THE ROLES OF PHOSPHORUS AND NITROGEN IN LAKE ECOSYSTEMS

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ABSTRACT

The Kodiak Limnology Laboratory has been analyzing water samples from lakes on Kodiak and Afognak Islands, the Alaska Peninsula, and the Aleutians since 2000. The limnology data generated are analyzed by various biologists to determine sockeye salmon *Onchorynchus nerka* stocking levels, lake fertilization levels, and to assess escapement goals of different salmon systems. Phosphorus and nitrogen are the two nutrients most critical in freshwater lakes. Many factors affect the levels of these nutrients, which in turn affect the productivity of the lake. This paper reviews the nutrients phosphorus and nitrogen and their various forms, explains how they cycle through the lake environment, and discusses implications this might have for the lake. The paper also discuss what the limnology data means and how these data can be used.

INTRODUCTION

The Kodiak limnology laboratory, located in the Kodiak Island Borough research center on Near Island, was established in 2000 to analyze the chemical, biological, and physical properties of water collected from the salmon-rearing lakes on Kodiak and Afognak Islands, the Alaska Peninsula, and the Aleutian Islands. The laboratory routinely measures the pH, alkalinity, total ammonia (TA), nitrate + nitrite, total phosphorus (TP), total filterable phosphorus (TFP), filterable reactive phosphorus (FRP), chlorophyll *a* (chl-a), phaeophytin *a* (phaeo-a), and occasionally measures total Kjeldahl nitrogen (TKN), of freshwater lakes. This paper is intended to inform the biologists and others who use the limnology data about the importance of the nutrients analyzed, how they are cycled through the environment, and the types of interactions they have with other chemicals or organisms. It will also provide some interpretation on the limnology data collected and options to bring about changes in nutrient levels. In addition, common limnological terms are defined (Appendix A).

pH

pH is a measurement of the acidity of a solution. Almost every chemical reaction in a lake is pH dependent. The pH of a lake is largely related to the carbon dioxide in the water and the buffering system of carbonate (CO_3^{2-}) and bicarbonate (HCO_3^-) present in the lake (Horne and Goldman 1994). Because so many chemical reactions are pH dependent, this buffering capacity, termed alkalinity, is important. Alkalinity is a measure of the waters' ability to resist changes in pH (Koenings et. al 1987).

CHLOROPHYLL A

Measurements of the algal pigment chlorophyll *a* can be used to estimate the phytoplankton standing crop (Koenings et. al 1987). As chlorophyll *a* degrades it is rapidly converted to phaeophytin *a*, another algal pigment. The amount of phaeophytin *a* can be used to determine the amount of degraded chlorophyll in the lake. Chlorophyll *a* is converted to phaeophytin *a* upon exposure to light and heat. Extended processing time of the sample may overestimate phaeophytin *a* levels and underestimate chlorophyll *a*. It must also be kept in mind that the chlorophyll *a* measurements tell us only about the standing crop of phytoplankton, not about the rate of primary production in the lake.

PHOSPHORUS

Phosphorus is the primary nutrient controlling lake productivity. The many forms of phosphorus and their relation to one another are shown in Figure 1. Three forms of phosphorus are measured at the Near Island laboratory; total phosphorus (TP), total filterable phosphorus (TFP), and filterable reactive phosphorus (FRP). FRP, or orthophosphate, is available for algal uptake. FRP and organic particular phosphate (OPP) are the two forms considered biologically active (Koenings et. al 1987).

Most phosphorus is held in a biologically unavailable form by particles in lake water, so although it is required in smaller amounts than other nutrients, phosphorus availability commonly limits phytoplankton growth. Phytoplankton can only absorb soluble phosphate (PO_4) or orthophosphate (PO_4^{3-}) because these are the only forms able to diffuse into the cell. Because of the limited availability of biologically available phosphorus (PO_4), the standing crop of phytoplankton is often proportional to the level of total phosphorus. A reason for this close correlation is that most TP in lakes is in particulate form and algae often constitute a large fraction of particulate matter (Horne and Goldman 1994).

The phosphorus cycle involves organic and inorganic, soluble and insoluble forms, and transfers between fractions (Figure 2). These transfers occur quickly. Most phosphorus inflow comes from erosion. PO_4 does not move readily through soil. It is deposited into lakes by streams, rivers, or in sewage (Horne and Goldman 1994). Once the phosphorus arrives in the lake, there is a net movement of the phosphorus to sediments. Important factors that affect the speed of phosphorus recycling from the sediments back to the waters are the sediments ability to retain phosphorus, the overlying water conditions, and any biota in the sediment that alter exchange rates (Wetzel 1983). By late spring, algal uptake usually reduces PO_4 to less than two micrograms per liter, much lower than that needed for optimal phytoplankton growth (~20 µg/L; Table 1). For the remainder of the year, soluble phosphorus is recycled back to phytoplankton via excretion by fish, zooplankton, and bacteria. Recycling of nutrients in lakes during summer and fall turnovers is likely the major phosphorus source. Even with recycling however, the TP in oligotrophic lakes sinks out of the epilimnion by the end of summer. In shallow waters or in the littoral zone PO_4 can be recycled from the sediments, whereas in deeper water only winter and spring mixing return phosphorus to the epilimnion (Horne and Goldman 1994).

The amount of PO_4 and the rate at which it can be used is affected by numerous factors. pH alters rates of PO_4 absorption by direct effects on enzymes, membrane permeability, or by changing the degree of PO_4 ionization (Wetzel 1983). As acidity increases, the most abundant PO_4 form shifts from orthophosphate (PO_4^{3-}), the most utilized form of inorganic phosphorus, to monophosphate (HPO_4^{2-}) and dihydrogen phosphate ($H_2PO_4^-$) which are not as easily assimilated (Horne and Goldman 1994). In anoxic sediments, PO_4 ions pass between the sediment pore waters and the lake waters at a rate dependent on the concentration gradient (Wetzel 1983; Horne and Goldman 1994). In oxic conditions the phosphate ions are precipitated from the water and pass to the sediments (Horne and Goldman 1994), which can retain phosphorus and other soluble components beneath an oxidized microzone that traps and prevents their transport to the water. As the oxygen content of the water near the sediment decreases, the oxidized microzone weakens (Wetzel 1983).

When algal growth is limited by phosphorus concentrations, the photosynthesis rate is determined by the amount of PO_4. Algae have developed several ways to cope with low phosphorus levels. The first, called luxury consumption, involves the assimilation of phosphorus when levels are high and storage of that phosphorus in polyphosphate granules for later use. Luxury consumption can provide sufficient phosphorus to maintain algal growth in the epilimnion for a short time, even though external phosphorus may be low or depleted (Wetzel 1983). A second coping strategy is the production of an enzyme called alkaline phosphatase. This enzyme cleaves the bonds between PO_4 and organic molecules (Horne and Goldman 1994) making more PO_4 available for algal use. Alkaline phosphatase activity is commonly high in spring and summer during the highest phosphorus demands (Wetzel 1983). A third strategy is simply the ability to assimilate and utilize low levels of phosphorus with no additional storage or enzymes.

A significant portion of the nutrient pool in a lake is held in living biomass. During egestion, nutrients are released in the form of soluble PO_4 ions, some organic phosphorus compounds, and NH_4^+ (Wetzel 1983). Zooplankters excrete around ten percent of their body phosphorus daily, one-half as PO_4 and one-half as organic phosphorus. In eutrophic lakes where zooplankton standing crops are large, they can supply PO_4 to most of the phytoplankton (Horne and Goldman 1994).

Wetland plants and rapid decay of macrophytes facilitate PO_4 transport from sediments to open water. The uptake of phosphorus by littoral vegetation and phytoplankton can be rapid (Horne and Goldman 1994). Within twenty minutes of phosphorus enrichment plankton take up 95% of the added phosphorus. The uptake of phosphorus from the water by phytoplankton is influenced by external factors. The initial absorption of phosphorus and subsequent uptake are greater in light, especially under carbon dioxide limitation. Phosphorus absorption rates are specific to groups and species of algae, however when biologically available phosphorus is in excess, the amount of phosphorus per cell is nearly constant between species (Wetzel 1983).

Variation in TP levels between lakes is high and related to regional geology. TP levels are lowest in mountainous regions of crystalline bedrock. They increase in lowland regions derived from sedimentary rock deposits. Lakes high in organic matter, such as bogs, tend to have high TP. The phosphorus content of precipitation is generally lower over unpopulated regions, so lakes in those areas may receive less phosphorus than lakes in urban areas (Wetzel 1983).

NITROGEN

The Kodiak limnology laboratory measures three forms of nitrogen: total ammonia (TA), nitrate and nitrite ($NO_3^- + NO_2^-$), and total Kjeldahl nitrogen (TKN). TA consists of ammonia gas (NH_3) and the ammonium ion (NH_4^+). Increases in temperature and pH shift the proportion of TA from NH_4^+, the primary nitrogen source in lakes, to NH_3, which is toxic to salmonids at levels above 0.016 mg/L. Since the pH of freshwater lakes is usually between 5 and 8 units, NH_4^+ is usually present in far greater concentrations than NH_3 (Koenings et. al 1987). Nitrate (NO_3^-), the most highly oxidized and usually most abundant form of inorganic nitrogen, is the secondary nitrogen source for phytoplankton. Nitrite (NO_2^-) is an intermediary and usually has insignificant concentrations (Horne and Goldman 1994). TKN is a measurement of both the organic nitrogen and TA content of the sample, but does not include other inorganic forms of nitrogen such as NO_3^- and NO_2^-.

Although NO_3^- is normally the most common form of inorganic nitrogen in lakes, NH_4^+ is the preferred nitrogen source for plant growth. This is because NO_3^- uptake is slow relative to NH_4^+ uptake. NO_3^- must be transformed by nitrate reductase before it can be metabolized, which requires additional energy. Despite the rapid uptake of NH_4^+ by algae, small quantities persist in water because of NH_4^+ excretion by aquatic animals. These low levels of NH_4^+ are often at the limits of detection, yet many plants can assimilate it. This recycling process can occur quickly. NH_4^+ excreted by aquatic animals has been known to stimulate phytoplankton metabolism (Horne and Goldman 1994), but this NH_4^+ source is quantitatively minor in comparison to that generated by bacterial decomposition. Heterotrophic bacteria generate NH_4^+ as the primary end product of decomposition of organic matter, either directly from proteins or from other nitrogenous organic compounds (Wetzel 1983).

NH_3 dissolves readily in water and forms ammonium hydroxide (NH_4OH), which is toxic to organisms unless it dissociates to NH_4^+ and OH^-. At a neutral pH and 15°C (normal conditions for Kodiak Lakes) only 0.27 percent of TA is toxic NH_4OH and NH_3. The majority of TA is in the form of NH_4^+ (99.7%). The percent of un-ionized ammonia (NH_4OH and NH_3) increases with pH and temperature (Table 2). Ammonium hydroxide toxicity varies with pH, temperature, dissolved oxygen levels, water hardness, and animal species and age. At a pH of 6-7 and a temperature of 5-10°C, rainbow trout fry are rapidly killed by NH_4OH if the TA concentration exceeds 0.3 mg/L. Minnows and other non-salmonid fish are more tolerant and can handle as much as 10 times the NH_4OH. *Daphnia* and other aquatic invertebrates can tolerate up to 8 mg/L. Increases in ammonia toxicity can result from increased nutrient supply when higher rates of photosynthesis remove CO_2 and increase pH. Susceptibility to ammonia poisoning is also increased at night when oxygen levels are low and the biological oxygen demand, associated with decomposition of waste, exceeds oxygen production. Fortunately ammonia levels usually are below 0.1 mg/L and toxic effects of naturally occurring ammonia are uncommon (Horne and Goldman 1994).

Nitrogen cycles between compounds in gaseous, soluble, and particulate forms in oxic and anoxic conditions (Figure 3). Although nitrogen is abundant, it is mostly present as N_2 gas which few organisms can use. NO_3^- and NH_4^+, the two most useful forms of nitrogen, are not always present in large enough amounts to support growth. The concentrations of most nitrogen compounds follow regular seasonal patterns (Horne and Goldman 1994). In spring and summer, biological uptake lowers the concentrations of usable nitrogen (NH_4^+ and NO_3^-) and heating of the epilimnion during summer thermal stratification decreases N_2 concentrations. In most oligotrophic lakes, recycling is the main source of nitrogen in summer. In winter, N_2 concentrations are usually at a maximum due to increased solubility at lower temperatures. During the winter nitrogen inputs from the sediments, tributary inflows, precipitation, and replenishment from the hypolimnion increase NO_3^- and sometimes NH_4^+ levels (Wetzel 1983; Horne and Goldman 1994).

The presence or absence of oxygen plays an important role in the cycling of nitrogen. Nitrogen fixation and denitrification are the ultimate sources and sinks, respectively, of combined nitrogen available to algae. Nitrogen fixation reduces atmospheric N_2 to NH_3 or NH_4^+. Denitrification converts NO_3^- back to N_2. Both processes involve enzymes requiring anoxic conditions and can occur only when oxygen is absent. In most aquatic systems the rate of denitrification is greater than the rate of nitrogen fixation. This results in considerable loss of nitrogen from the system. A third process, nitrification, requires oxygen. Nitrification oxidizes NH_3 or NH_4^+ to NO_3^- or NO_2^- (Horne and Goldman 1994). This process occurs until concentrations of dissolved oxygen decline to about 0.3 mg/L. In acid bogs and acidic bog lakes, where the pH is five or less, nitrification is slow. Certain dissolved organic compounds, such as tannins and their decompositional derivatives also inhibit the process. In these conditions the NO_3^- produced is probably utilized as fast as it is formed so that most of the time only very low or undetectable quantities are found (Wetzel 1983).

Heterocysts are cells developed by some algae that exclude oxygen and allow nitrogen fixation to occur, even when oxygen is present in the surrounding environment. Formation of heterocysts is induced when the carbon to nitrogen ratio in the cells exceeds 8:1 (Horne and Goldman 1994) and is greatly stimulated when there is a deficiency of combined nitrogen, particularly NH_4^+. Blue-green algae (cyanobacteria) with heterocysts can satisfy their nitrogen requirements and grow, even where NO_3^- and NH_4^+ levels are low, as long as there is adequate PO_4 (Van den Hoek et. al 1995). Nitrogen fixation in the heterocyst also requires iron and molybdenum for increased respiration (Horne and Goldman 1994). Molybdenum is also required for metabolism of NO_3^- (Wetzel 1983).

Only some blue-green algae, and bacteria with the capability of nitrogen fixation, can utilize nitrogen gas. Nitrogen fixation in the open waters is light dependent. In full sunlight the rate of nitrogen fixation is often inhibited at the surface. It reaches a maximum some depth below the surface, then shows a rapid, nearly exponential decrease with greater depth (Wetzel 1983). It is also strictly correlated with the presence of cyanobacteria that possess heterocysts (Wetzel 1983; Horne and Goldman 1994). Nitrogen fixation can be a major source of new, usable nitrogen. It requires the reducing power and ATP generated by photosynthesis. The numbers of heterocysts correspond approximately to observed nitrogen-fixing capacity. As cyanobacterial populations decrease rates of nitrogen fixation decline quickly. Often there is an inverse relationship between the rate of nitrogen fixation by cyanobacteria and the amount of combined nitrogen in the water (Wetzel 1983).

Major allochthonous nitrogen sources include precipitation onto the lake surface, nitrogen fixation in water and sediments, and inputs from surface and groundwater drainage. Nitrogen can enter the lake as an organic compound, as NH_4^+ adsorbed to inorganic particulate matter, or as dissolved N_2, nitric acid, NH_3, or NO_3^- (Wetzel 1983). The concentration of available nitrogen, and its rate of supply, is intimately connected with land use practices in the watershed. Changes in vegetation, such as floods, fires, or clearing increases NO_3^- levels (Horne and Goldman 1994). A flooded river or stream will often have relatively large quantities of NH_4^+. No direct relationship has been found between the volume of rainfall or snowfall and the quantity of nitrogen influx per area of land or water. Nitrogen is lost from the lake by effluent outflow, reduction of NO_3^- to N_2 by bacterial denitrification, and permanent sedimentation loss (Wetzel 1983). It is common that more than one half of the total dissolved nitrogen found in lakes is organic nitrogen. Overall, nitrogen levels generally show no seasonal or depth variations except those resulting from temperature changes (Horne and Goldman 1994).

DISCUSSION

Nitrogen and phosphorus are the two nutrients most often limiting to algal production in lakes. The normal nitrogen to phosphorus ratio in a lake is 10:1. A higher ratio indicates a deficiency in phosphorus and a lower ratio indicates a deficiency in nitrogen (Horne and Goldman 1994). Even though NO_3^- absorption is independent of PO_4 concentrations, optimal growth of many algae requires higher PO_4 concentrations when NO_3^-, rather than NH_4^+, is the nitrogen source (Wetzel 1983). This is because it takes more energy to metabolize NO_3^- than NH_4^+ and higher levels of phosphorus to provide enough energy to do so.

There are four main reasons for phosphorus limitation. The first is that little biologically available phosphorus is released into streams and lakes from rock breakdown. A second cause of limitation is that the root zone on land intercepts and retains most of the soluble phosphorus compounds. The phosphorus cycle contains no gaseous phase; thus rainwater contains little phosphorus compared to other nutrients. Lastly, any soluble PO_4 released into the water is rapidly adsorbed onto particles or precipitated with other compounds and not readily available to algae. These causes of phosphorus limitation are not easily reversible and application of a fertilizer is likely the best way to increase phosphorus levels. It is critical to have steady phosphorus loading to sustain increased productivity (Wetzel 1983).

In watersheds with high erosion due to geologically unstable soil or absent groundcover, PO_4 sorbed to clay is carried off with silt to the lake, providing high phosphorus input (Horne and Goldman 1994). Pollution from detergents or agricultural runoff can also elevate phosphorus levels in a lake. In a lake receiving continuous phosphorus loading, reducing phosphorus inputs below phosphorus losses decreases algal growth most effectively (Wetzel 1994). A method to reduce phosphorus levels is the addition of aluminum. At a near-neutral pH, such as that of most lakes, aluminum precipitates soluble PO_4 causing it to sink to the lake bed, making it unavailable for phytoplankton growth. This makes a lake more oligotrophic. Caution must be taken when using this method because large amounts of aluminum become toxic when the pH drops below 6.2. This is due to the release of soil bound aluminum ions combined with lake acidity (Horne and Goldman 1994). Phosphorus is technologically easier to remove from water than nitrogen and it does not have major reservoirs in the atmosphere.

NH_4^+ can enter the lake from inflowing rivers, precipitation, atmospheric dust, and nitrogen fixation (Horne and Goldman 1994). It was once thought that nitrogen fixation alone could overcome a lack of NO_3^- or NH_4^+ if PO_4 levels were high, but it has become clear that the stimulation of nitrogen fixation is a more complex process. Formation of nitrogen-fixing heterocysts is induced not only when there is a deficiency of combined nitrogen in the surrounding environment (Van den Hoek et. al 1995), but when the intracellular carbon to nitrogen ratio exceeds eight to one (Horne and Goldman 1994).

Automobile exhaust in precipitation can increase NH_4^+ levels, but this is not easily manipulated. The types of plants surrounding the lake can also increase the NH_4^+ levels. For instance, alders or legumes that have nitrogen-fixing bacteria in their root nodules provide a majority of the nitrogen to nearby lakes from leaching through the soil and fallen leaves in autumn (Wetzel 1983). In rice patties, blue-green algae in a symbiotic relationship with higher plants are more effective than free-living blue-green algae of the same genus at elevating nitrogen levels (Van den Hoek et. al 1995).

Adult salmon returning to a system to spawn also supply significant amounts of nutrients to a lake (Gross et. al 1998). This input can be offset by departure of nutrients with outmigrating salmon smolt. The level of nutrients in the system from this source is determined by whether more nutrients leave the lake with smolt or return with adults.

When interpreting data from the limnology laboratory it is important to remember what each measurement means. TP is a measurement of all the phosphorus present in a lake. Most forms of phosphorus are biologically unavailable. Only FRP and OPP (Figure 1) can be used by organisms (Koenings et. al 1987). Although TP can correlate with chlorophyll *a*, this holds true only for lakes in which phosphorus is the limiting nutrient.

TFP represents all phosphorus that is dissolved in the water, or small enough to pass through the filters used. Only a fraction of TFP is biologically available as FRP, or orthophosphate.

FRP is the most common phosphate at normal pH levels (Horne and Goldman 1994). The measurement of FRP may not accurately reflect the amount of soluble PO_4 since dissolved reactive phosphorus (DRP) and colloidal reactive phosphorus (CoRP; Figure 1) can vary according to lake type (glacial, organically stained, and clear). A small fraction of the measurement may actually represent other condensed PO_4 that is hydrolyzed unavoidably in the sample processing (Koenings et. al 1987; Horne and Goldman 1994).

The ADF&G limnology laboratory in Kodiak has the ability to determine total particulate phosphorus (TPP) (OPP + IPP (inorganic particulate phosphorus)), but individual determination of OPP would require additional chemicals and equipment.

The measurement of TA determines the amount of nitrogen in the form of NH_3, which is toxic, and NH_4^+, which is the primary nitrogen source (Koenings et. al 1987). The proportion of NH_4^+ (non-toxic) to NH_3 + NH_4OH (toxic) can be estimated using a combination of pH and temperature (Table 2). NO_3^- is the secondary nitrogen source after NH_4^+.

Cadmium columns are used to measure both NO_3^- and NO_2^-. NO_2^- is a less common form and requires more energy. It can be determined separately and NO_3^- can be quantified by the difference. Since NO_2^- levels are normally insignificant, and utilization by organisms is inefficient, the combined measurement of NO_3^- + NO_2^- is usually sufficient for our purposes.

TKN measures the combination of TA and organic nitrogen. Organic nitrogen can easily be recycled to NH_4^+ by decomposition and reused (Wetzel 1983). It does not measure NO_3^- or NO_2^-.

Although N:P ratios can indicate which nutrient is limiting, the numbers alone are not conclusive. There is often a direct relationship between the concentration of the growth limiting nutrient and the maximum crop of phytoplankton, which can be estimated from chlorophyll-*a* measurements (Horne and Goldman 1994). An increase or decrease in phytoplankton growth upon experimental addition or reduction of a nutrient can tell whether or not the nutrient is limiting.

Lakes are classified as oligotrophic, mesotrophic, eutrophic, or hypereutrophic depending on their nutrient levels (Table 3). In non-polluted natural waters the TP can range from less than 1 µg/L in freshwater lakes to more than 200 mg/L in some closed, saline lakes. However, in most uncontaminated surface waters the TP levels are between 10 g/L and 50 µg/L (Wetzel 1983). The relative fertility of a lake can be reflected in the sediment samples of a lake. The soluble interstitial PO_4 in the sediment is usually between 0.06 mg/L and 10.0 mg/L, while the overlying waters usually have between 0.002 mg/L and 0.05 mg/L of soluble PO_4. Generally there are two types of oligotrophic lakes. Phosphorus or silicon limited lakes where nitrate remains constant, and nitrogen limited oligotrophic lakes where nitrate falls to almost zero. Most eutrophic lakes are nitrogen limited and the nitrate falls to almost zero, while in the majority of mesotrophic lakes nitrate levels fall, but not enough for it to become a limiting nutrient (Horne and Goldman 1994). Limnology data collected by the Alaska Department of Fish and Game from numerous lakes in the Kodiak Management Area from 1987 to 1998 (Schrof et al. 2000) suggest that these lakes are oligotrophic. For a more specific picture of what is happening to the nutrients of these lakes, each nutrient in each lake needs to be looked at individually, keeping in mind all the factors that have gone into the creation of the chemical and biological aspects of the lake.

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Table 1. Phosphorus concentrations required for algal growth (Adapted from Wetzel, 1983).

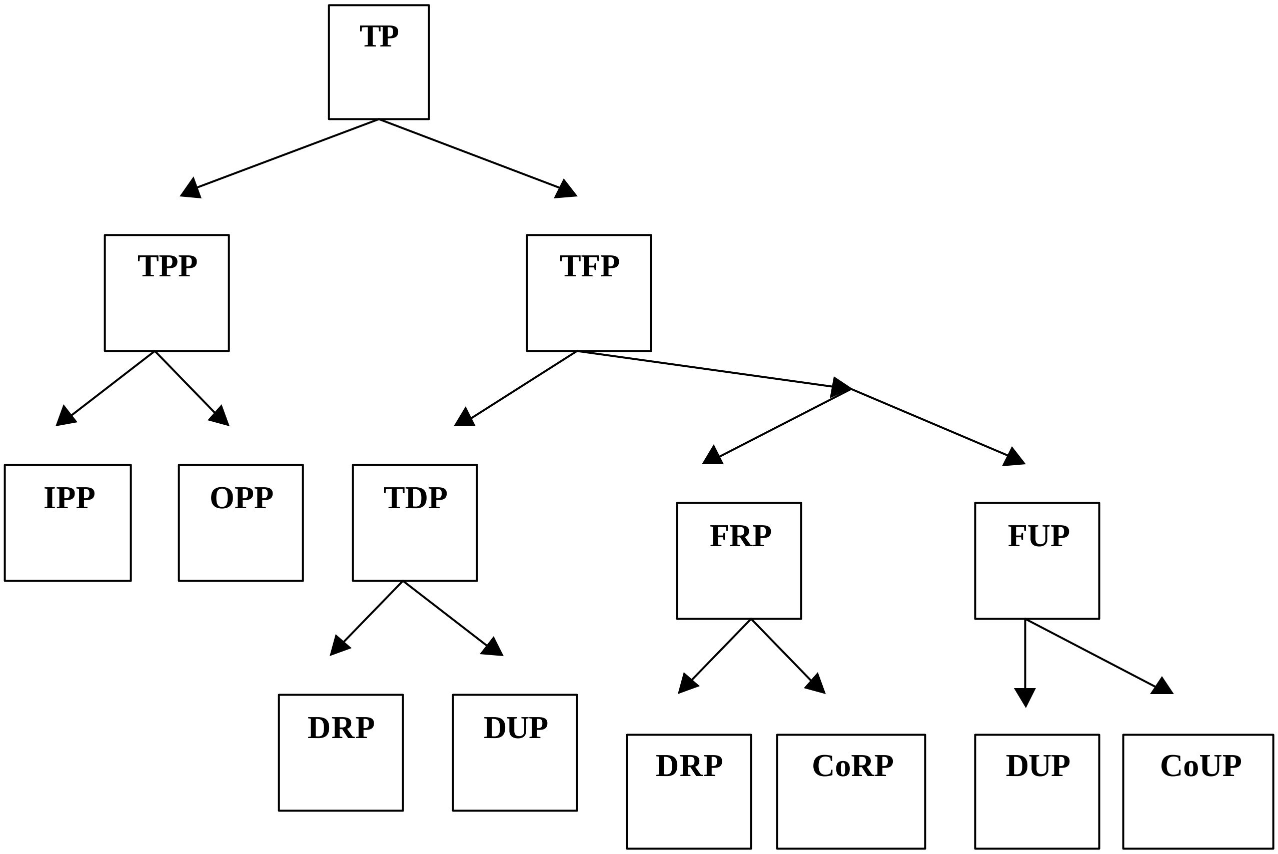
	Phosphorus levels	
Algal type	Optimum growth (µg/L P)	Upper tolerance (µg/L P)
Uroglena some *Chara* (macroalgae)	Below 20	Below 20
Asterionella Other diatoms	Below 20	Above 20
Green algae Many others	Above 20	Above 20
Tabellaria, *Fragilaria* (diatoms)	45	-
Scenedesmus (green)	500	-
Oscillatoria (blue-green)	3000	-

Table 2. Percent of un-ionized ammonia ($NH_4OH + NH_3$) in freshwater at varying pH and temperature levels (Horne and Goldman, 1994).

	Temperature °C				
pH	5	10	15	20	25
6.5	0.04	0.06	0.09	0.13	0.18
7.0	0.12	0.19	0.27	0.40	0.55
7.5	0.39	0.59	0.85	1.24	1.73
8.0	1.22	1.83	2.65	3.83	5.28
8.5	3.77	5.55	7.98	11.2	15.0
9.0	11.0	15.7	21.4	28.5	35.8

Table 3. General trophic classification of lakes and reservoirs in relation to phosphorus and nitrogen (Wetzel 1983).

	LAKE TYPES			
Parameter (annual mean values)	**OLIGOTROPHIC**	**MESOTROPHIC**	**EUTROPHIC**	**HYPEREUTROPHIC**
Total Phosphorus (µg/L)				
Mean	8.0	26.7	84.4	-
Range	3.0-17.7	10.9-95.6	16-386	750-1,200
N	21	19	71	2
Total Nitrogen (µg/L)				
Mean	661	753	1,875	-
Range	307-1,630	361-1,387	393-6,100	-
N	11	8	37	-
Chlorophyll a (µg/L) Of phytoplankton				
Mean	1.7	4.7	14.3	-
Range	0.3-4.5	3-11	3-78	100-150
N	22	16	70	2
Chlorophyll a peaks (µg/L) ("worst case")				
Mean	4.2	16.1	42.6	-
Range	1.3-10.6	4.9-49.5	9.5-275	-
N	16	12	46	-
Secchi transparency depth (m)				
Mean	9.9	4.2	2.45	-
Range	5.4-28.3	1.5-8.1	0.8-7.0	0.4-0.5
N	13	20	70	2



TP= total P
TPP= total particulate P
TFP= total filterable P
IPP= inorganic particulate P
OPP= organic particulate P
TDP= total dissolved P

FRP= filterable reactive P
FUP= filterable unreactive P
DRP= dissolved reactive P
DUP= dissolved unreactive P
CoRP= colloidal reactive P
CoUP= colloidal unreactive P

Figure 1. Phosphorus fractions comprising the total phosphorus (TP) in natural lake waters (Koenings et al. 1987).

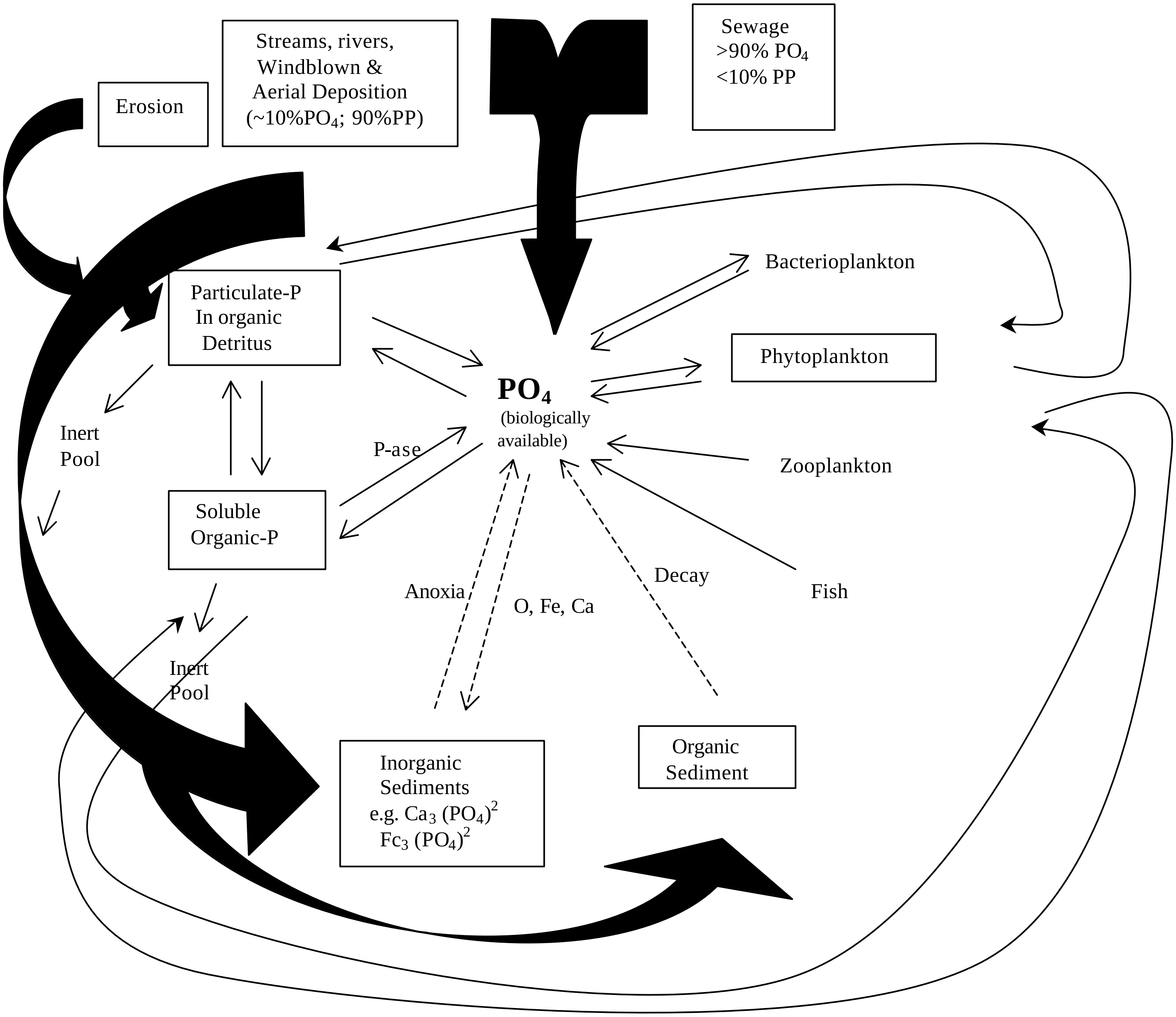
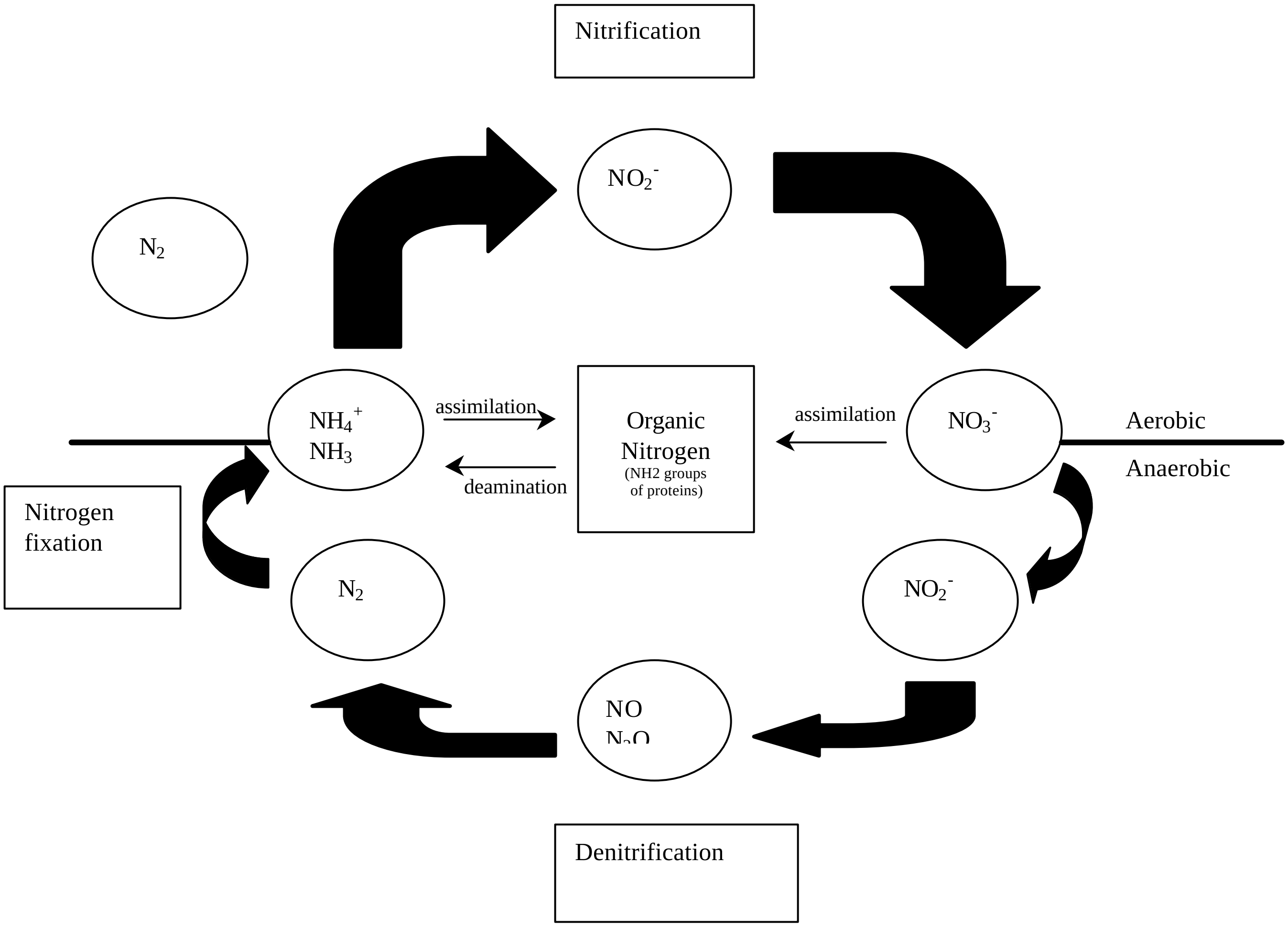


Figure 2. The phosphorus cycle in lakes. [Heavy lines indicate external loading; dashed lines internal loading; other lines internal recycling] (Horne and Goldman 1994).



NH_3 : ammonia gas
NH_4^+ : ammonium ion
N_2 : nitrogen gas
NO : nitrous oxide
NO_2^- : nitrite
NO_3^- : nitrate

Figure 3. The generalized nitrogen cycle.

APPENDIX

Appendix A. Definition of terms.

Allochthonous:	from an external source
Anoxic:	no oxygen present
Decomposition:	the bacterial process of breaking down dead organic matter
	$\text{Organic N} \longrightarrow \text{organic N} + NH_4^+$
Denitrification:	the process by which nitrates are reduced to nitrous oxide or nitrogen gas
	$\text{Reduced C} + NO_3^- \longrightarrow \text{oxidized C} + (NO_2^- \text{ or } N_2O \text{ or } N_2)$
Epilimnion:	a warmer, less dense upper layer of water in a lake
Eutrophic:	nutrient rich with abundant algal growth and limited oxygen
Heterocyst:	a type of cyanobacterial cell in which oxygen is excluded and nitrogen fixation can take place
Hypolimnion:	a cooler, lower layer of water in a lake
Limnology:	the study of inland waters
Littoral:	the portion of a lake from shore to the depth where well mixed, warm surface waters still reach the lake bed in summer
Metalimnion:	a dense middle layer of water in a lake that contains the thermocline and separates the hypolimnion and epilimnion
Nitrification:	the process by which ammonia or ammonium ions are oxidized to nitrites or nitrates
	$NH_4^+ + O_2 \longrightarrow NO_2^- \qquad NO_2^- + O_2 \longrightarrow NO_3^-$
Nitrogen fixation:	the reduction of atmospheric nitrogen gas to ammonia
	$N_2 + H \longrightarrow 2NH_3 + H_2 \text{ and } NH_4^+$
Oligotrophic:	nutrient poor with little algal growth and low productivity
Oxic:	oxygen available
Thermocline:	the region in a lake where temperatures change rapidly