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Lakes are discrete, largely isolated ecosystems in which the interplay between physical, biogeochemical and organismal processes can be studied, understood, and put to use in effective management.

Introduction

Lakes are inland bodies of water that lack any direct exchange with an ocean. Lake ecosystems are made up of the physical, chemical and biological properties contained within these water bodies. Lakes may contain fresh or salt water (in arid regions). They may be shallow or deep, permanent or temporary. Lakes of all types share many ecological and biogeochemical processes and their study falls within the discipline of 'limnology'. Lakes are superb habitats for the study of ecosystem dynamics: interactions among biological, chemical and physical processes are frequently either quantitatively or qualitatively distinct from those on land or in air. Because the boundaries between water and land, and water and air are distinct, there is tight coupling among many ecosystem components.

Although lakes contain 50.01% of all the water on the Earth's surface, they hold 49.98% of the liquid surface freshwater. Many organisms depend on freshwater for survival, and humans frequently depend on lakes for a great many 'goods and services' such as drinking water, water removal, fisheries, agricultural irrigation, industrial activity, and recreation. For these reasons lakes are important ecosystems.

Lake ecosystems are influenced by their watersheds, the geological, chemical and biological processes that occur on the land and streams that lie uphill. The movement of chemicals, sediments, detritus, and of many organisms, is typically unidirectional from the watershed to the lake, but fish may migrate upstream, and aquatic insects may emerge and disperse on to land. A lake and its watershed are often considered to be a single ecosystem (Likens, 1985).

Lake Thermal Structure

During summer, sunlight increases the temperature of lake surface water. Water at greater depths is warmed less. Wind at the surface causes the top several metres of lake water to mix homogeneously

to form a warm surface layer called the 'epilimnion'. Below the level of wind mixing, temperature drops rapidly through a zone called the thermocline, and below this is a region of homogeneously

Secondary article

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cool water called the 'hypolimnion'. This two-layer physical structure is called 'thermal stratification'. Summer stratification does not occur in shallow water bodies, nor in high latitude or high altitude lakes where summers are short. In winter, surface water directly under the ice is about 0°C and deeper water is slightly warmer. Wind cannot mix water below the ice so winter stratification persists while the lake is frozen. Winter stratification does not occur in tropical or subtropical lakes, in many large temperate-zone lakes, or in many salt lakes.

Lakes that stratify during summer and winter mix from top to bottom during spring and autumn in events called 'turnover'. Lakes that do not stratify in winter, and those that do not stratify in summer, mix continuously throughout their unstratified periods. Tropical lakes may stratify every day and mix every night.

Summer thermal stratification divides the lake environment into two distinct parts: an illuminated and warm epilimnion where phytoplankton (algae and photosynthetic

cyanobacteria) carry out photosynthesis, and a dark and cool hypolimnion where this production is decomposed. Decomposition also dominates under the ice of lakes that freeze over. When the amount of decomposing organic matter is large, anoxic conditions (no dissolved oxygen) can prevail.

Lake Habitats and Food Chains

In the pelagic zone (open-water region) of the lake, phytoplankton carry out photosynthesis at the base of the food web. These unicellular or simple colonial algae or cyanobacteria sink only very slowly and are easily resuspended by wind-driven water movements. Very small phytoplankton and bacteria are consumed by unicellular zooplankton; larger phytoplankton are consumed by larger zooplankton. Some taxa are generalists that filter most algae encountered (e.g. *Daphnia*) and can have a major impact on phytoplankton densities in lakes. Other taxa tend to select the more nutritious phytoplankton to consume.

Fine detritus (dead plankton) suspended in the pelagic zone is colonized by heterotrophic bacteria, which then

consumed by protists (ciliates and flagellates) and generalist grazers. The protists are in turn consumed by other protists or by copepods. This return of energy to the pelagic food chain is called the 'microbial loop'. Its ultimate importance in lake ecosystems remains a point of debate. Other detritus produced in the epilimnion may be trapped at the thermocline or sink into the hypolimnion where it is decomposed by bacteria.

Grazing zooplankton are consumed by predatory invertebrates (rotifers, cyclopoid copepods, some cladocerans, and insect larvae of the genus *Chaoborus*) or vertebrates (typically fish). Zooplanktivorous fish also consume predatory invertebrates. Piscivorous fish (consume other fish) sit atop the natural food

webs of most lakes although in some cases there are piscivorous birds, otters, seals, crocodiles or alligators. Humans act as top predators in a great many lakes worldwide.

Submersed rooted plants (macrophytes) growing at the lakemargin define the littoral zone, and provide habitat for attached algae (epiphytes), insects and other invertebrates, and fishes that use this area for breeding, cover and foraging. Some fish consume rooted plants, but most eat invertebrates or other fish. The littoral zone captures much of the chemicals, sediments and detritus washing in from the watershed and processes these materials before they reach the pelagic zone. Because macrophytes require light to grow up from the lake bottom each spring, the distance the littoral zone extends into the lake depends upon how steeply the lake bottom drops off near shore, and how turbid the lake water is with phytoplankton or suspended sediments.

The profundal zone is the bottom water and sediments of deep lakes where there is insufficient light for photosynthesis. In this region bacteria and fungi obtain energy by decomposing detritus, or by chemoautotrophy (breaking energy-rich chemical bonds in inorganic molecules). Insect larvae (typically dipterans) and annelid worms (oligochaetes) live in the soft bottom sediments and consume detritus. All organisms that live in, on, or in association with the lake bottom are called 'benthos'.

There are exchanges among all lake habitats. Nutrients and dissolved organic carbon ('DOC') molecules released by macrophytes in the littoral zone diffuse to the pelagic zone where they are used by algae and bacteria. Detritus from the epilimnion sinks to the hypolimnetic profundal zone where nutrients are released. Nutrients in the hypolimnion are returned to the epilimnion via

The Role of Nutrients

Identifying the determinants of algal growth in lakes is crucial both for understanding lake ecosystem functioning,

and because extensive algal blooms are an unsavory

phenomenon that can be caused by human activity. Primary production in lake ecosystems depends on nutrients and light as essential resources. Phytoplankton take up nutrients dissolved in

lake water; rooted macrophytes obtain nutrients from the sediments. Primary producers are potentially limited by carbon, nitrogen or phosphorus. Of these, carbon is the most common element in algal tissue and is also the

most abundant in solution in lake water (CO_2 , HCO_3^- , or CO_3^{2-}). Nitrogen (NO_3^- , NH_4^+ , N_2) and phosphorus

diffuse, turbulent mixing across the thermocline, and at turnover. Planktonic animals migrate between the epilimnion and hypolimnion on a daily cycle, excreting nutrients as they travel. Fish move between the littoral and pelagic zones feeding and breeding in one place and excreting and defecating nutrients in another.

(PO_4^{3-}) are much less available, suggesting that phosphorus, followed by nitrogen, is most likely to limit algal production in lakes.

Limitation by other nutrients can occur: for example diatoms, algae characterized by hard cell walls containing silica, can be limited by silica availability. Light is also taken up and consumed like other algal resources. Light limitation can occur during algal blooms when cells close to the surface shade algae deeper in the water column, or when phytoplankton shade the lake bottom and prevent macrophyte growth.

Phosphorus

Phosphorus is essential in nucleic acids, phospholipids, adenosine triphosphate (ATP) etc., but is scarce in bio-accessible forms in lakes. Whereas carbon and nitrogen enter lakes by exchange of CO_2 and N_2 from the atmosphere, the only natural source of phosphorus is weathering from the watershed of PO_4^{3-} ions, which dissolve only poorly in water. Thus, bio-available phosphorus occurs in extremely low

concentrations in fresh-water and is taken up quickly by phytoplankton. In water containing dissolved oxygen, PO_4^{3-} can combine with iron to form insoluble salts that sink to the lake bottom, making phosphorus still less available to algae. Under anoxic conditions in the hypolimnion or in sediments, PO_4^{3-} becomes soluble again (a process called 'internal loading') and can stimulate algal growth through mixing processes. The paramount importance of phosphorus as a resource for primary producers in lakes has been shown (1) as a close relationship between phosphorus supply to lakes worldwide and the abundance of algae they contain (Schindler, 1978), (2) through studies of lakes polluted with phosphorus-containing human waste and laundry detergents, where phosphorus removal has eliminated noxious algal blooms (Edmondson, 1991), and (3) through whole lake experiments in which enrichment with both phosphorus and nitrogen resulted in a bloom of cyanobacteria much higher than the growth of algae observed in a lake enriched only with nitrogen (Schindler, 1974). The important role

played by phosphorus in lake algal production is generally accepted today, and successful management of many lake ecosystems depends upon controlling phosphorus inputs.

Nitrogen

Algal cells require nitrogen to synthesize proteins. Typically, nitrogen is available in lakes in higher concentrations than phosphorus. Most algae take up NH_4^+ ions (from decomposition) or NO_3^- ions (from bacterial nitrification of NH_4^+). However, many species of cyanobacteria can also use N_2 diffusing across the air-water boundary in a process called nitrogen fixation which forms NH_4^+ . Lake ecosystems are not as frequently nitrogen limited as marine or terrestrial ecosystems. Lakes can only be nitrogen limited if the relative supply of phosphorus is greater than that of nitrogen. Adding wastewater from sewage to a lake can create this condition, which in turn favours the growth of nitrogen-fixing cyanobacteria because they have an alternative source of nitrogen. This is why lakes with excessive phosphorus input tend to have noxious blooms of cyanobacteria.

Trophic Control of the Food Chain

The enrichment of algal growth by nutrients, and the resulting enhanced production of grazing zooplankton, predatory invertebrates and fish, is called 'bottom-up control' because nutrients flow from the base of the food chain up through the trophic levels. However, an alternative regulation of algal abundance and primary production can come from 'top-down control'. When grazing zooplankton, especially *Daphnia*, are abundant, algal biomass can be suppressed by consumption even when nutrient concentrations are high. Large-bodied and abundant zooplankton occur in lakes that have a relatively low number of zooplanktivorous fish (Brooks and Dodson, 1965). And low zooplanktivorous fish density is found in lakes with high numbers of piscivorous fish. Thus, an alternative to reducing phosphorus inputs as a means of regulating the abundance of algae is to increase the density of stocked piscivorous fish. Managing fisheries has become

a tool for controlling phytoplankton biomass in lakes (Carpenter and Kitchell, 1993).

In natural lakes both bottom-up and top-down processes operate. Their relative importance may vary among lakes or can change seasonally within a lake. For example, in many temperate-zone lakes in spring the disappearance of ice increases light availability and turnover which mixes nutrients throughout the water column. The result is a

bottom-up driven algal bloom. *Daphnia* then grows in abundance to the point where it suppresses algal densities and causes the water to become quite transparent in a seasonal top-down event called the 'clear water phase' (Lampert *et al.*, 1986).

Within these broad generalizations, there is ecologically important variation among taxa. Only some phytoplankton can fix nitrogen. Not all phytoplankton species are equally edible for grazing zooplankton: cyanobacteria can be of poor nutritional quality (low in essential fatty acids), often contain toxins, and grazers have reduced impact on these cells. Similarly, not all zooplankton species are equally vulnerable to predation. Fish are generally visually-orienting predators that feed during the day on the largest prey in the water. Small zooplankton and those that migrate into the dark hypolimnion during the day can escape detection but still graze on phytoplankton. Still other zooplankton grow spines that defend them against predation by invertebrates, and zooplanktivorous fish may grow sufficiently large that piscivores are unable to capture and consume them.

The rates and even the occurrence of many ecosystem processes, such as transfers of nutrients and energy from one trophic level to

the next, depend not only on the physical and chemical environment, but also critically on the characteristics of the species present.

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