Course Handout on Limnology

Limnology: the study of lakes and rivers.

Limnology encompasses everything from the geologic origins of lakes to the development of a lake in prehistoric times (Paleolimnology) to the structure of food webs. As do oceanographers, limnologists generally specialize in physical, chemical or biological limnology. Modeling is a tool that can reach across the boundaries of these specialty areas. There are three major limnological topics that are covered here: (1) temperature structure of lakes, (2) food webs, and (3) eutrophication. Environmental and civil engineering students should review this material in the textbook for CE3501/CE3503.

1. Temperature Structure in Lakes

The fact that water is most dense at 4^{o}C (rather than at the freezing point as for most other liquids) has enormous importance for lakes. You will recall that this behavior results from the formation of hydrogen bonds between water molecules that spaces the molecules further apart at cold temperatures; because the hydrogen bonds are weak, they are broken by the movement of water molecules at temperatures above 4^{o}C. In winter, this behavior results in the coldest water being at the top of the lake (Fig. 1) and forming a protective barrier that itself cools as a result of contact with cold air and keeps the whole lake from becoming even colder. This situation is called **inverse stratification**. Also as a result, ice floats on top of lakes rather than forming from the bottom up. Ice not only acts as a thermal barrier, it also prevents the wind from mixing the lake waters (and thereby slows further cooling) as well as preventing oxygen from contacting and dissolving into the lake water. In shallow or highly productive lakes, all of the oxygen can be used up during winter by bacteria decomposing the organic matter in the sediments; the result can be an under-ice fish-kill in such lakes.

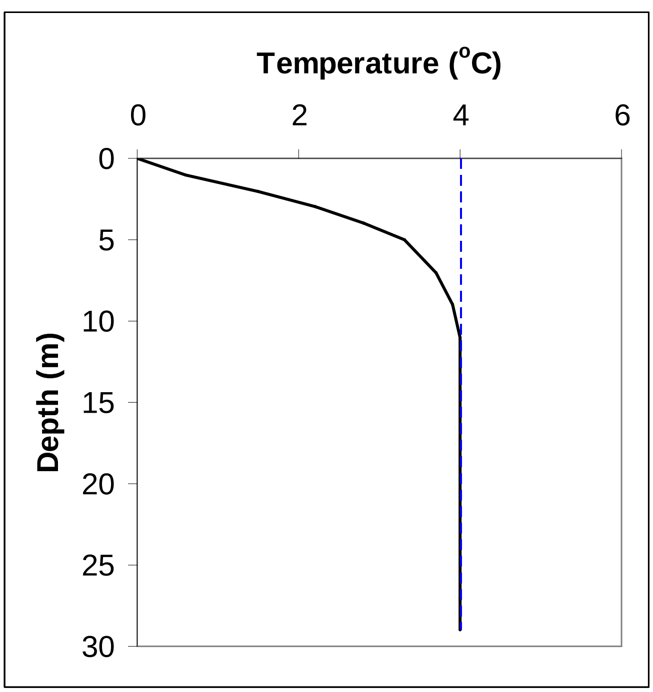

Figure 1. Temperature profile in winter.

In summer, just the opposite occurs. The cold, dense water is at the bottom of the lake, and the warmer water sits on top. Again, this allows the warm layer to get warmer and shields the cold layer from the warmth of the atmosphere. The cool, deep water provides a refuge for many fish species. This temperature profile is stably stratified because the least dense water is on top. Often, wind energy is sufficient to mix the upper waters and create an upper layer of nearly uniform temperature. The upper, warm layer is termed the **epilimnion**, the cold deep layer is called the **hypolimnion**, and the zone of transition is called the **metalimnion**. The depth at which the maximum temperature change occurs is called the **thermocline**.

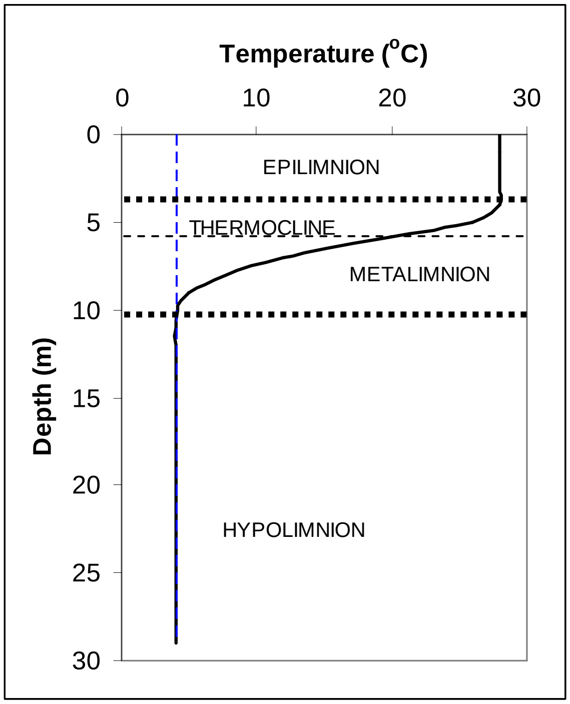

Figure 2. Summer temperature profile.

There are numerous effects of summer **stratification** upon a lake. Any pollutants brought into a lake in summer are diluted into a much smaller volume while the lake is stratified. Stratification makes it possible to swim in summer even in northern latitudes. Any nutrients lost from the epilimnion during summer (e.g., via settling of dead algal cells) will not be available for algal growth again until the lake mixes in fall. Because the hypolimnion does not have contact with the atmosphere, it must rely on diffusion across the metalimnion (a slow process) to resupply any oxygen that is consumed within the bottom waters. In productive lakes, oxygen consumption can be faster than oxygen transfer across the metalimnion, and the bottom of the lake can go **anoxic**. This anoxia kills most organisms except bacteria in the bottom waters and sediments. In the absence of oxygen, the bacteria must use other electron acceptors, and, as a result, substances such as dissolved iron, hydrogen sulfide (the molecule that gives rotten eggs their odor), and methane may build up in the hypolimnion. Anoxia has a huge effect on phosphorus, generally the most important nutrient in lakes. When oxygen is present, phosphorus in the sediments adsorbs on the surface of iron oxides. Under anoxic conditions, the iron oxides dissolve and the phosphorus is released to the water and becomes available to support further algal growth. This phosphorus release from anoxic sediments is a type of positive feedback that promotes **eutrophication** (see below) in lakes.

Spring and fall are periods of transition between the two temperature profiles shown above. At some point, the whole lake will reach 4°C, and at this point there is the least hindrance (from buoyancy) to complete mixing of the lake. The period of complete mixing is termed **overturn** or **holomixis**. In spring and fall, the epilimnion gradually thickens as the thermocline is driven deeper by wind energy. Around Houghton, spring holomixis generally occurs between mid-April and mid-May, and fall holomixis occurs between late September and mid-November.

The timing and pattern of lake mixing and stratification depend on climate. The pattern of mixing twice (**dimictic**) per year as described above occurs in temperate latitudes. Further north, lakes may never stratify in summer, and further south many lakes never stratify in winter; these patterns are called cold **monomictic** and warm **monomictic**. Very shallow lakes may stratify and be mixed by the wind numerous times in a year and are called **polymictic**. By the equator or at high latitudes, lakes tend to be permanently stratified and mix only rarely (oligomictic) if at all (amictic) either because of continuous ice cover or continuous warm weather.

2. Food webs

A **food web** is the trophic linkages among organisms in an ecosystem. **Trophic interactions** refer to feeding relationships or who eats whom (predator-prey relationships). The energy source fueling most ecosystems is sun light; this electro-magnetic energy is converted into chemical energy through photosynthesis. In a few ecosystems (e.g., deep sea vents, hot springs), chemosynthetic bacteria are able to create organic compounds using energy from inorganic compounds present in the environment (e.g., sulfide, reduced iron, methane). Organisms that are able to create all of their organic compounds using the sun's energy are termed photosynthetic **autotrophs**. All organisms that are not autotrophic are **heterotrophic**, i.e., they obtain their organic carbon from other organisms. In other words, the autotrophs must feed the rest of the world. In lakes, **algae** (also called **phytoplankton**), **blue-green algae** (or **cyanobacteria**), and **macrophytes** (macroscopic, usually vascular, plants) comprise the autotrophs. Algae may be classified either phylogenetically (i.e., by the similarity of their DNA and hence physical and biochemical features) or by size. The major groups of algae include diatoms, green algae, chrysophytes, dinoflagellates, cryptophytes, red algae, and brown algae. The blue-green algae are really bacteria (prokaryotes), not plants. Often we speak of net plankton (> 20 µm), nanoplankton (2-20 µm), and picoplankton (< 2 µm).

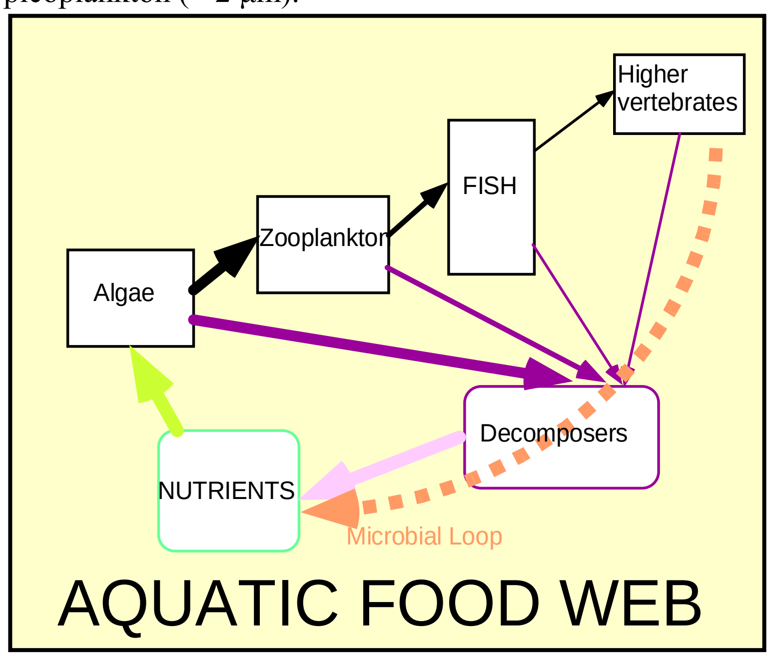

Figure 3. Simplified sketch of an aquatic food web.

Autotrophs are consumed by grazing organisms or **herbivores**. In lakes, the herbivores may be either **planktonic** (free floating or swimming **zooplankton**) or **benthic** (bottom dwelling). The major zooplankton are crustaceans, and fall into either the subclass of Cladocerans (e.g., daphnia, the water flea) or the suborder Copepods. These organisms range in size from less than 1 mm to over 2 cm. Herbivores are, in turn, consumed by **planktivorous** organisms that may be either small fish or larger zooplankton. The planktivores are, in turn, eaten by larger organisms. Planktivorous fish are consumed by **piscivorous** fish such as lake trout, walleye, northern pike, large mouth bass, etc. Juvenile fish may be planktivorous and then become increasingly piscivorous as they become larger.

Were there no mechanism for recycling the carbon and nutrients in dead organisms, the biosphere would long ago have ground to a halt as all available carbon and nutrients would have been consumed. It falls to the **detritivores** and **heterotrophic** bacteria and fungi to consume the dead organic matter and to recycle the carbon and nutrients. Detritivores include fish (e.g., suckers, sturgeon), a wide variety of insect larvae, and benthic crustaceans among others.

The biosphere as well as engineering students must obey the laws of thermodynamics. Whenever there is a transformation of energy from one form to another (e.g., from electromagnetic radiation to chemical energy), some of the energy is irreversibly lost to heat and increased entropy. At each step in a food web, there is this loss of energy. A very rough rule of thumb is that 90% of the energy is lost at each trophic transfer. Thus, the longer is the food chain, the fewer top carnivores will be produced. This phenomenon results in a **trophic pyramid**, a reduced biomass of organisms present in successively higher trophic levels. The total biomass of bacteria and detritivores within an ecosystem typically ranges from about half to larger than the biomass of autotrophs. Interestingly, environments with low nutrient levels (**oligotrophic**) often have a larger bacterial biomass than autotrophic biomass. Oligotrophic aquatic ecosystems (including Lake Superior) often have inverted trophic pyramids; the biomass of herbivores exceeds the biomass of autotrophs. How is this possible?

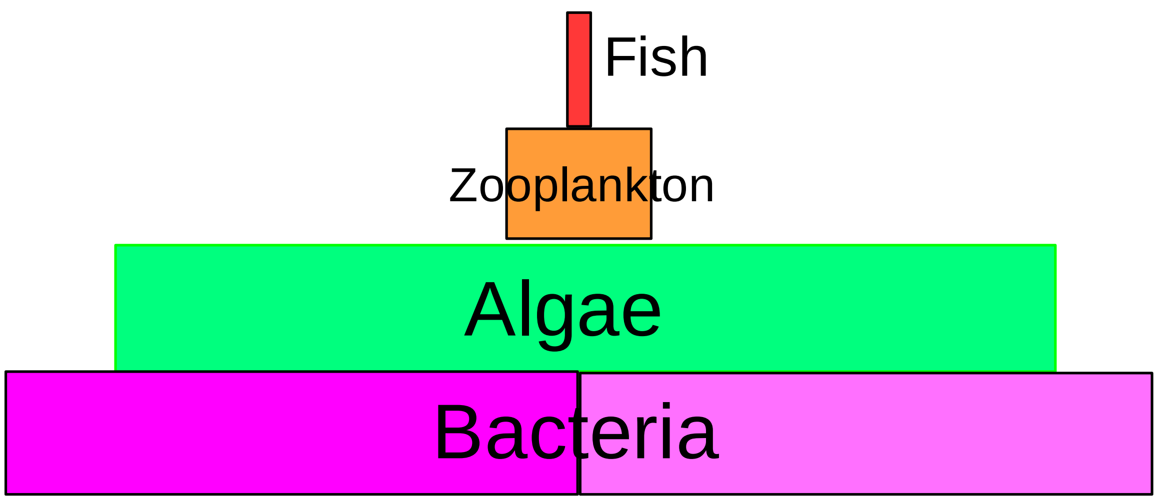

Figure 4. Illustration of a trophic pyramid.

3. Eutrophication

The fertility of an ecosystem is referred to as its **trophic status**. Thus, **eutrophic** systems have abundant nutrients, **mesotrophic** systems have an intermediate availability of nutrients, and **oligotrophic** systems have few nutrients. Based on the discussion of trophic pyramids above, a eutrophic ecosystem should be able to produce more biomass of top predators than would a mesotrophic or oligotrophic system. However, this often is not the case. Eutrophic conditions are often aesthetically unpleasant and also create chemical conditions inimical to many life-forms. As a result, mesotrophic ecosystems are often the most productive in terms of production of biomass in upper trophic levels. Accordingly, eutrophic conditions in lakes are generally regarded as undesirable, and it often falls to environmental/civil engineers to restore eutrophic lakes to mesotrophic conditions. Below are listed a few of the cascade of effects that renders eutrophic lakes unpleasant and unproductive.

High rates of nutrient inputs to lakes generally lead to enhanced algal growth. The green appearance of a highly productive lake itself may be less desirable than the blue color of a less productive lake. Furthermore, the algae that often appear in eutrophic lakes are undesirable species including forms that may produce toxins, undesirable tastes and odors, or undesirable scum on the surface or shoreline. The abundant algal growth has to be accompanied by a corresponding increase in decomposition of algal biomass. Enhanced decomposition rates cause accelerated uptake of oxygen. If the oxygen demand exceeds the rate at which oxygen can be supplied to the lake, then anoxic conditions may result. (Recall that oxygen transfer into the hypolimnion is a slow process.) Anoxic conditions often result in production of biochemicals with unpleasant tastes or odors. High concentrations of dissolved iron or manganese that may develop under anoxic conditions give water undesirable color and taste. Hydrogen sulfide has an even more obnoxious taste and odor and is toxic. Anoxic conditions cannot support higher life forms (i.e., life-forms above bacteria), and hence eutrophic lakes often have few benthic organisms, few fish in the hypolimnion, and the sediments are unable to support the hatching of fish eggs much less of producing food to support benthivorous fish. The animal species capable of living under low-oxygen conditions (e.g., carp, rat-tailed maggot) are generally undesirable. Anoxic conditions in the hypolimnion enhance release of phosphorus from the sediments, and this further exacerbates the abundance of nutrients.