensitive lakes), and from the respiration of organic matter by all of the organisms in the lake (see below).

Dissolved mineral nutrients are absorbed from the water by algae and from the water and the sediments by higher plants. Typically, the most important nutrients are phosphorus and nitrogen, because they are present in very low concentrations unless there are sources of pollution (see **trophic state** section) and are typically low enough to limit the growth of algae. Other minerals essential to life, such as the major ions (calcium, magnesium, sodium, and potassium) and certain trace metals (iron, cobalt, molybdenum, manganese, copper, boron, and zinc), are usually present at sufficient concentrations. Silicon is required by **diatoms** and a few other groups of algae and is usually, though not always, present at sufficient levels. Another mineral required by all living things, sulfur (in the form of sulfate), is typically not deficient in lakes.

The whole interaction of photosynthesis and respiration by plants, animals, and microorganisms represents the food web. Food webs are usually very complex and, in any one lake ecosystem, hundreds of different species can be involved. Because the available energy decreases at each trophic level, a large food base of primary producers (mostly plants) is necessary to support relatively few large fish.

These plants may die and decompose or be eaten by **primary consumers** – the second trophic level. This link in the food chain typically involves zooplankton grazing on algae but also includes larval fish eating zooplankton and a variety of invertebrates that eat attached algae (**periphyton**) and higher plants. Other animals, such as small fish, **secondary consumers** (third trophic level) eat the primary consumers and thus are considered secondary consumers. Still larger consumers such as large fish, ospreys, and people are **tertiary consumers** (fourth trophic level). Thus, energy and nutrients originating from the photosynthetic production of **biomass** and energy cascade through the food web (Figure 15). There is some recycling of nutrients back up to the top of the cascade. Respiration, the oxidation of organic material, releases the energy that was originally captured from sunlight by photosynthesis. Both plants and animals respire to sustain their lives, and in doing so, consume oxygen. Microorganisms (bacteria and fungi) consume a large fraction of available oxygen in the **decomposition** of excreted and dead organic material.

Decomposers are sinks for plant and animal wastes, but they also recycle nutrients for photosynthesis. The amount of dead material in a lake far exceeds the living material. Detritus is the organic fraction of the dead material, and can be in the form of small fragments of plants and animals or as dissolved organic material. In recent years, scientists have recognized that zooplankton grazing on **detritus** and its associated bacterial community represent an additional important trophic pathway in lakes.

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Primary Producers

Much of modern limnological study revolves around the **primary productivity** of lakes. The ecology of plant growth is of great importance to the character and history of lakes and to all other organisms that live in lakes. The major threat to lakes involves the excessive growth of primary producers due to nutrient inputs caused by poor **landuse** management. Therefore, it is worth a closer look at these organisms.

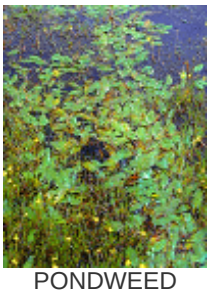
The **littoral** zone is defined by the growth of rooted and floating aquatic plants, or **macrophytes**. Figure 17 provides examples of common macrophytes found in Minnesota lakes. The macrophyte community can also include large **algae**, such as *Chara,Nitelle,*or*Cladophora.*In shallow, clear lakes, macrophytes may represent most of the green plant material present and may account for most of the **photosynthesis**.

SOME COMMON MACROPHYTES
click on the photos to see larger images

FLOATING

WATER LILY
Nymphaea

DUCKWEED
Spirodela


PONDWEED
Potamogeton

SUBMERGENT

STONEWORT
Chara

COONTAIL
Ceratophyllum

BLADDERWORT
Utricularia

EMERGENT

CATTAIL
Typha

BULRUSH
Scirpus

WILD RICE
Zizania

EXOTICS

PURPLE LOOSESTRIFE
Lythrum salicaria

EURASIAN WATER MILFOIL
Myriophyllum spicatum

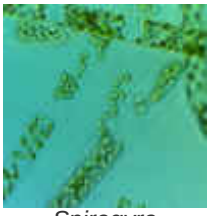
Figure 17.
Photos from the **University of Florida's Aquatic, Wetland, and Invasive Plant Information Retrieval System**

There may be few macrophytes in a lake when the bottom is too rocky or too sandy for the plants to anchor themselves, wave action too severe, or the water too deep. Also, sunlight may not reach the bottom even in shallow areas if the concentration of algae or silt is high.

Algae constitute the other main group of primary producers (Figure 18). They come in countless forms and live in nearly all kinds of environments. Most are microscopic, growing as single cells, small colonies, or filaments of cells. Suspended algae are called **phytoplankton**, while attached algae are called **periphyton**. Phytoplankton grow suspended in open water by taking up nutrients from the water and energy from sunlight. If their populations are dense, the water will become noticeably green or brown and will have low transparency

ALGAL PHOTOS
click on the photos to see larger images

Ankistrodesmus



Spirogyra

Fragillaria

Synedra

Dinobryon

Peridinium

Cryptomonas

Anabaena

Aphanizomenon

Microcystis

Oscillatoria

Figure 18.
Images courtesy of the **Susquehanna University Algal Image Archive and Cyanosite** (Purdue University).

Phytoplankton are classified into groups by the type of pigments they use to perform photosynthesis. While **chlorophyll**-a is common to all groups there are many other accessory pigments that allow the algae to capture different types of light. Green algae are considered the most closely related to higher plants. Within this group alone there is a great diversity of size, shape, and growth form (single celled, colonial, filamentous, and flagellated). **Diatoms** belong to a large group, classified as the golden-brown algae, which also includes chrysophytes and dinoflagellates. The most striking characteristic of diatoms and chrysophytes is the ability to form silica (glass) cell walls. **Diatoms** cell walls are similar to a **petri dish**, having two halves that fit together. Some chrysophytes have elaborate silica scales, spines, or vase-like shells called **loricas**. Diatoms are **non-motile** (unable to swim), so they depend on water turbulence to remain suspended. Chrysophytes have **flagella** (whip-like appendages) that allow them to control their position in the **water column**. There are other important algal groups containing **motile** forms.

Dinoflagellates are another group of golden-brown algae that also have flagella. These cells are capable of moving very rapidly; positioning themselves where light and nutrients are optimal for growth. Another flagellated group called the cryptomonads are very small algae and contain pigments that enable them to photosynthesize under very low light conditions, either very deep in the water column or during those times of the year when sunlight isn't very strong.

Blue-green "algae" are technically referred to as **cyanobacteria** since, except for their chlorophyll-based photosynthesis, they are bacteria. They generally receive the greatest amount of research and management attention because of their ability to form **nuisance blooms** in **eutrophic lakes**. It is important to remember, however, that blue-green algae are very important primary producers in both freshwater and marine systems, despite often being a nuisance.

Blue-greens have several characteristics that often enable them to dominate and create nuisance or noxious conditions. Some blue-green species have the ability to adjust their buoyancy. They can float or sink depending on light conditions and nutrient supply. All plants, including all algae, typically satisfy their nitrogen requirement by absorbing nitrate (NO_3^-) and/or ammonium (NH_4^+) from the water. However, some blue-greens can **fix** molecular nitrogen (N_2) derived from the atmosphere and dissolved in the water and convert it to ammonium in the cell through a process called **nitrogen fixation**. This allows them to maintain high rates of growth when other forms of nitrogen are sufficiently depleted to limit growth by other types of algae. Blue-green algae typically are well-adapted to **phosphorus** deficiency because of their ability to absorb and store excess phosphorus when it is available -- enough to last days to weeks in some cases.

Unlike the green algae and diatoms, the blue-green algae are less suitable food for **primary consumers**. This is partly because some blue-greens can form large colonies of cells embedded in a gelatinous matrix which may pose handling problems for **grazers**. They also may produce chemicals that inhibit grazers or

makes them "taste bad" to the grazers. Consequently, blue-greens have advantages over other algae at using nutrient and light resources, as well as avoiding being eaten.

Aphanizomenon flos-aquae is a common species of filamentous blue-green algae (see Figure 18) with the ability to regulate its buoyancy, fix nitrogen, form large inedible colonies, and form algal blooms. Other common bloom genera are *Anabaena* (N_2-fixing filamentous algae) and *Microcystis* (colonial; not a N_2-fixer). These bloom-forming algae are known to produce toxins in farm ponds that can poison cattle and, more recently, have been found to produce potent neurotoxins and hepatotoxins that may be a greater public health concern than previously realized.

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Chlorophyll - A Measure of Algae

An in-depth microscopic enumeration of the dozens of species of **algae** present in a **water column** each time a lake is sampled is prohibitively costly and technically impossible for most monitoring programs. Further, in many lakes a large portion of the algal **biomass** may be unidentifiable by most experts (these are appropriately called LRGTs or LRBGTs -- little round green things and little round blue-green things). However, measuring the concentration of **chlorophyll**-a is much easier and provides a reasonable estimate of algal biomass. Chlorophyll-a is the green pigment that is responsible for a plant's ability to convert sunlight into the chemical energy needed to **fix** CO_2 into carbohydrates. To measure chlorophyll-a, a volume of water from a particular depth is filtered through a fine glass-fiber filter to collect all of the particulate material greater than about 1 micron (1/1000th of a millimeter) in size. The chlorophyll-a in this material is then extracted with a **solvent** (acetone or alcohol) and quantified using a spectrophotometer or a fluorometer.

Note regarding Water on the Web: Although the RUSS units do not currently have chlorophyll sensors, a prototype sensor is being developed by Apprise Technologies, Inc. and the **Natural Resources Research Institute** at the University of Minnesota Duluth. In the interim, surface water (0-2 meter composites) values of chlorophyll-a are being determined at 2-4 week intervals at Ice Lake and Grindstone Lake (by NRRI) and at two week intervals at Lakes Independence and Minnetonka during the ice-free season (by **Hennepin Parks Natural Resources**). These data, along with secchi disk depth data and ancillary nutrient data are posted on the WOW Web site as they become available (**Data/Other**).

Both chlorophyll-a and secchi depth are long-accepted methods for estimating the amount of algae in lakes. Secchi depth is much easier and less expensive to determine. However, care must be used in interpreting secchi data because of the potential influence of non-algal particulate material, such as silt from stream discharge or re-suspended bottom sediment. Also, the tea color of some lakes that's due to dissolved organic matter from bogs, can have an effect on secchi depth readings as well. Even if chlorophyll-a is measured, it may be important to also examine the algal community microscopically on occasion, since the mix of species may influence lake management decisions.

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Algal Succession

A lake's biological characteristics are determined in large part by physical characteristics of the **water column**. Important physical characteristics include temperature, light transparency, and wave action, as well as the total abundance of **inorganic** nutrients, which is largely a watershed characteristic. In addition, preceding populations influence successive populations by assimilating critical nutrients. Populations also have varying susceptibilities to grazing by **zooplankton**, which vary seasonally in type and abundance. As physical, chemical, and biological conditions in the lake change over time, some species will be effectively eliminated from a lake because they cannot tolerate the new conditions. Other species will be out-competed by organisms that are better adapted to the new environment.

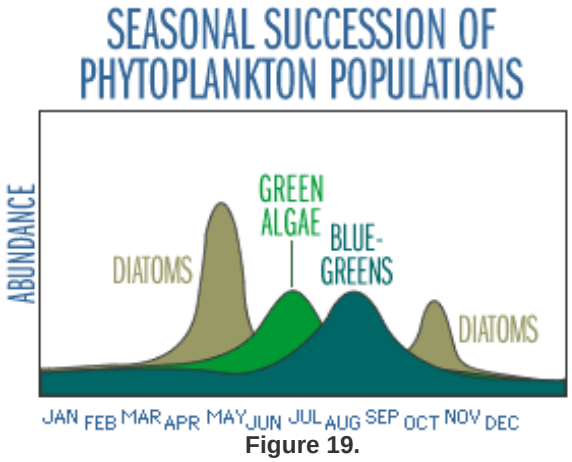

Figure 19.

These changes represent an important ecological pattern in lakes known as algal succession. In most natural systems the seasonal succession of **algae** (and macrophytes) is a recurrent, if not exactly repetitive, yearly cycle. A typical algal succession is shown in Figure 19. Some species flourish for a period of time and then give way to other species more compatible with changed conditions, such as warmer water, more daylight, or lower concentrations of **phosphorus** or nitrogen. Short-lived plankton communities are characterized by these seasonal fluctuations; longer-lived organisms, such as fish, must be tolerant of lake conditions all year.

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Consumers

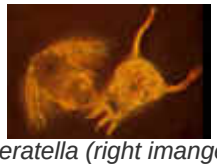
Zooplankton, small animals that swim about in open water (Figure 20), are **primary consumers**. They graze on **algae**, bacteria, and **detritus** (partially decayed **organic** material). Some species can be seen with the naked eye, although they are more easily observed with a hand lens or low-power microscopes. If you wish to see them, stare into the water of a pond or lake on a calm night with a flashlight beam shining from above.

Secondary consumers, such as planktivorous fish or predaceous invertebrates, eat **zooplankton**. While **photosynthesis** limits plant growth to the sunlit portions of lakes, **consumers** can live and grow in all lake zones, although the lack of **oxygen** (**anoxia**) may limit their abundance in bottom waters and sediments.

ZOO PLANKTON
click on the photos to see larger images

Daphnia Pulicaria

Diaptomus


Keratella (right imange)

Chaoborus

Figure 20

Images courtesy of University of Minnesota Limnology

Benthic organisms are major consumers and are also important recyclers of nutrients otherwise trapped in the sediments. **Benthic** organisms include invertebrates and bottom-feeding fish. Their feeding strategies vary widely. Some, such as clams, filter small bits of organic material from water as it flows by. Others eat detritus that has sunk to the bottom. The spread of the exotic invader, the zebra mussel, has caused dramatic changes in the water quality and ecology of Lake Erie in the past decade due to its high rates of filtration and high reproductive rate (See **Ohio Sea Grant**).

Not all organisms are easily classified as planktonic or benthic. For example, *Chaoborus,***Dipteran** insect larvae, remain near the sediments in daytime and migrate to upper waters at night. These transparent predators ("phantom midges") migrate upward to feed on zooplankton, and are, themselves, a favorite food for fish. Mysid shrimp behave in a similar fashion and have been shown to migrate enormous distances (>100 meters) in Lake Tahoe each night.

The best known group of aquatic consumers is fish. Many small fish, such as sunfish and perch, primarily eat zooplankton. **Tertiary consumers** that prey on the smaller fish include larger fish and other carnivorous animals (loons, grebes, herons, and otters). Different species exploit different habitats (niches). Bass and pike are found in lakes that have beds of aquatic **macrophytes** suitable for spawning. Walleyes, on the other hand, spawn on a gravel bottom. Lake trout live only in very clear lakes with cold, well-oxygenated deep water. In contrast, carp are adapted to warm turbid, low oxygen lakes with mucky, high organic matter bottoms. View images of fish, **Figure 21**.

Decomposers

Decomposers, which include bacteria, fungi, and other microorganisms, are the other major group in the **food web**. They feed on the remains of all aquatic organisms and in so doing break down or decay organic matter, returning it to an **inorganic** state. Some of the decayed material is subsequently recycled as nutrients, such as **phosphorus** (in the form of phosphate, PO_4^{-3}) and nitrogen (in the form of ammonium, NH_4^+) which are readily available for new plant growth. Carbon is released largely as **carbon dioxide** that acts to lower the **pH** of bottom waters. In **anoxic** zones some carbon can be released as methane gas (CH_4). Methane gas causes the bubbles you may have observed in lake ice.

The decomposers can be found in all biological zones of a lake, although they are the dominant forms in the lower **hypolimnion** where there is an abundance of dead organic matter. Oxidation of organic matter by the decomposers (respiration) in the hypolimnion is responsible for the depletion of **dissolved oxygen** over the course of the summer, potentially leading to anoxic conditions (no dissolved oxygen). There is no source of oxygen in the hypolimnion to replace oxygen lost through **decomposition**. **Stratification** prevents atmospheric oxygen from being mixed deeper than the **thermocline**, and it is usually too dark for photosynthesis. Consequently, a large volume of organic matter from a variety of sources (e.g., wastewater, sinking algae, dying macrophytes, and organic sediment washed in from the watershed) leads to faster oxygen depletion and often complete removal of oxygen in the hypolimnion. The resulting **anoxia** has a profound effect on both the chemistry and the biology of the lake.

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Trophic Status

Since the early part of the 20th century, lakes have been classified according to their trophic state. "**Trophic**" means nutrition or growth. A **eutrophic** ("well-nourished") lake has high nutrients and high plant growth. An **oligotrophic** lake has low nutrient concentrations and low plant growth. **Mesotrophic** lakes fall somewhere in between eutrophic and oligotrophic lakes. While lakes may be lumped into a few trophic classes, each lake has a unique constellation of attributes that contribute to its trophic status. Three main factors regulate the trophic state of a lake:

1.Rate of nutrient supply

- Bedrock geology of the watershed
- Soils
- Vegetation
- Human **landuses** and management

2.Climate

- Amount of sunlight
- Temperature
- **Hydrology** (precipitation + lake **basin turnover time**)

3.Shape of lake basin (**morphometry**)

- Depth (maximum and mean)
- Volume and surface area
- Watershed to lake surface area ratio (A_w : A_o)

Trophic status is a useful means of classifying lakes and describing lake processes in terms of the **productivity** of the system. Basins with infertile soils release relatively little nitrogen and **phosphorus** leading to less productive lakes, classified as **oligotrophic** or **mesotrophic**. Watersheds with rich organic soils, or agricultural regions enriched with fertilizers, yield much higher nutrient loads, resulting in more productive, **eutrophic** (even hyper-eutrophic) lakes.

Eutrophication, the progress of a lake toward a eutrophic condition, is often discussed in terms of lake history. A typical lake is said to age from a young, oligotrophic lake to an older, **eutrophic lake**. Geological events, such as glaciation, created lakes in uneven land surfaces and depressions. The landscapes surrounding lakes were often infertile, and thus many lakes were oligotrophic. Eventually some of the **shoreline** and shallow areas supported colonizing organisms that decomposed unconsolidated materials into reasonably fertile sediments. Active biological communities developed and lake basins became shallower and more eutrophic as decaying plant and animal material accumulated on the bottom. Shallow lakes tend to be more productive than deep lakes, in part because they do not stratify, thereby allowing nutrients to remain in circulation and accessible to plants. They also tend to have a smaller lake volume, so nutrient loading from their watershed has a larger impact. There are undoubtedly

exceptions to this typical progression from oligotrophy to eutrophy,where geology, **topography**, and lake morphology caused eutrophic conditions from the start.

This concept of lake aging has unfortunately been interpreted by some as an inevitable and irreversible process whereby a lake eventually "dies." In fact, many oligotrophic lakes have persisted as such since the last glaciation and some ultra-oligotrophic lakes, such as Lake Tahoe may have been unproductive for millions of years. Furthermore, research in **paleolimnology** has provided evidence that contradicts the idealized version of a lake becoming more and more eutrophic as it ages. Studies of sediment cores have suggested that the algal productivity of Minnesota lakes actually may have fluctuated a great deal during the past 12 - 14,000 years (the period since the last glaciation). Changes in climate and watershed vegetation seem to have both increased and decreased lake productivity over this period. Some lakes probably experienced high rates of **photosynthesis** fairly soon after glacial retreat and then became less productive until recent times. It is also possible that water sources for some lakes have changed over the past thousands of years through diversions of stream flow, for example. In such cases water supplies to a lake (and therefore nutrient supplies) could have changed, leading to changes in the lake's productivity.

However, lakes may be culturally eutrophied by accelerating their natural rate of nutrient **inflow**. This occurs through poor management of the watershed and introduction of human wastes through failing septic systems. Such changes may occur over periods of only decades and are reversible if **anthropogenic nutrient loading** can be controlled. In the 1960s this was a serious issue, exemplified by the hyper-eutrophic condition of Lake Erie. Although it was pronounced "dead," it eventually returned to less eutrophic conditions, when major point sources of phosphorus were controlled in the early 1970s (by spending millions of dollars to build advanced wastewater treatment plants).

In North America, most of the problems associated with the direct discharge of domestic wastewater have been successfully mitigated. Now the regulatory focus is on the much more difficult problem of controlling **non-point sources** (NPS) of nutrient pollution such as agricultural drainage, stormwater runoff, and inadequate on-site septic systems. NPS pollution is particularly difficult to address because it is diffuse, not attributable to a small number of polluters, and associated with fundamental changes in the landscape, such as agriculture, urbanization and shoreline development.

An excellent discussion of the factors and issues relating to natural versus cultural eutrophication is a paper called:

The Algal Bowl- A Faustian View of Eutrophication, (by J.R. Vallentyne, 1972, Federation Proceedings, Vol 32 (7), pp1754-7. American Society of Biological Chemists Symposium on Man and his Environment at the 56th Annual Meeting of the Federation of American Societies for Experimental Biology, Atlantic City, NJ, USA, April 10, 1972).

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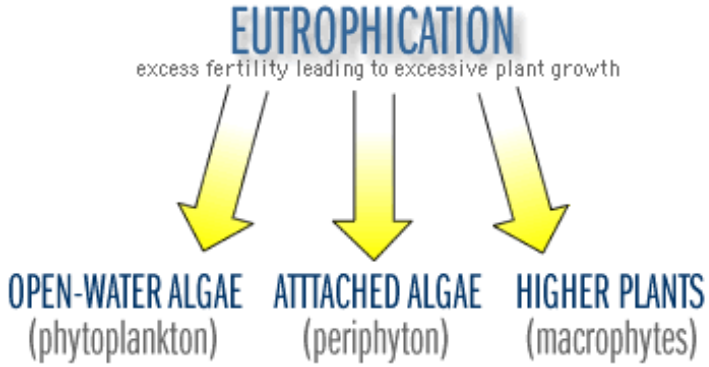

Figure 22.

WATER QUALITY IMPACTS ASSOCIATED WITH EUTROPHICATION

- Noxious **algae** (scums, blue-greens, taste and odor, visual)
- Excessive macrophyte growth (loss of open water)
- Loss of clarity (secchi depth goes down)
- Possible loss of **macrophytes** (via light limitation by algae and **periphyton**)
- Low **dissolved oxygen** (loss of habitat for fish and fish food)
- Excessive **organic** matter production (smothering eggs and bugs)
- Blue-green algae inedible by some zooplankton (reduced **food chain** efficiency)
- "Toxic" gases (ammonia, H_2S) in bottom water (more loss of fish habitat)
- Possible toxins from some species of blue-green algae
- Chemical treatment by lakeshore homeowners or managers may result (copper, diquat, 2,4-D, etc.)
- Drinking water degradation from treatment disinfection byproducts
- Carcinogens, such as chloroform (from increased organic matter reacting with disinfectants like chlorine)

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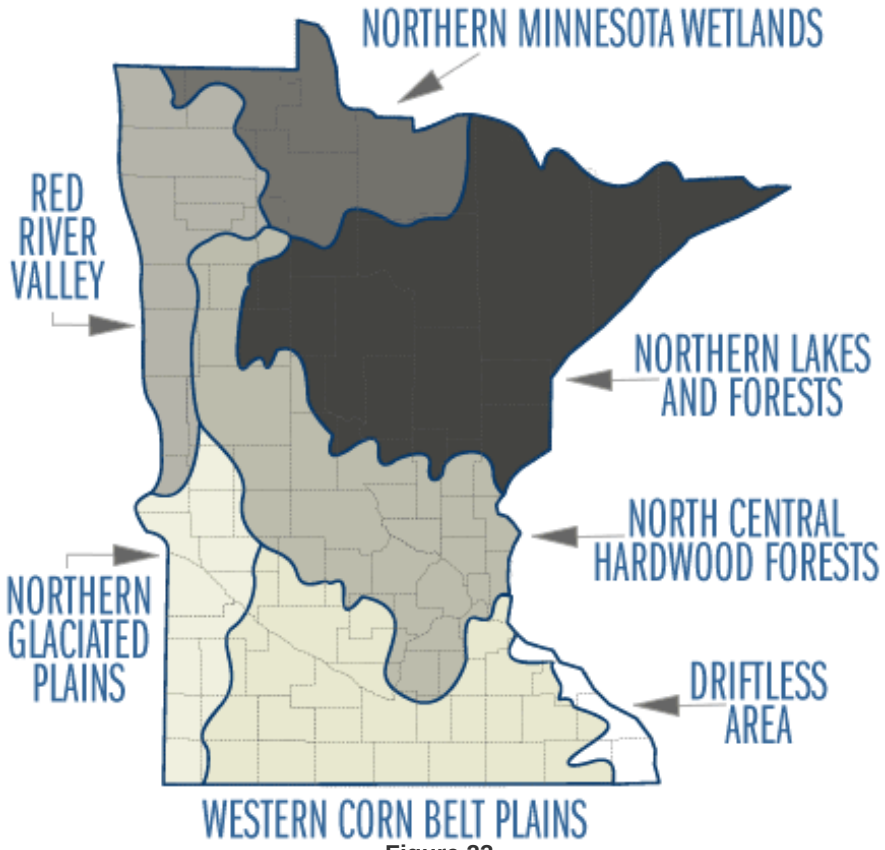

Figure 23.

Observations of lake characteristics that are geographically-distinct have led to the **ecoregion** approach of lake classification developed by the U.S. Environmental Protection Agency (EPA) Research Laboratory at Corvallis, Oregon. Ecoregions are areas of relative homogeneity based on **landuse**, soils, land and surface form, and potential natural vegetation. Minnesota is divided into seven ecoregions (Figure 23), but most of its lakes are found in four of these. Minnesota Pollution Control Agency (MPCA) researchers found regional patterns in numbers of lakes, lake water quality, **morphometry**, and watershed characteristics (Table 5) among these ecoregions. For example, lakes of the Northern Lakes and Forests ecoregion have significantly lower total **phosphorus** and **chlorophyll** than lakes in the Western Corn Belt Plains ecoregion. Furthermore, the MPCA discovered through lake-user surveys that user perception of water quality varied by ecoregions. This has led to ecoregion-specific criteria for phosphorus and, in general, helped to clarify expectations and goals for protecting lakes in Minnesota.

Table 5
Ecoregion lake data summary
Values are typical for surface water (0-2 m) in summer (June-September).

PARAMETER	Northern Lakes and Forests	North Central Hardwood Forests	Western Corn Belt Plains	Northern Glaciated Plains
Total Phosphorus (µg/L)	14 - 17	23 - 50	65 - 150	130 - 250
Chlorophyll-mean (µg/L)	< 10	5 -22	30 - 80	30 - 55
Chlorophyll-max (µg/L)	< 15	7 - 37	60 - 140	40 - 93

Secchi Disk (m)	2.4 - 4.6	1.5 - 3.2	0.5 - 1.0	0.3 - 1.0
Total Kjeldahl - N (mg/L)	< 0.75	< 0.60 - 1.2	1.3 - 2.7	1.8 - 2.3
[Nitrite + Nitrate]-N (mg/L)	< 0.01	< 0.01	0.01 - 0.02	0.01 - 0.1
Alkalinity (mg/L)	40 - 140	75 - 150	125 - 165	160 - 260
Color (Pt-Co units)	10 - 35	10 - 20	15 - 25	20 - 30
pH	7.2 - 8.3	8.6 - 8.8	8.2 - 9.0	8.3 - 8.6
Chloride (mg/L)	< 2	4 - 10	13 - 22	11 - 18
TSS (mg/L)	< 1 - 2	2 - 6	7 - 18	10 - 30
Turbidity (NTU)	< 2	1 - 2	3 - 8	6 - 17
EC (uS/cm)	50 - 250	300 - 400	300 - 650	640 - 900
TN:TP ratio	25:1 - 35:1	25:1 - 35:1	17:1 - 27:1	7:1 - 18 - 1

* Summer averages by ecoregion, based on interquartile range (25th - 75th percentile) for ecoregion reference lakes. Derived in part from Heiskary, S.A. and C.B. Wilson (1990).

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Biological Differences

Populations of **algae** and the animals that feed on them are lower in **oligotrophic** lakes because of low nutrient concentrations. Thus the water remains clear. Decay of the relatively small amount of **organic** matter in oligotrophic lakes does not completely deplete the hypolimnetic supply of **dissolved oxygen**. Therefore, lack of oxygen does not restrict animals from living in the **hypolimnion** of oligotrophic lakes. Lake trout, for example, require cold, well-oxygenated water and primarily live in the hypolimnion of oligotrophic lakes. Minnesota's oligotrophic lakes are found in the northeast region of the state, where infertile soils are covered with mixed conifer forests.

Extremely deep oligotrophic lakes such as Lake Superior and Lake Tahoe have hypolimnia that remain completely saturated with **oxygen** the entire year. However, many moderately deep lakes (with maximum depths greater than about 30 meters) may develop **anoxia** in the lower hypolimnion during late summer but may still be classified as oligotrophic because of their very low nutrient concentrations, low algal abundance, and relatively high transparency (high secchi depth). These lakes may have a **two-story fishery**, with warm and cool water fish in the **epilimnion** and **metalimnion** and cold water fish (such as trout) in the cold, oxygen rich portion of the hypolimnion. The cold-water fishery is therefore very sensitive to increased inputs of organic matter from sewage or erosion (external inputs), and to increased algal and macrophyte production (internal inputs) due to **eutrophication** since these factors will accelerate the rate and extent of **hypolimnetic oxygen depletion** in the summer.

Algae or **macrophytes** grow so thickly in some **eutrophic lakes** that light penetrates only a short distance and nutrients below that depth are not assimilated. As discussed earlier, **phosphorus** is typically the limiting nutrient in freshwater lakes, meaning that the plants deplete all available phosphorus before depleting other nutrients. In a hypereutrophic lake, algae may become so abundant that they suffer from self-shading. In those cases, **photosynthesis** is limited by light rather than by nutrients. When a great abundance of phosphorus is available in a lake, nitrogen may become limiting. In such lakes, certain species of blue-green algae that can **fix** atmospheric nitrogen have a clear competitive advantage and frequently become dominant. They dominate the algal community until another nutrient, or usually light, becomes limiting. In many infertile lakes in northeastern Minnesota, both phosphorus and nitrogen may be extremely low during midsummer. Since most sources of either point source or nonpoint-source pollution involve increased inputs of **both** N and P, these lakes are extremely sensitive to such pollution, irrespective of which is technically "most" deficient.

Eutrophic lakes show wide seasonal changes in their biological and chemical conditions. Because of the great amount of organic matter produced in these lakes, the decay rate is high in the hypolimnion, causing oxygen to be depleted. Therefore, eutrophic lakes frequently show a complete loss of dissolved oxygen below the **thermocline** during summers. Clearly, fish and most other animals cannot live in the hypolimnion of such lakes. Warm-water fish that can live in the epilimnion, however, can be quite productive. Bass, panfish, northern pike, walleye, carp, and bullheads thrive in many of Minnesota's eutrophic lakes. Complete or nearly complete oxygen depletion below the thermocline may also be a common feature of many moderately deep (10 to 30 m) **mesotrophic** lakes, if deep enough to stratify throughout the summer. Therefore, virtually complete anoxia below the thermocline does not necessarily mean that the lake is eutrophic.

> Ice Lake, one of our WOW lakes, is an example of a mesotrophic lake that becomes **anoxic** below the thermocline in the summer, (see **Ice Lake** section) as is Hale Lake, a somewhat less productive lake immediately downstream of Ice Lake. Both are ~16-18 meters deep.

Another oxygen-related problem in eutrophic lakes is **winterkill**. A dense snow cover over the ice reduces light penetration and keeps oxygen-producing photosynthesis from occurring. The high organic content of the water, however, provides considerable food for the decomposers. If the decomposers succeed in

using all the available dissolved oxygen, a fish kill can occur.

In certain cases, a winterkill may lead to a more balanced fishery and possibly even improved water quality. Fish that survive a winterkill will have reduced competition for food for a period of time and so may grow faster and to a larger size. Fewer small fish reduces predation on the larger **zooplankton**, such as the water flea, *Daphnia sp.,* leading to increased zooplankton grazing on algae and a resultant increase in water **clarity**. This general scheme, involving fishery manipulations to reduce the abundance of zooplanktivorous fish, has been termed **biomanipulation**, and is being tried in many urban lakes where it is economically impractical to reduce nutrient inputs enough to significantly reduce algae. In these situations the offending fish may be removed by intense stocking of gamefish, by intensive netting and trapping, or even by poisoning the entire fishery and starting over with greatly reduced **planktivores**.

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