ZOO401 Limnology

Diversity of aquatic ecosystems, Comparison of fresh, brackish and marine ecosystems. Unusual and extreme habitats, hydrology, physiography and physical properties like temperature, light, turbidity, currents, density, their interactions and relations with aquatic life. Chemical properties like dissolved oxygen, carbon dioxide, pH, alkalinity, hardness, inorganic and organic substances, their distribution, dynamics and influence on aquatic ecosystem. Status and forms of nutrients like nitrogen, sulphur, phosphorus and carbon in natural waters; nutrients use and remineralization with special reference to processes controlling the levels of nitrogen, phosphorus and sulpher in aquatic ecosystem. Stichiometry of autographs and heterotrophs; concepts of trophic state, aquatic productivity & eutrophication. Managing eutrophication in freshwater habitats. Biodiversity of fresh waters. Ecological classification of aquatic biota. Limnological importance of biota. Adaptations and characteristics of aquatic life. Quantitative and qualitative changes in spatial and temporal distribution of aquatic biota.

Textbook: Wetzel, R.G. 2001. Limnology: Lake and River Ecosystems, Third Edition. Academic Press

Course Notes

Lecture 1 - Introduction

I. Introduction; Syllabus Review/Background

II. What is limnology and why study it?
- A. Limnology – study of inland waters
  1. Standing waters – lentic
  2. Flowing waters – lotic
- B. Interdisciplinary science -- geology, chemistry, physics, biology
- C. Greater diversity of freshwater systems than of oceans
  1. Size
  2. Origin
  3. Temperature
  4. Age
  5. Color

6. Chemistry
7. Biology is often determined by the rest of the limnological parameters

D. Water distribution (Table 1-1, Wetzel)

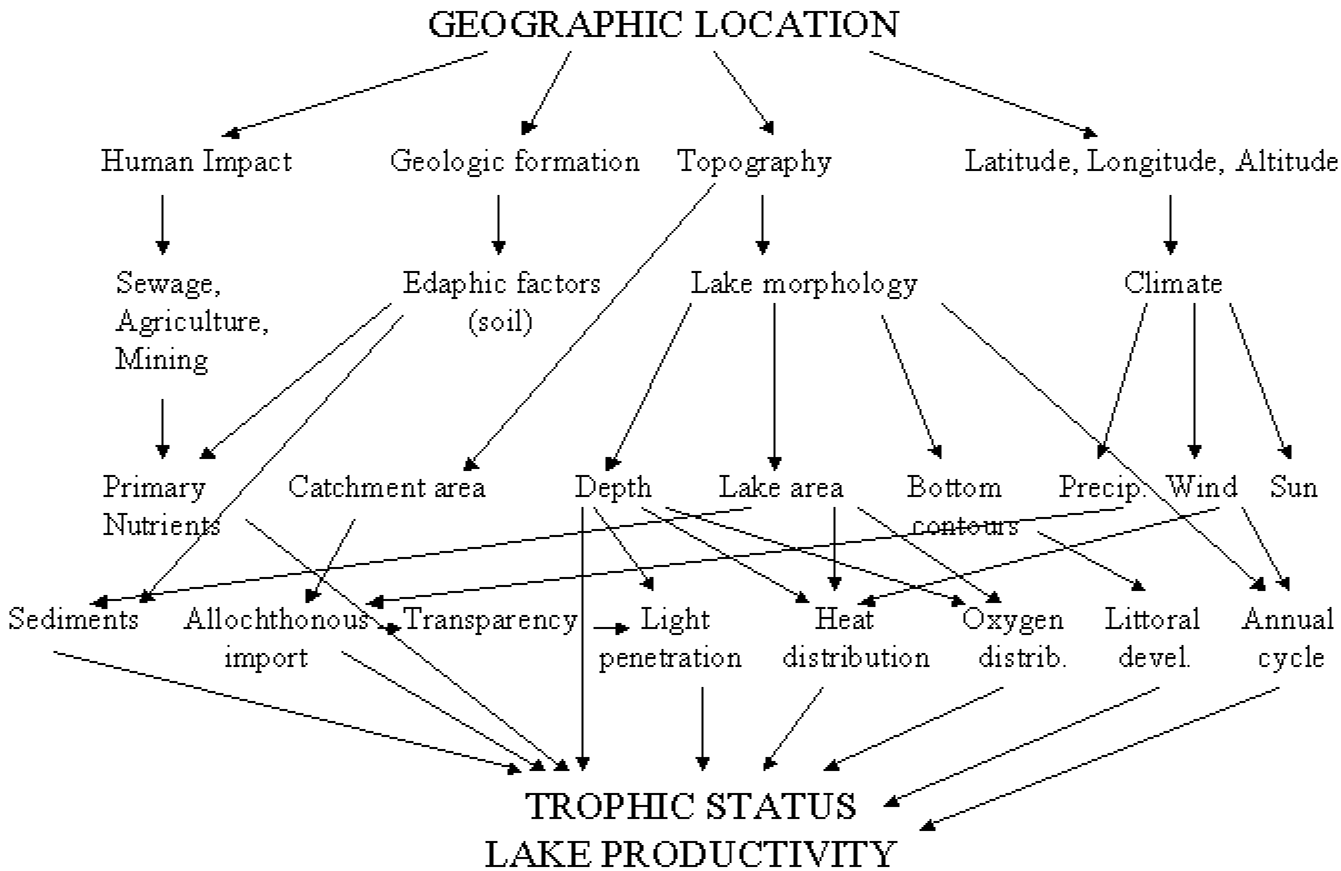
Water in the Biosphere

From Table 1-1 in Wetzel	Volume (Thousands of km^3)	% of Total	Renewal Time
Oceans	1,370,000.0	97.61000	3100 y
Glaciers	29,000.0	2.08000	16,000 y
Groundwater	4,000.0	0.29000	300 y
Freshwater lakes	125.0	0.00900	1-100 y
Saline lakes	104.0	0.00800	10-1000 y
Soil moisture	67.0	0.00500	280 d
Rivers	1.2	0.00009	12-20 d
Atmosphere	14.0	0.00090	9 d

E. Water usage

F. Environmental Problems -- e.g., acid rain, pollution, eutrophication, climate change, exotic species...

G. Lake systems are a web of interconnected processes



Interaction of factors that influence the biota (from Rawson 1939, Cole 1983)

H. Lakes are good places to study ecology
1. easier boundaries
2. easy to sample
3. shorter-lived organisms
4. field experiments easier to perform than in oceans

III. History of Limnology (don't worry about the names!)

A. F.A. Forel, "Father of Limnology"
1. Lac Leman (Lake Geneva) -- began biological studies
2. Influenced by oceanography

B. S.A. Forbes, Illinois Natural History Survey (1887)
1. "Lake as a Microcosm"
2. Beginnings of ecosystem ecology

C. US -- Birge and Juday -- Wisconsin school of limnologists
1. sampled many lakes -- comparative approach
2. 'the data will speak' versus hypothesis testing

D. Europe -- Thienemann and Naumann
1. Lake classification
2. Continuation of ecosystem ecology

E. G.E. Hutchinson
1. Treatise of Limnology (1957 first volume)
2. theories and processes; modeling
3. influential in founding modern ecological thought
4. fight between Wisconsin school and Hutchinson

F. Current -- integration of research on lakes, streams, rivers and their watersheds --

ecosystem approaches; human influences on freshwater systems

IV. Limnology and the development of Ecology
A. Standing crop, biomass, productivity
1. 'Dynamical ecology'
2. Not just what's there, but how fast it's growing
B. Ecosystem Ecology
C. Paleoecology
D. Trophic dynamics (Lindeman) -- Food webs and energy flow

Origin of Lakes

I. General background
A. There are a few large lakes, but ponds dominate numerically (85%)
B. **Lake districts**

C. Necessity of positive water balance

Precipitation + Inflow > Evaporation + Outflow

C. Processes in lake formation
1. **Constructive**
2. **Destructive**
3. **Obstructive**

D. Significance of lake formation

1. Hydrology
    Including **renewal time**

2. Basin shape
3. Chemistry
4. Trophic state
    a. **eutrophic**
    b. **mesotrophic**
    c. **oligotrophic**
    d. **dystrophic**
5. Paleolimnology
6. Endemic species
    relict lakes
        Lake Baikal, Russia
        Lake Tanganyika, Tanzania

<u>TYPES OF LAKES</u>

1. TECTONIC BASINS

A. **New land lakes**
  1. uplifting of marine sediments
  2. often large and shallow
      Lake Okeechobee, Florida

B. **Structural basins**
  1. **Grabens**
    a. lake in a downfaulted depression
    b. often long, narrow and deep

    Lake Baikal, Lake Tanganyika, Lake Tahoe, Pyramid Lake (Nevada), Lake Ohrid (Yugoslavia), Dead Sea, Lake Kinneret (Sea of Galilee)

  2. **Tilted fault blocks**
    a. Fault on only one side

        Abert Lake, Oregon

  3. **Reverse drainage basins**
    a. Uplifting forms a dam
    b. Dendritic lake

    Lake Kioga, Uganda

4. **Upwarping**
    a. Uplifting around entire basin
    b. Large but fairly shallow lake

Lake Victoria, East Africa

5. **Subsidence**
Local depression due to earthquakes

New Madrid Quakes, Reelfoot Lake

2. LAKES ASSOCIATED WITH **VOLCANIC** ACTIVITY
A. **Craters** in cinder cones

B. **Calderas**
1. collapsed or exploded volcanoes
2. surrounded by rim of lava; deep
3. oligotrophic

Crater Lake, OR (608 m deep)
Tagus Lake, Galapagos

C. **Maars**
1. explosion craters
2. often small, round and not as deep as calderas

Eifel lake district (Black Forest of Germany)

D. **Lava flow lakes**
collapsed lava flow cavern

E. **Volcanic damming**
lava or ash dams a stream

Lake Kivu, central Africa

3. LAKES FORMED BY **LANDSLIDES**
· landslides block a river or stream
· often short-lived lakes

Quake Lake, Yellowstone

4. LAKES FORMED BY **WIND**

A. **deflation basins**

1. **pan lakes** (animals remove cover and trample; wind blows away dirt)
2. **playas** (wind erosion in arid basins)
3. often shallow and large

B. sand dune lakes

5. LAKES FORMED BY **RIVERS**

A. **plunge pools**

includes basins of old waterfalls in now dry river systems

Falls Lake, WA (from ice break on glacial Lake Missoula in Grand Coulee region of WA)

B. **oxbow lakes**

1. bends in river that become isolated
2. shallow and oddly shaped
3. often interesting organisms in these lakes

C. **floodplain** or **varzea** lakes

1. some are in depressions in the flood plain area
2. some are due to sediments deposited across mouths of inflowing streams

6. LAKES FORMED BY **GLACIERS** AND **ICE**

A. Existing glaciers or ice

1. pockets of meltwater on the surface of or below glaciers
2. lakes at the front of a receding glacier
   a. irregularly shaped
   b. silty
3. glacier dams a valley
4. **permafrost lakes** (cryogenic lakes)

B. Past glaciers

1. **fjords**
   a. glacially deepened valley or fault adjoining the sea
   b. may be isolated from the sea
   c. may be dammed

2. glacial carved basins
   a. **ice scour lakes** (piedmont lakes)

(1) often on originally flat rock (not in mountains)
(2) lake basin on rock – may have poor drainage

many Canadian lakes (including Great Slave Lake)
Laurentian Great Lakes (scour and rebound)

b. **cirque lakes**
(1) common on formerly glaciated mountains
(2) small, round, steep sided (amphitheater-shaped)
(3) small drainage area
(4) reduced number of species
(5) **paternoster lakes** – series of cirques down a hill

3. **moraine lakes**
a. material pushed by glaciers leaves dams of rock and dirt as the glacier retreats

Finger Lakes
Lake Mendota, WI

4. **kettle lakes**
a. depressions in glacial till
b. sometimes due to melting ice block, sometimes irregularities in the moraine
c. irregularly shaped

Walden Pond
Linsley Pond

7. SOLUTION LAKES
A. Formed by dissolution of soluble rock (often limestone) by percolating water

e.g., $CaCO_3 + CO_2 + H_2O \longleftrightarrow Ca^{2+} + 2HCO_3^-$

B. Areas with numerous solution lakes are known as **'Karst topography'**
C. **sink holes** – may form quickly and be short-lived (dolines)
D. cave ponds and mound springs - often have strange and unique biota

8. LAKES ASSOCIATED WITH **SHORELINES** on shores of oceans and large lakes
A. **deltaic lakes** – sedimentation as river currents slow when they enter a large lake

or the ocean – may isolate lakes on deltas

B. **coastal lake --** movement of sand in spits and bars may enclose basins

9. LAKES FORMED BY **METEOR IMPACT**

A. Can be very large

B. Perfectly round

Chubb Crater, Canada; 3.4 km diameter; 1.4 million years old

10. BIOGENIC LAKES

A. buffalo wallows

B. beaver ponds

C. coral reefs

D. bog lakes

E. HUMAN MADE LAKES

1. dams -- >40,000 reservoirs with dams over 15 m high; 60,000 with >0.1 km3 surface area;
10% of the volume of natural lakes
2. borrow pits
3. surface mine lakes
4. bomb craters

LAKE MORPHOMETRY AND ZONATION

I. Morphology of Lakes

A. **Bathymetric** maps

contour lines = **isobaths** (iso-equal; bathy-depth)

surveying and sonar

B. **Morphometry**

1. Maximum depth = z_m
2. Maximum length = l
3. Maximum width = b
   at right angles to the maximum length line
4. Area
   A_0 - surface area
   A_z - area of contour at depth z

5. Volume

V = volume of the whole lake

V_z = volume below depth z

6. Mean depth $\bar{z}$

7. Relative depth

ratio of maximum depth (z) to the mean diameter of the lake at the surface, expressed as a percentage

8. Shoreline development.

L = length of shore line

9. **Hypsographic** curve

area at each depth – m^2 or %

can use to calculate the volume

10. Depth-Volume curve

volume at each depth – m^3 or %

sediment water interactions

II. Lake and Stream Zonation -- See page 132 of Wetzel

A. Lakes

1. **Epilittoral -**
2. **Supralittoral -**
3. **Littoral -** extends from the seasonal high water level down to where the vegetation doesn't grow due to a lack of light

eulittoral

upper littoral

middle littoral

lower littoral

4. **Littoral-Profundal -** no higher plants (can be algae)
5. **Profundal -** sediment free of vegetation; low light
6. **Pelagic** - open water

a. **trophogenic (euphotic) -** enough light for production > respiration

b. **tropholytic -** darker – respiration > production

B. Streams

1. **Eucrenon -** the origin of the stream
2. **Hypocrenon**

3. **Rithron** - stony stream zone
4. **Potamon** - lower energy part of the stream - river
5. **Riparian zone**
5. Drainage classification
   stream orders

C. Biological groups associated with zones (lakes only)

1. **Pelagic**
   a. **Seston** - all particulate matter in the open water
      (1) bioseston -- the living component
      (2) tripton -- non living seston = <u>detritus</u>
   b. **Nekton** - can swim against currents
   c. **Plankton** - movement influenced by turbulence
      (1) **euplankton** - spend whole life cycle in open water
         (a) **bacterioplankton**
         (b) **phytoplankton**

         (c) **zooplankton**
      (2) **meroplankton** - periodically enter the plankton, but can't spend their whole life cycle there
      (3) **pseudoplankton** - organisms that don't really live in pelagic, but are swept there accidentally
2. **Benthos** - organisms that live on the sediment water interface
   a. Phytobenthos - 'macrophytes' higher plants; algae
   b. Zoobenthos
3. Other
   a. **Pleuston** - at the air-water interface
   b. **Neuston** - microscopic pleuston
   c. **Periphyton** - plants (and bacteria) that live on the substrates
      (1) **epiphytic**
      (2) **epipelic**
      (3) **epilithic**
      (4) **epipsammic**
   d. **Psammon** - interstitial fauna -- they live between sediment grains

BONUS QUESTION OF THE WEEK (Due *at beginning of class* 3 Sept. 2003):

Name a lake formation type that often has very irregularly shaped basins. Would you predict that lakes of this type tend to be eutrophic or oligotrophic? (Say which and describe why in one or two sentences)

Hydrologic Cycle

I. Global Hydrologic Cycle
  A. Pools
    1. Atmosphere
    2. Oceans
    3. Ice
    4. Groundwater and soil moisture
      i. **Infiltration capacity**
      ii. **Water table**
      iii. **Vadose water** or **soil moisture**
      iv. **Groundwater**

    5. Lakes
    6. Rivers

  B. Fluxes
    1. Evaporation
    2. Evapotranspiration (plants)
    3. Precipitation
    4. Runoff –
      i. often seasonal patterns
      ii. **Overland flow**
      iii. subsurface stormflow
      iv. stream hydrographs
        a. baseflow
        b. **discharge** – volume passing through the cross-sectional area of a stream or river per unit time

        c. rising limb
        d. peak
        e. falling limb

        f. variability
        f. effects of clearcutting and landuse

      v. 10 largest rivers = 40% of world's runoff

  C. Water in the Biosphere (Table 1-1, Wetzel)

Water in the Biosphere

From Table 1-1 in Wetzel	Volume (Thousands of km^3)	% of Total	Renewal Time
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Rivers	1.2	0.00009	12-20 d
Atmosphere	14.0	0.00090	9 d

renewal time = residence time

D. Hydrologic Cycle diagram (see Figure 4-1, Wetzel)

II. Global distribution of water

A. Global weather patterns

1. Hot air rises and then cools, causing precipitation
2. Rain at tropics
3. Deserts at ‘horse latitudes’
4. Rain in temperate areas

B. Effects of mountains near the sea

1. Moist air rises at mountain and cools
2. Lots of precipitation on windward side of mountain
3. Dry air on lee side of mountain

4. Example of state of Washington precipitation patterns
5. Global precipitation patterns – result of weather patterns and mountain ranges

C. 3 regions on earth in terms of water balance:

1. **exorheic --**

2. **endorheic** –

3. **arheic** –

III. Lake Water Balance

A. Closed versus open lake systems

1. **closed** –
2. **open** –
   - i. drainage
   - ii. seepage

B. Water balance

1. Inputs
   - a) Runoff from watershed
   - b) Precipitation directly on lake surface
   - c) Groundwater inputs – seepage or springs

2. Outputs
   - a) Drainage from outlet (stream)
   - b) Evaporation and evapotranspiration
   - c) Seepage through floor of lake

<> C. Modeling control by rainfall and evaporation

Simple equation balancing precipitation and evaporation on lake and catchment, and outflow from lake to yield water level change

$$A_L D_z = A_L (P_L - E_L) + (A_C - A_L) (P_C - E_C) - (A_L) (O)$$

where:

D_z = change in depth of the lake
A_L = Area of the lake
A_C = Area of the catchment
P_L = Precipitation on the lake
P_C = Precipitation on the catchment
E_L = Evaporation from the lake
E_C = Evaporation from the catchment
O = outflow per unit lake area

e.g., when Dz increases, then

$$(P_L - E_L) + \frac{(A_C - A_L)}{A_L} (P_C - E_C) - O > 0$$

This blue term is key. If A_L is greater than 1/2 A_C, then the value of the blue term is less than 1,
and the catchment watershed becomes less important

– Importance of basin shape and watershed size

IV. Human Impacts on the Hydrologic Cycle
- A. Irrigation, industrial and domestic use of groundwater
- B. Human increases in evaporation (reservoirs, irrigation) –
  humans account for 3-10% of continental evaporation today;
  projected 50% in 100 years
- C. Discharge amount and seasonality of rivers
  1. land use
  2. water projects
- D. Aral Sea example

Light in Lakes

LIGHT IN LAKES

I. Why study light in lakes?
- A. Drives photosynthesis and lake metabolism
- B. Affects thermal structure
- C. Regulates biota
- D. Can damage biota

II. Electromagnetic spectrum

A. Background
SEE FIGURE 5-1, WETZEL

1. **photosynthetically active radiation**
2. **Insolation** – solar radiation
3. **Radiant flux** – quantity of electromagnetic energy flow over time (quanta/sec)
4. **Irradiance** – all wavelengths of light; intensity of radiant flux; flux per unit of surface area (quanta x sec^{-1} m^{-2})
5. Wavelengths and energy (note, not all symbols display accurately on all

browsers -- double check equations from notes printed off the web)

$E = h\nu$ (Planck's Law)

h = Planck's constant = 6.63 X 10-34 J s

ν = frequency (cycles per sec)

Wavelength, $\lambda = c/\nu$

c = speed of light (3×10^8 m s^{-1})

Therefore $E=hc/\lambda$ so photons have less energy at longer wavelengths

B. Dual nature of light

1. **Energy** – heat flux
   energy/time/area
   e.g., cal/min/cm^2 or Joules/min/cm^2
2. **Particle** – biochemical processes
   Photons (quanta)
   1 mol photons = 1 Einstein

C. **Solar constant**

Amount of radiation reaching the earth's outer atmosphere

~1.94 cal/cm^2/min (or 1353 W m^{-2}) reaches earth

Most common ('maximum') wavelength is ~480 nm

III. Intensity and Quality of Light

A. Factors affecting light intensity and quality

1. Latitude
2. Solar angle (time of day and season)
3. Altitude
4. Atmospheric transparency – haze, smoke, particles
5. Cloud cover

B. Processes affecting light intensity and quality

1. **Scattering**
   a. Atmosphere and water
   b. Dependent on wavelength (for small particles it is proportional to $1/\lambda^4$)
   c. Selective scattering of short wavelengths
   d. Decrease of UV bands (200-400 nm)

   e. <u>Rayleigh</u> – scattering due to small molecules (why sky is blue)
   f. <u>Mie</u> – scattering due to dust (forward scattering preferentially)

2. **Refraction** – speed of light changes in different substances

a. Speed of light changes in medium (generally cited speed is for a vacuum)

b. This causes the angle of light to change when it enters a new media, based on the refractive index

c. $\dfrac{\sin(\text{angle})_{air}}{\sin(\text{angle})_{water}} = \dfrac{n_{water}}{n_{air}} = \dfrac{(1.33)}{(1.00028)}$

d. Refractive index is affected by temperature, salt content

e. Net effect is to move the angle closer to vertical in the water

3. **Reflection**
   a. angle of light
   b. wave height and foam
   c. ice and snow

4. **Absorption**
   a. decrease of light energy by transformation to heat
   b. atmospheric gases, O_2, O_3, H_2O
   c. water itself

5. Attenuation of light in the water column – due to absorption and scattering

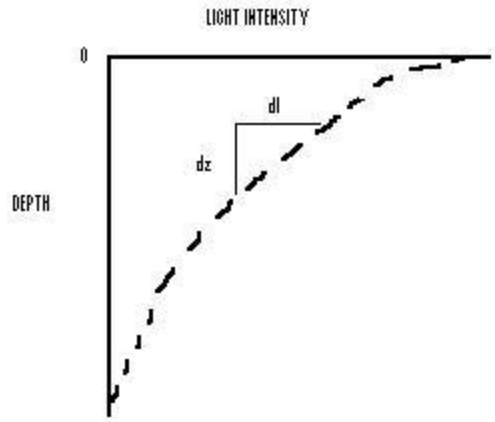
   a. **Transmittance** (amount of light left) = $I_z / I_0 \times 100$
   where I = irradiance,
   I_0 = irradiance just below surface
   I_z = irrad. at depth z

   b. **Absorbance** $[100 \times (I_0 - I_z)]/I_0$

   c. Attenuation equation

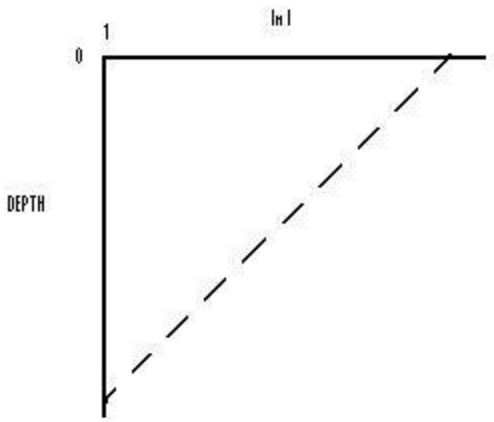
   i. $I_z = I_0 e^{-kz}$
   where e = natural logarithm
   k = attenuation coefficient (extinction coefficient; use η in Wetzel)

   ii. characteristic for each water body and each wavelength



iii. often converted to a linear plot by taking the log of both sides:

$\ln I_z = \ln I_0 - kz$



d. components of the attenuation/extinction coefficient

$K_\lambda = K_{abs} + K_{scattering}$
$K = K_{water} + K_{dissolved\ organics} + K_{particulates}$

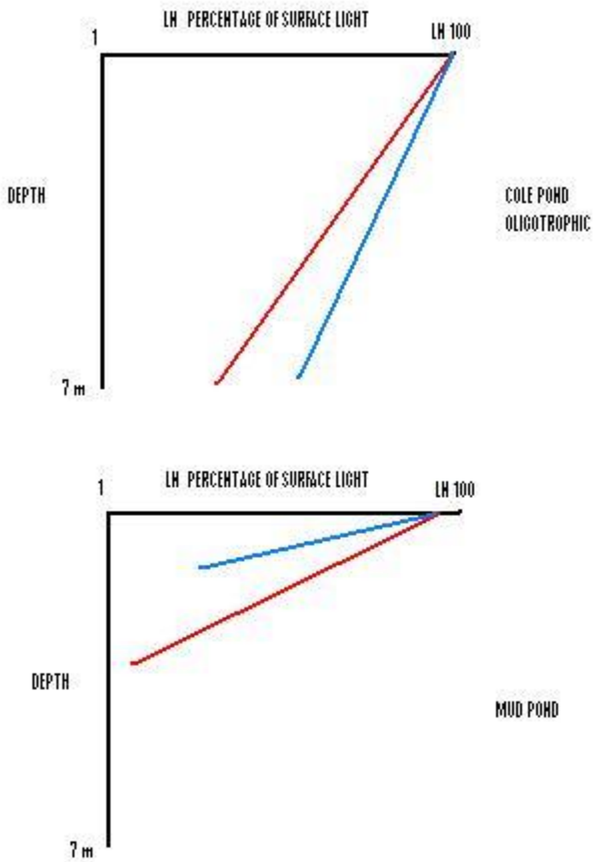
1) **K_{water}**
- for pure water, absorption at long wavelengths dominates (>550 nm; red and IR)
- So, IR disappears in the top 1-2 m of most lakes
- Scattering at short wavelengths, <380 nm
- Pure water does not absorb UV (only scatters it)
- Dissolved salts do not increase attenuation

2) **$K_{dissolved\ organics}$**
- dissolved organics "Gelbstoff" -- humic and fulvic acids
- absorb strongly at short wavelengths -- blues and UV's (<500 nm)

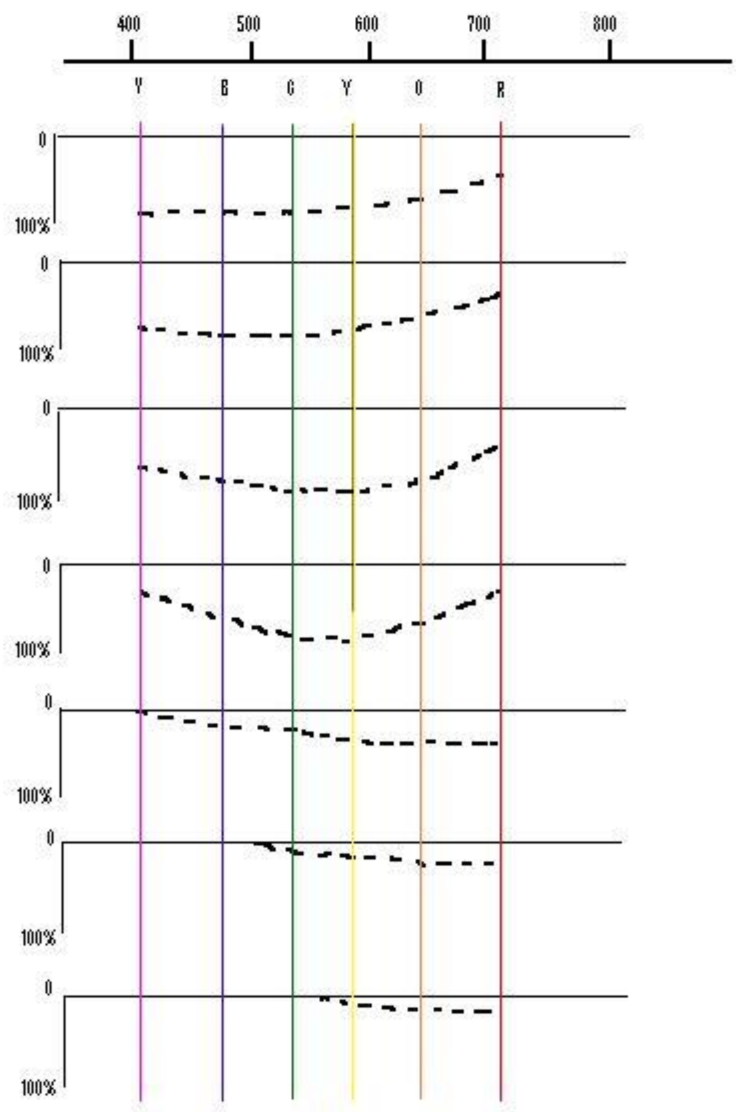
3) **$K_{particulates}$**
- absorbs light evenly over the entire spectrum

- often the particulates are predominantly tripton and phytoplankton
-detritus may have higher absorbance at the blue end

4) Examples from various natural lakes with different amounts of dissolved substances



Modified from Kilham and Likens (1968)



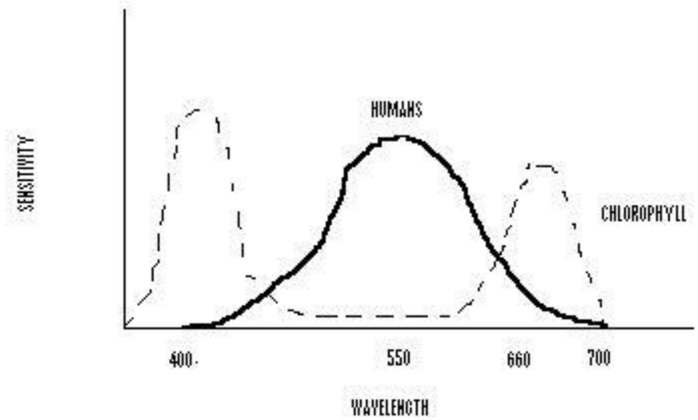
IV. Other interesting facts about light in lakes

A. Measurement of light

1. **Secchi disc**

- Visual contrast between light reflected off the disc and all other upwelling irradiance, so it is independent of surface light intensity
- Has been used to predict chlorophyll a (within lake measurements)
- Good way to communicate light penetration information to non-scientists

B. Old measures - lumens



C. Complications

Lagged attenuation coefficients

Interested in Light in Aquatic Systems? A good additional reference is:

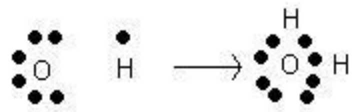
Kirk, J.T.O. 1994. *Light and photosynthesis in aquatic systems.* 2nd edition. Cambridge University Press

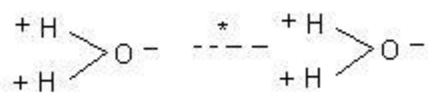
Thermal Stratification

I. Properties of Water

A. Bonding -- dipole moment

high dipole moment; electrons associate with O with a higher probability than with H





H-O-H angle is 104.5 degrees
hydrogen bonds

good **solvent** for salts and polar organic molecules

B. Characteristics of water

1. **specific heat**
   - capacity to absorb thermal energy per unit change in temperature
   - water takes 1 cal/g to raise the temperature 1 degree C

2. **latent heat of vaporization**
- amount of thermal energy needed to change from water to gas
- for water this is 540 cal/g
- for heat of sublimation (ice to gas) is 679 cal/g

3. **latent heat of fusion**
- amount of thermal energy needed to be removed to change 1 g. of material from liquid (water) to solid (ice)
- for water this is79.7 cal/g

So these attributes make water a **good thermal buffer**

4. density – See Figure 2-3 in Wetzel

- Density = rho = ρ□= g x cm^{-3}
- Temperature of maximum density is 3.98 degrees C
- Ice lattice has more space and so ice less dense
- Density vs. temperature - nonlinear

Density-temperature relationship is affected by:

a) dissolved salts -- increased density with increasing salts

b) particulates

c) dissolved gases

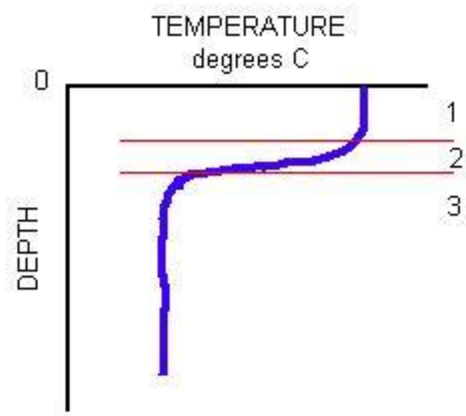
d) pressure -- increase of pressure decreases the temperature of maximum density.

5. **Viscosity** – water is 775 times density of air and more viscous; [viscosity decreases as temperature increases]

6. Surface tension high

II. Thermal Stratification

A. Layering



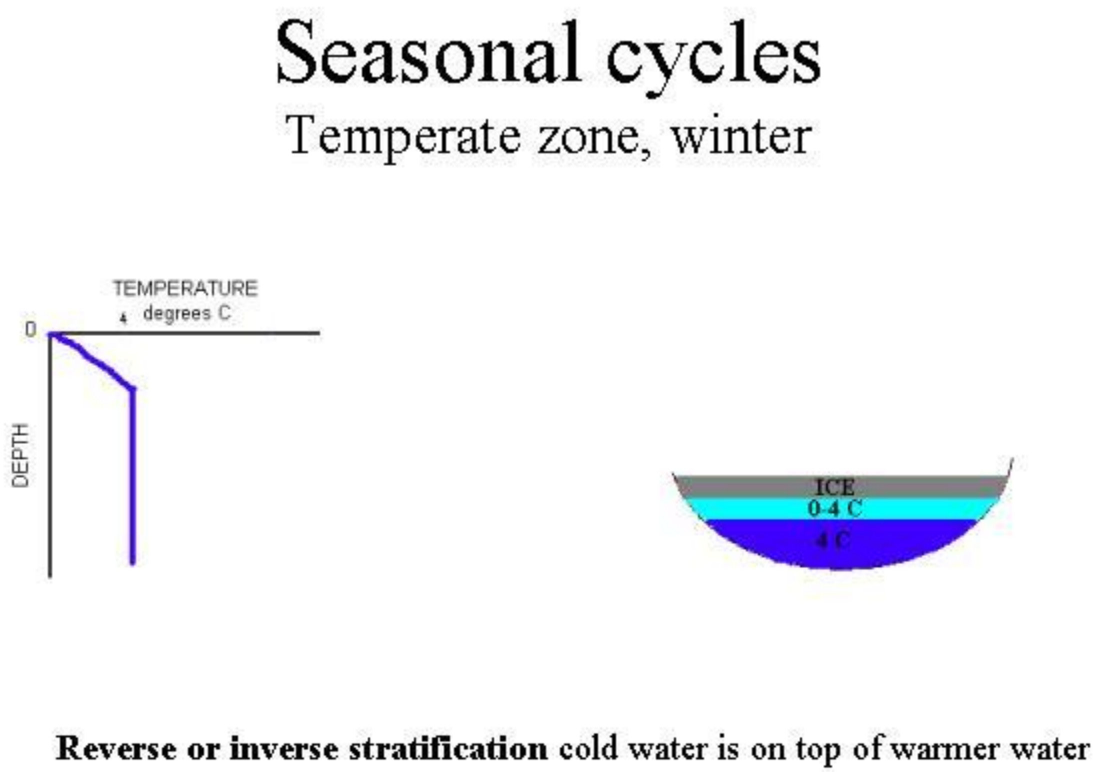
1. **epilimnion** -- upper mixed layer -- warmer water (less dense)

2. **metalimnion** -- middle layer -- where temperature changes
   - **thermocline** is the <u>plane</u> where dT/dz is maximum

3. **hypolimnion** -- lower layer -- cooler water (more dense)

HOW ARE THESE LAYERS FORMED?

B. Seasonal cycles for a temperate lake
   1. winter

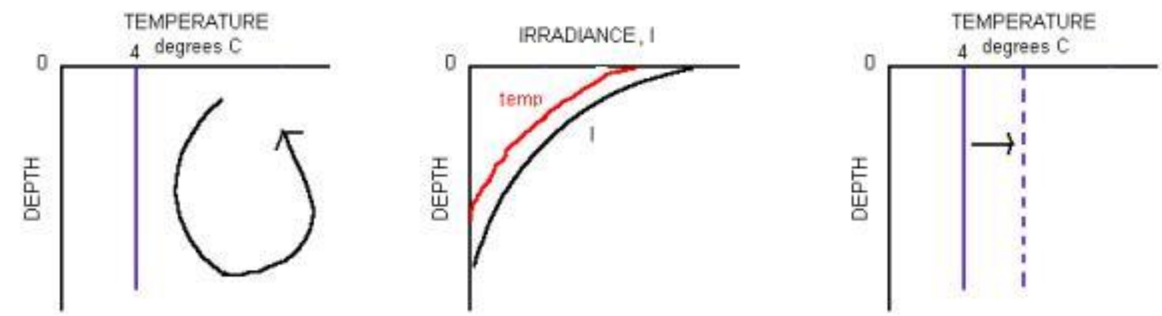


reverse stratification or **inverse stratification** cold water is on top of warmer water

2. early spring
spring turnover or overturn

Seasonal cycles

Temperate zone, early spring



Isothermal
spring overturn or
turnover

Energy from light

Isothermal warming

Mixing determines pattern of ion and gas transport
Can mix organisms (meroplankton) and resting eggs

Isothermal

3. late spring –
incipient stratification

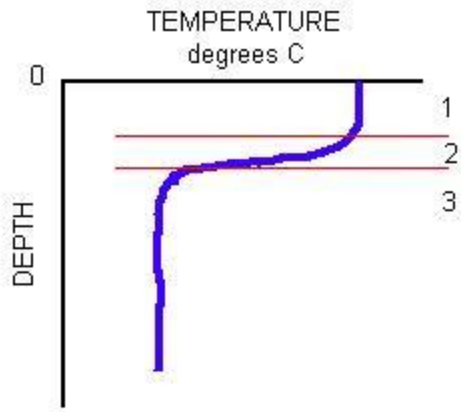
Seasonal cycles

Temperate zone, late spring

Incipient stratification heat input and thermal resistance to mixing become greater than the wind energy
Resistance to mixing is proportional to $d\rho/dz$

Resistance to mixing proportional to $d(\rho)/dz$

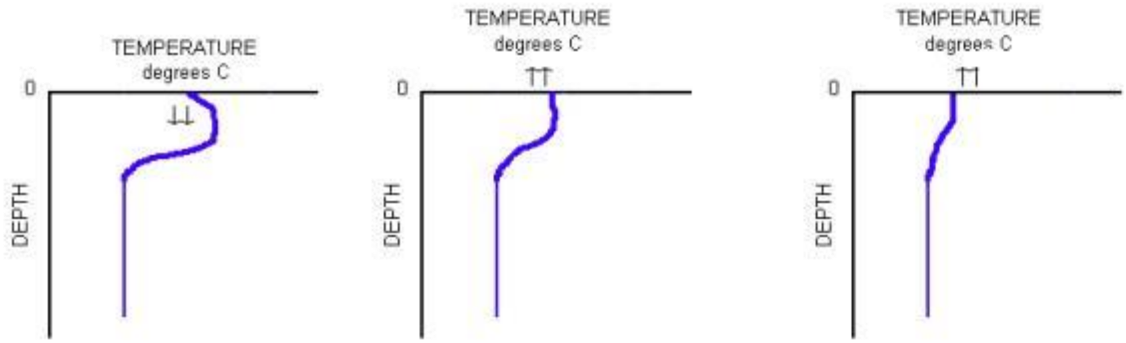
4. early to mid-summer
   summer stratification



Why is hypolimnion temperature in summer often more than 4 degrees C?

5. early fall

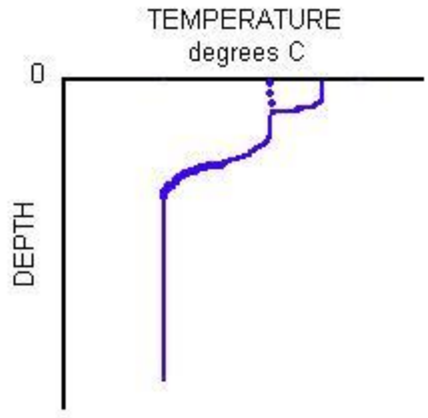
Seasonal cycles
Temperate zone, fall



6. fall overturn

7. return to winter and inverse stratification

8. complex summer temperature profiles

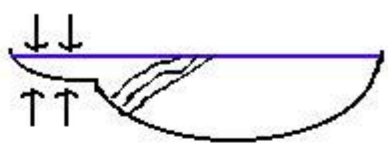


C. Factors affecting the mixing cycle

1. morphology

fetch

thermal bars -- in a large lake with shallow water nearshore, the shallow area will warm faster



2. geography

3. water clarity

4. weather

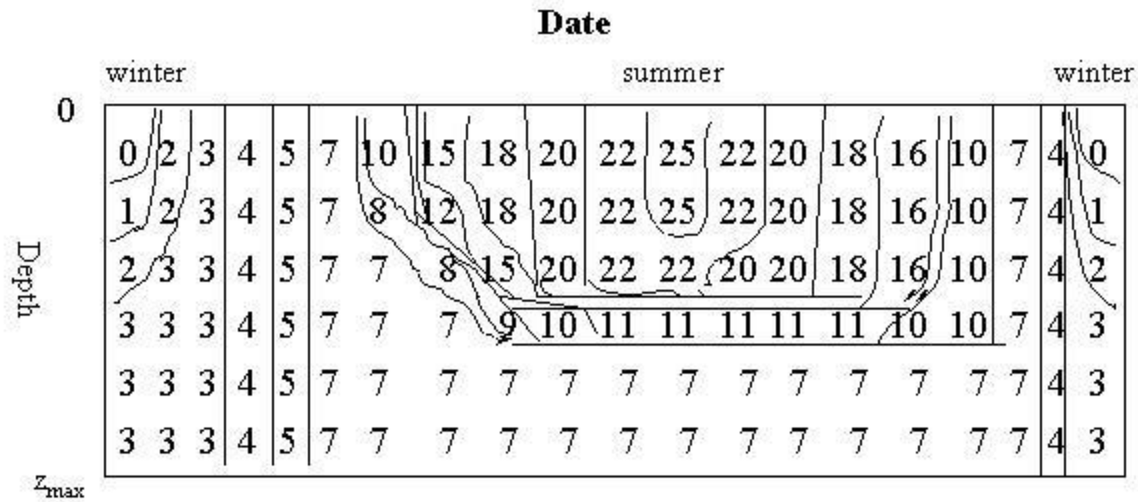
III. Patterns of stratification

holomictic --

depth-time diagram of isotherms

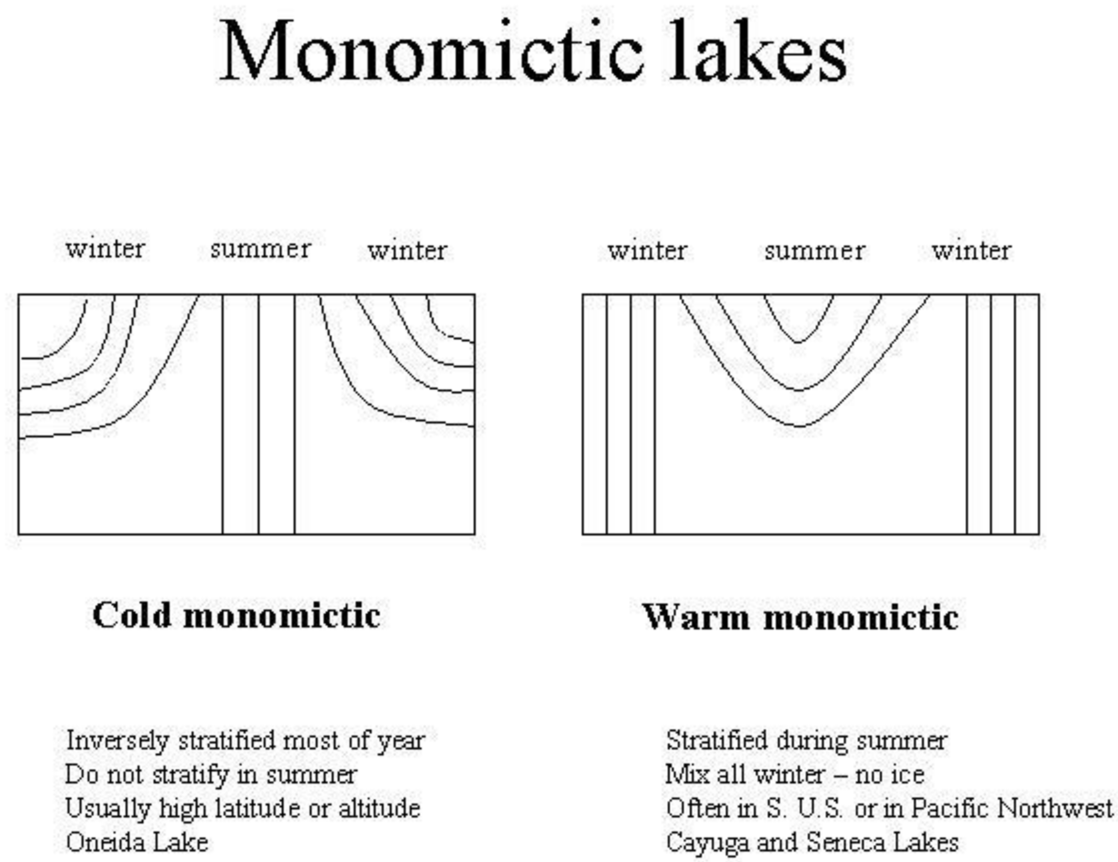
A. **Dimictic --**

Summary of mixing in dimictic lake



isotherms

B. **Monomictic**



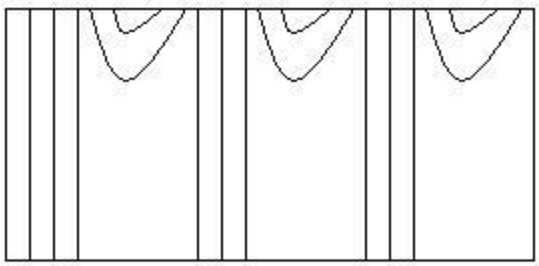
1. **cold monomictic**

2. **warm monomictic**

C. Special considerations in **tropical lakes**

D. **Polymictic**

Polymictic lakes



Cold – are 4 degrees top to bottom; stratify briefly in summer

Warm – stratification breaks down often

Can mix daily or with storms

Oligomictic – mix every few years – unusual, irregular, short circulation
Lake Ohrid, Yugoslavia; some deep tropical lakes
Amictic – always frozen

1. **cold polymictic**

2. **warm polymictic**

E. **Oligomictic**

F. **Amictic**

G. **Meromictic** (mero=partial)

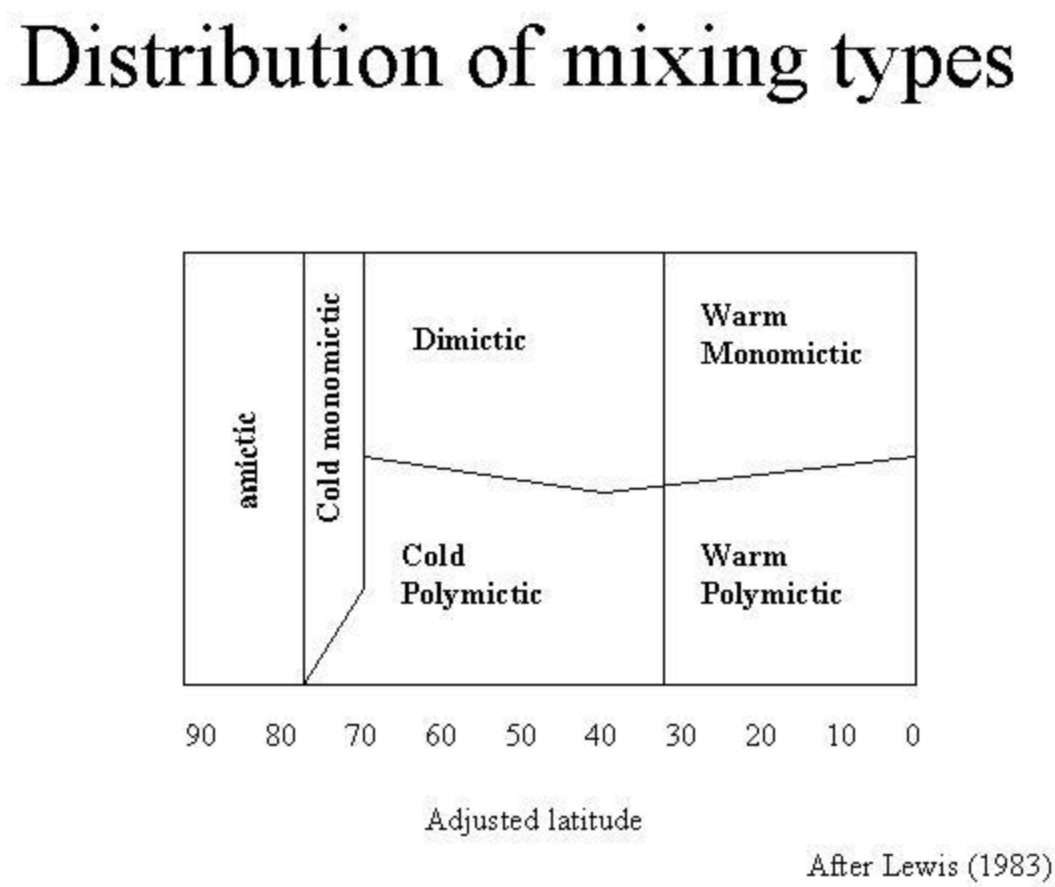
mixolimnion -- shallow layer that mixes
monimolimnion -- deep layer that doesn't mix
pycnocline -- region of maximum density change
chemocline -- region of change in density due to change in salinity; dissolved salts or organics

1. ***ectogenic*** -- external event brings salt water into a freshwater lake or freshwater into a saline lake

2. ***crenogenic*** -- submerged saline springs release dense water to deep portions of lake basins

3. ***biogenic*** -- accumulation of salts due to decomposition in the sediments, sinking organic matter,
and photosynthetic precipitation of carbonate

H. Patterns of lake mixing types



- Updated version of figure 6-7 in Wetzel from Hutchinson and Loffler, 1956

IV. Resistance to mixing and stability

A. Resistance to mixing proportional to $d\rho/dz$

B. **Stability** – the resistance to mixing; the amount of work that would be required to mix an entire lake to uniform density without adding or subtracting heat in the process.

1. **Whole lake stability** – determines if the whole lake will mix; is the amount of energy required to mix the entire lake to uniform density (KJ/cm^3)

a. $$S = 1/A_0 \sum_{Z_0}^{z_{max}} (\rho_z - \rho_{average})(z - z_{\rho average})(A_z)\, dz$$

where Σ is actually an integral symbol (apparently non-existent on my html font file for now!)

where A_o = the surface area in cm

A_z = the area at some depth z (in cm)

$\rho_{average}$ = the final or mean density that would result if the lake were completely mixed

ρ_z = the density at depth z

$z_{\rho average}$ = the depth (cm) where the final (mixed) mean density exists prior to mixing

z_{max} = maximum depth in cm

z_0 = surface or zero depth

2. **Richardson's stability** – determines whether or not two fluids will mix

a. $Ri = (g \times d\rho/dz) / \rho_{average} (du/dz)^2$

Where g = acceleration of gravity

ρ = density

u = horizontal velocity

b. Ri > 0.25 then no mixing -- numerator dominates

c. Ri < 0.25 then will mix -- denominator dominates (energy of mixing)

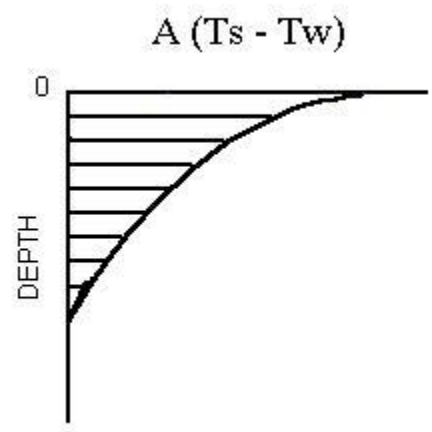
C. Heat in lakes

1. **Annual heat budget** (Birgean heat budget) – record of the heat content of the lake

- Winter heat income – amount of heat required to warm a dimictic lake from winter stratification to isothermal mixing in spring

- Summer heat income – amount of heat required to heat the lake from spring mixing to its maximum summer heat content

A = Area at depth z
T_s = maximum summer temperature at depth z
T_w = minimum winter temperature at depth z



integrate

2. **Analytical heat budget** – budget based on identification of all the sources and sinks for heat to or from a lake

D. Streams and Heat

WATER MOVEMENTS

I. Why would a biological limnologist be interested in water movements?
-Distribution of organisms
-Distribution of dissolved gases and nutrients
-Distribution of temperature

We will deal with 5 basic categories of physical factors that describe water motion or the movement of substances in water :
SIMPLE DIFFUSION
TURBULENT VERSUS LAMINAR FLOW
CONVECTION / ADVECTION
CURRENTS

WAVES
MORE COMPLEX COMBINATIONS OF CURRENTS AND WAVES

II. **Diffusion** – molecular movement of substances in water, but not movement of water itself

Fick's first law of diffusion:

$$FLUX = -K_S \frac{dS}{dx}$$

Where ***flux*** equals bulk movement – the amount that can pass through a given area in a given time

K_s = diffusivity coefficient; $cm^2 \times \sec^{-1}$

dS = change in [solute]; $g \times cm^{-3}$

dx = change in distance; cm

Always check to make sure that the units cancel out!

$$g \times cm^{-2} \sec^{-1} = \left(cm^2 \times \sec^{-1}\right) \times \frac{\left(g \times cm^{-3}\right)}{cm}$$

Heat diffusion

K_T is thermal diffusivity – Fourier's Law

$K_{T\ (heat)}$ for water is 1.5 X 10^{-3} cm^2 sec^{-1}

K_s most dissolved substances is ~1 X 10^{-5} cm^2 sec^{-1}

III. Laminar Flow versus Turbulent Flow

A. **Laminar flow**

B. **Turbulent Flow**

Particles move in highly irregular manner, even though the bulk fluid is traveling on average in one direction – this is
the 'statistical' nature of turbulence

Similar for heat and dissolved substances (whole water parcels exchanged) – unlike diffusive processes

C. How do you predict whether laminar or turbulent flow will occur?

Reynold's number (dimensionless)

$$REYNOLDS\# = \frac{\overline{U} \times LENGTH \times \rho}{\mu}$$

where $\overline{U}$ = mean velocity (cm s^{-1})
ρ = density (g cm^{-3})
μ = viscosity (gm cm-1 sec-1)

$$REYNOLDS\# < 500 \equiv LAMINAR$$
$$REYNOLDS\# > 2000 \equiv TURBULENT$$

most flow generates turbulence
important for small organisms

Viscosity and Temperature

IV. **Convection** -- – flow arising from density differences (independent of externally supplied velocity gradients)

Advection – bulk movement of water and its contents

1. Heat source
2. Evaporation
3. Cooling
4. Salinity

V. **Eddy diffusion**

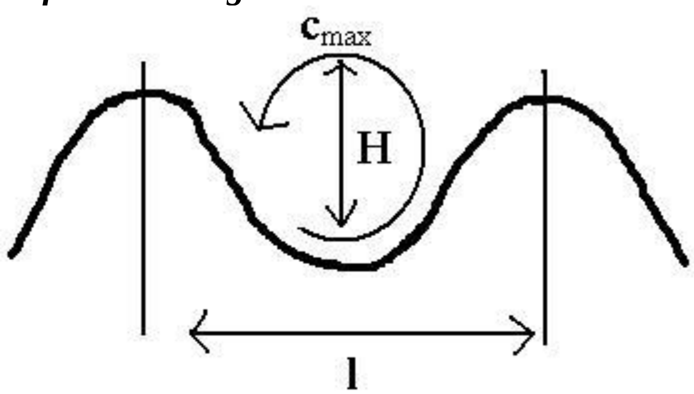
Measure of rate of exchange or intensity of mixing across a density layer (thermal or salt)
Result of molecular diffusion + turbulent flow + advection

Disorganized flow of water on different spatial scales
"Big whirls have lesser whirls that feed on their velocity and lesser whirls have smaller whirls and so on 'til viscosity"

Richardson's number (see mixing section)
$R_i = (g \times d\rho/dz) / (\rho \times du/dz)^2$

VI. **<u>Waves</u>** - periodic movement, but not much unidirectional flow

A. ***Surface traveling waves***



h = height that a water molecule moves
h is halved for each λ/9 of depth in the water column

1. wave velocity $C_w = l / T$; T= period
2. particle velocity $\overline{C_p} = \frac{\pi \times H}{T}$
3. **Stokes limit**

$$\frac{C_p}{C_w} = \frac{\pi \times H}{l} \approx \frac{3H}{l}$$

$if \frac{H}{l} > \frac{1}{7}$, then waves will tend to break up (Stokes Limit)

4. potential versus kinetic energy
   Energy in deep water is mostly <u>potential</u>
   Nearshore it is converted to <u>kinetic</u>, can get damage

5. <u>capillary waves</u> – capillarity is a calming force. At higher windspeeds you get <u>gravity waves</u> (>1.75 cm in height or 6.28 cm in length) where gravity is a calming force.

B. ***Standing Waves***

1. <u>**Surface seiche**</u>

<> pressure of wind pushes water to one side
when wind stops, oscillation begins (also earthquakes and pressure systems)

period of seiche $$T_n = \frac{2l}{n(g\bar{z})^{1/2}}$$

where l = length of basin
n = number of nodes
g = gravity
z = mean depth

setup of surface seiches $S_h=3.2X10^{-6}*l*[u^2]/(g*z_{max})$

2. <u>Internal seiche</u>

If the wind causes a 1 cm set-up at the surface, the pressure at depth will increase by ρgh. To get an equivalent pressure difference, the slope of the thermocline would have to be 1000X greater (you have displaced air with water), so a 1 cm setup leads to a ~10 m internal seiche!

i. set-up
- a. winds
- b. pressure differences
- c. rain, river inputs, landslides

ii. amplitude

Internal seiches have amplitudes much larger than surface seiches, and the period is much longer

internal seiches ($A_i=S_h*(\rho_h/(\rho_h-\rho_e))$)

Will get floating organisms piling up on the end toward which the wind is blowing

iii. period

$$T_i = \frac{2l}{\left(\dfrac{g(\rho_h - \rho_e)}{\dfrac{\rho_h}{z_h} + \dfrac{\rho_e}{z_e}}\right)^{1/2}}$$

l = length of basin
ρ_h = density of hypolimnion
ρ_e = density of epilimnion
z_h = thickness of hypolimnion
z_e = thickness of epilimnion

Characteristics of internal seiches are strongly dependent on basin morphology, and so there is more than one formula to calculate the period of a seiche.

Upwelling

Can get *internal waves* along thermocline

VII. **Currents** -- non-periodic movements generated by external forces (but *do* have flow in one direction, unlike waves)

A. **Coriolis force**

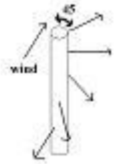
Coriolis acceleration $= 1.46 \times 10^{-4} (v)(\sin \phi)$

Tendency to drift to right of wind or velocity direction in Northern hemisphere

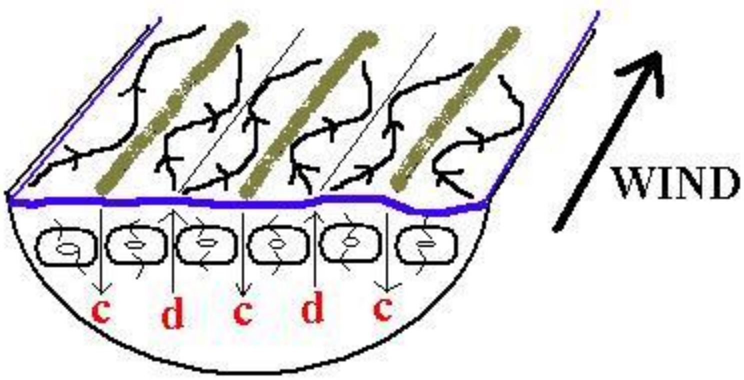
Not a true force

Usually small in lakes

B **Ekman spirals**



C. **Langmuir circulation**



Very common: form of organized advection, controls distribution of organisms as well as mixes

Streak of convergence – floating matter (flotsam); **wind rows**

Divergence – things that sink – algae, zooplankton (upwelling)

Can think of the cells as rotation of gears. Each of the rotating circles is known as a Langmuir Cell

VIII. Combination of waves and currents

Kelvin and Poincaré waves

Interaction of internal waves and Coriolis effect

<u>Kelvin waves</u> – currents along a line parallel to the shore; decrease in amplitude away from shore

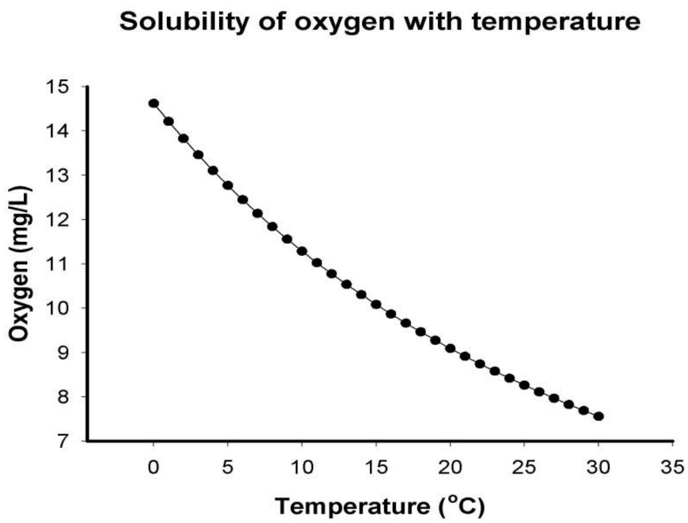
<u>Poincaré waves</u> – in large lakes where long waves travel without influence of shore and make a standing wave pattern across the basin, rotating clockwise once a wave cycle; continue away from shore

cture - Water Chemistry -- Dissolved Gases -- Oxygen

I. Properties of dissolved gases

A. Solubility -- How much gas will dissolve in water?

1. Pressure -- as pressure increases, solubility increases
2. Temperature -- as temperature increases, solubility decreases



3. Salts -- as TDS increase, solubility decreases exponentially
4. Concentration -- Henry's law

At constant temp. the amount of gas absorbed by a given volume of liquid is proportional to the pressure in atmospheres that the gas exerts

[gas] = K_H ρ_{gas}

K_H (Henry's constant) is a solubility factor, varying from gas to gas

O_2 in atmosphere ~20.3% = 0.203 atm

K_H @ 20oC = 1.39 $\frac{mmolO_2}{kgH_2O \times atm}$ (for pure water)

will dissolve in water at 20°C

$$[O_2] = (0.203\,atm)\left(\frac{1.39\,mmolO_2}{kg \times atm}\right) = 0.282\,\frac{mmolO_2}{kg} = 9.03\,\frac{mgO_2}{kg}$$

B. Oxygen

1. Used in respiration
2. Important in chemical reactions
3. Oxygen dynamics:

    (a) respiration uses oxygen

(b) bacterial decomposition uses oxygen

(c) photosynthesis makes oxygen ($6CO_2 + 6H_2O \xrightarrow{light} C_6H_{12}O_6 + 6O_2$)

(d) atmosphere contains a large reserve of oxygen

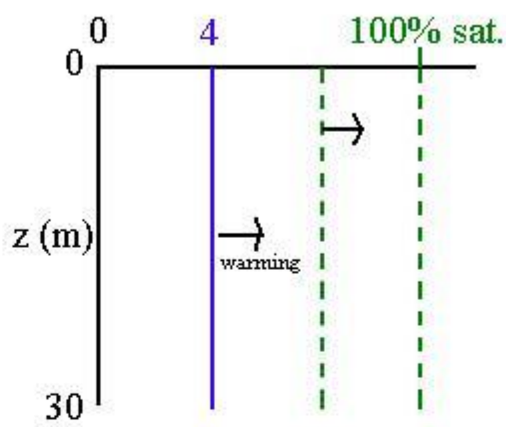
C. Carbon dioxide -- about 200 X more soluble than oxygen.

II. Seasonal Cycles of Oxygen

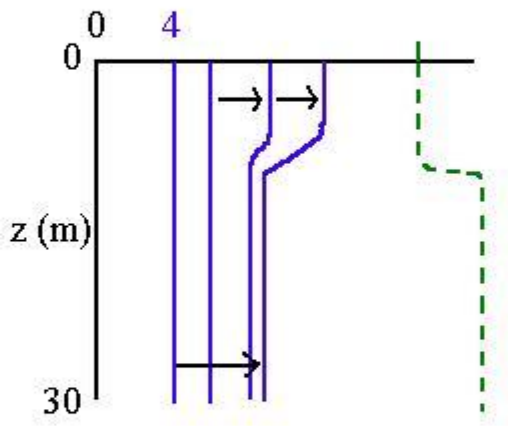
Dimictic pattern for a mesotrophic or eutrophic lake

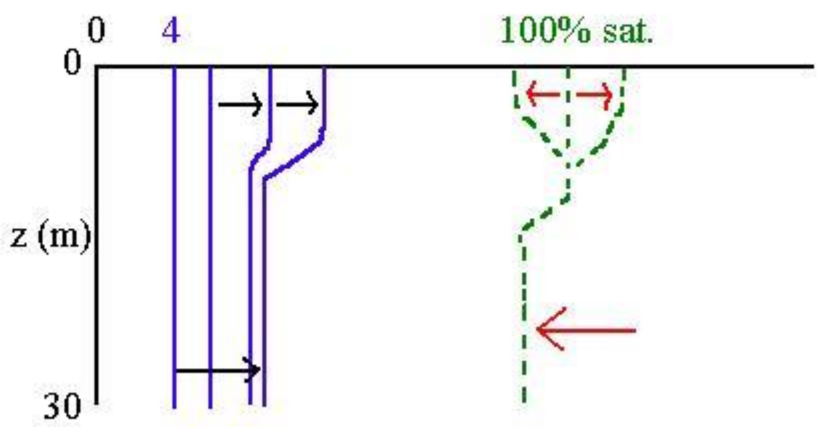
A. Spring turnover

- Ice cover locked in oxygen over winter.
- Some depletion occurs over winter (decomposition and respiration)
- Oxygen increases until 100% saturation is reached
- Summer oxygen debt -- this occurs if stratification sets up before the lake is saturated with oxygen



B. Spring stratification

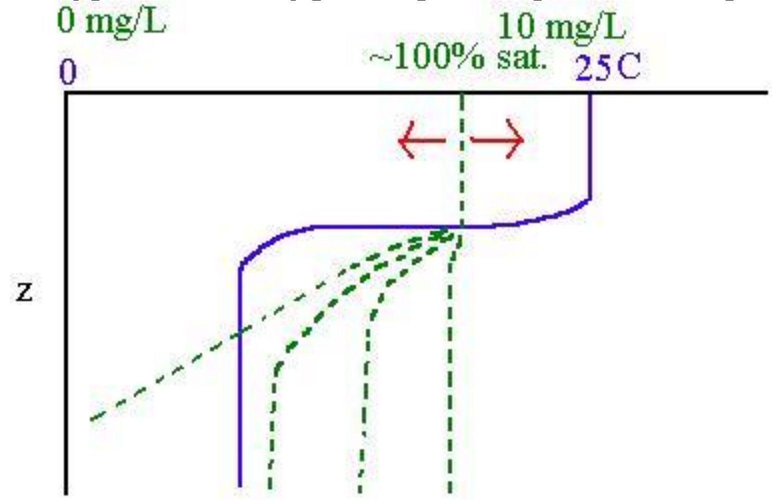




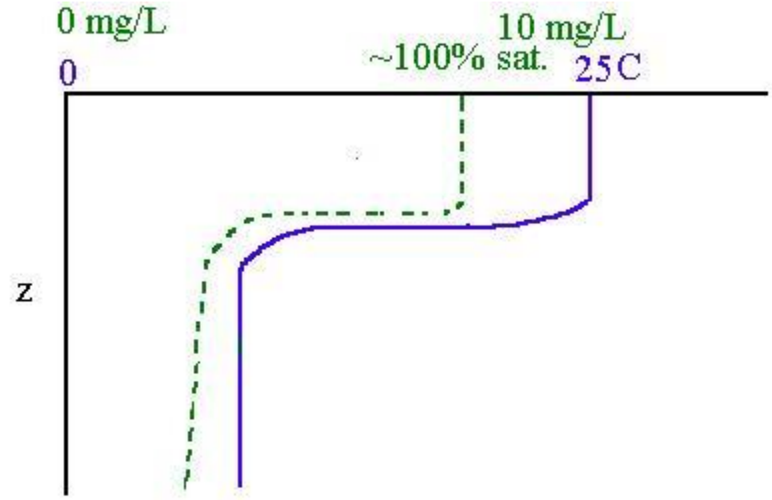
- Follows the 100% saturation curve.
- Organism effects:
  i. Respiration
  ii. Photosynthesis

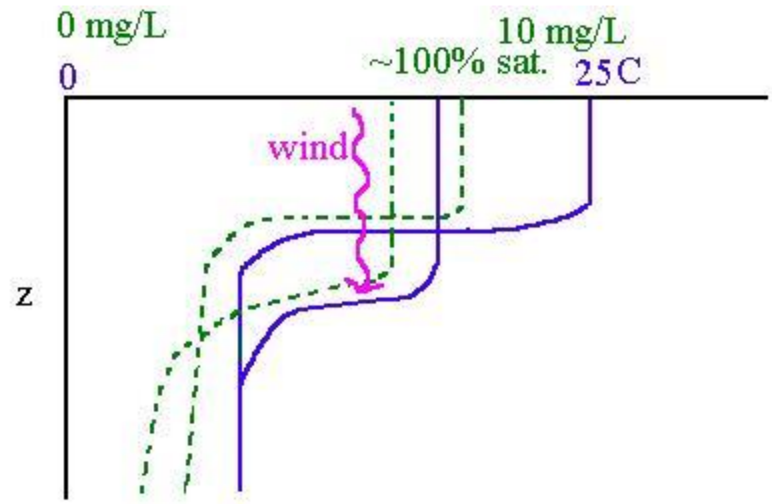
C. Summer stratification
- epilimnetic oxygen fluctuates due to balance of photosynthesis, respiration, and wind mixing

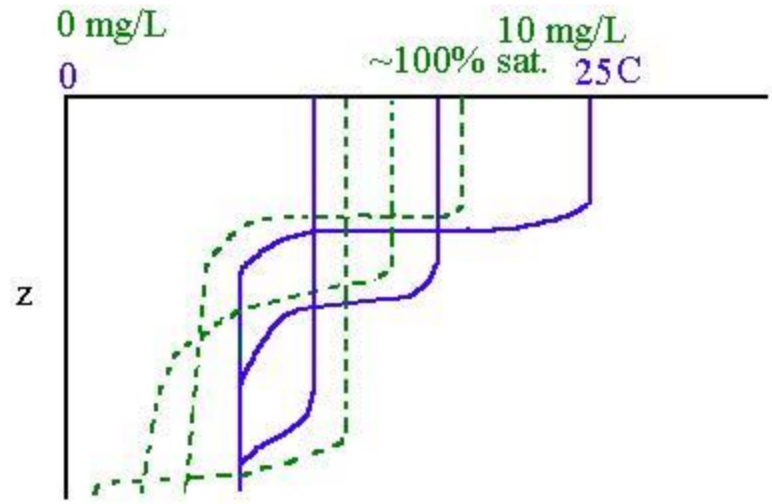
- hypolimnetic oxygen drops -- respiration is important



D. Breakdown of stratification

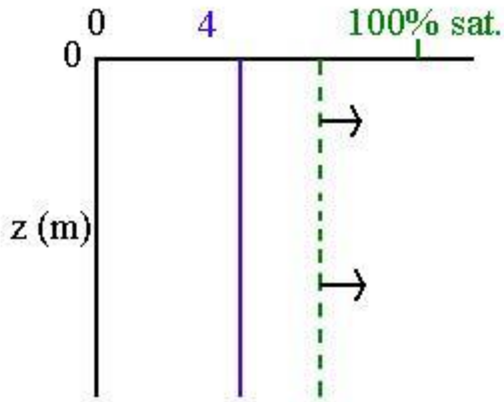






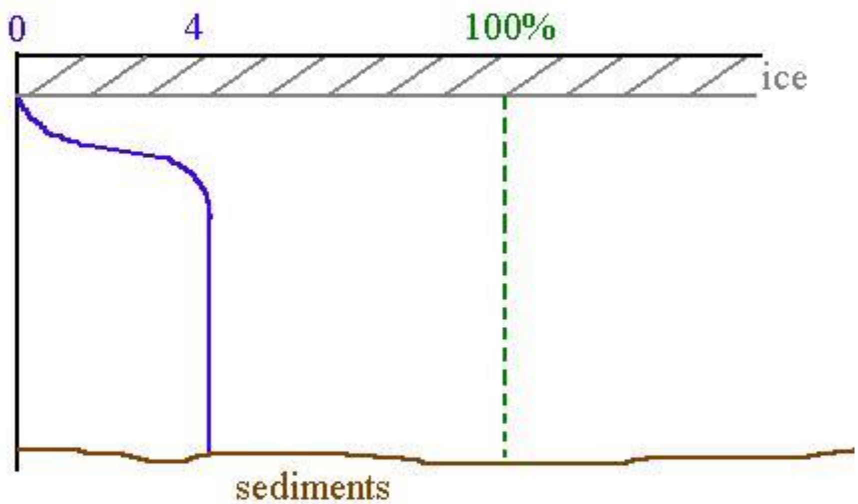
- epilimnetic oxygen decreases slightly as oxygen poor water is mixed to the surface
- hypolimnetic oxygen continues to decrease

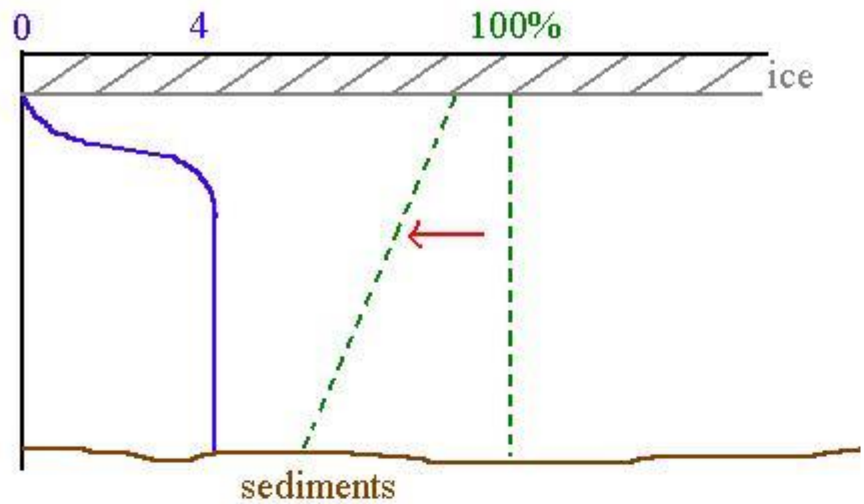
E. Day of turnover

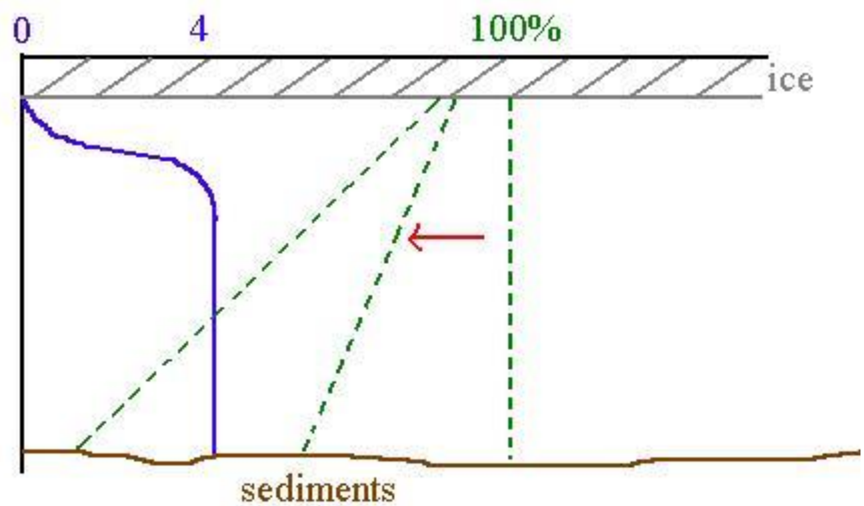


- temperature >4 degrees C because of leftover summer heat
- oxygen <100% because of respiration in hypolimnion
- oxygen goes toward 100% by wind pumping
- but, if ice sets in early, whole lake may not come to 100%, and this is a 'winter oxygen debt'

F. Winter



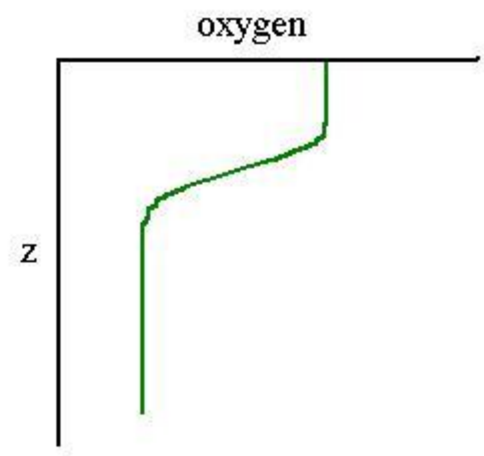




- Inverse stratification
- most intense respiration is in and near the sediments
- '***winter kills***' possible

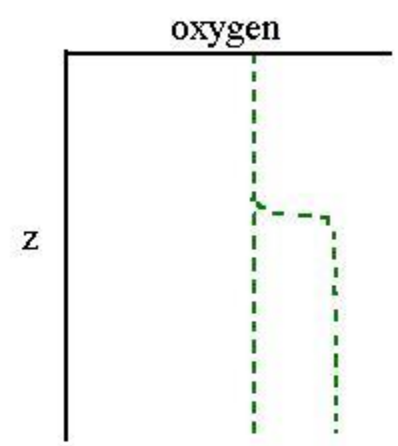
III. Oxygen curves

A. **Clinograde**

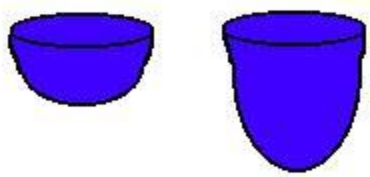


- Hypolimnetic oxygen depletion
- Respiration and decomposition increase as lake productivity increases

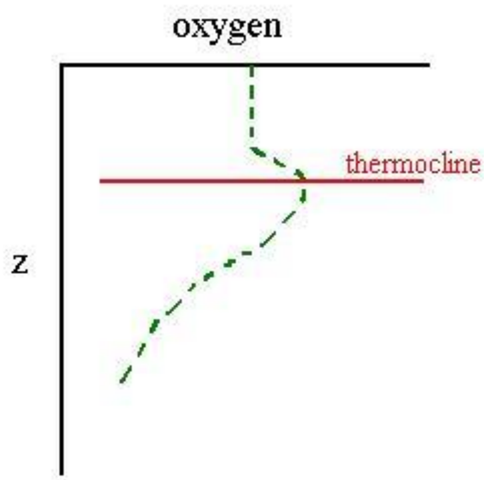
B. **Orthograde**



- oligotrophic lakes -- low production, little respiration
- Also higher oxygen solubility due to lower temperature
- If two lakes have the same productivity on an areal basis, one may be clinograde and one orthograde based on basin shape



C. **Positive heterograde**



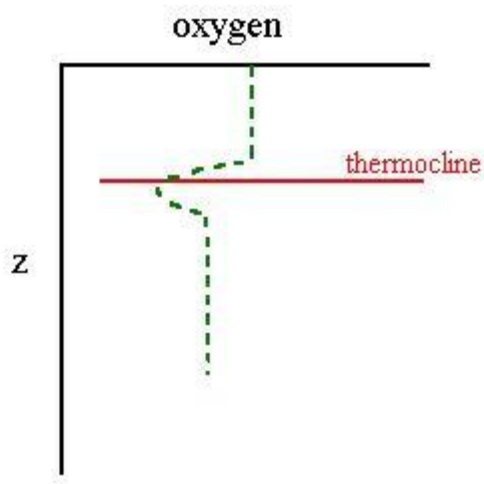
- due to photosynthesis at the thermocline
- light penetration to metalimnion where there is slow mixing so that any oxygen produced stays around and builds up;

some input of nutrients from hypolimnion increases growth

from hypolimnion increases growth

- 'deep chlorophyll layer' - depends on water transparency
- could also be due to input of oxygen-rich river water that is denser than surface water

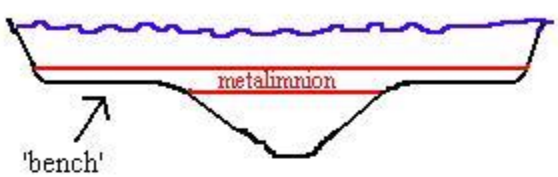
D. **Negative heterograde**



1. can be due to respiration of algae at night, or respiration of dense layer of zooplankton but also can be caused in other ways:

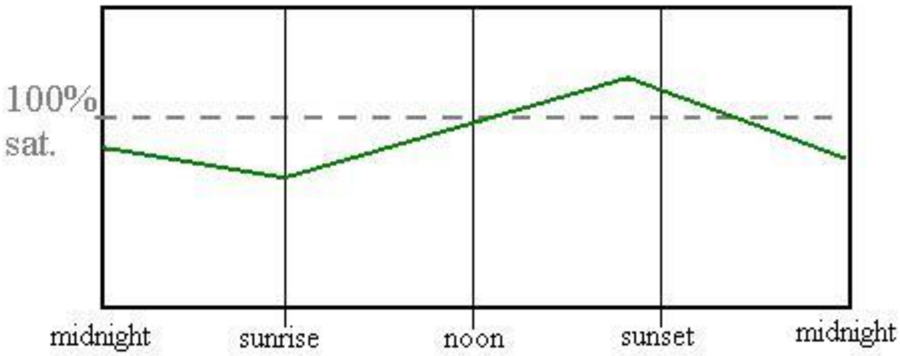
2. density gradient -- rain of detritus ('marine snow') is slowed by density gradient around thermocline, more respiration of organic matter

(could also be effluent output there)



3. morphology -- bench; more sediment area per water volume at a given depth so lots of respiration at that depth

E. Diel cycle of epilimnetic oxygen content



F. **Oxygen deficit --** how much oxygen is used up from decomposition of material falling from the productive trophogenic zone

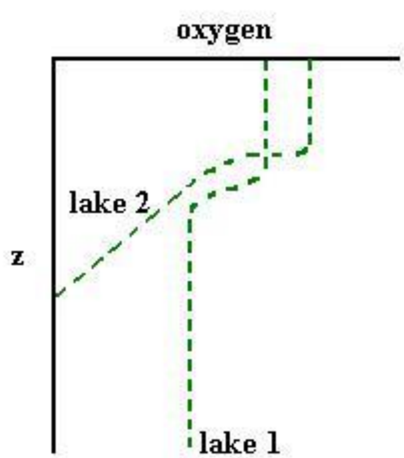
to the tropholytic zone

amount of oxygen consumed by decomposition in the hypolimnion gives an estimate of the productivity of the lake

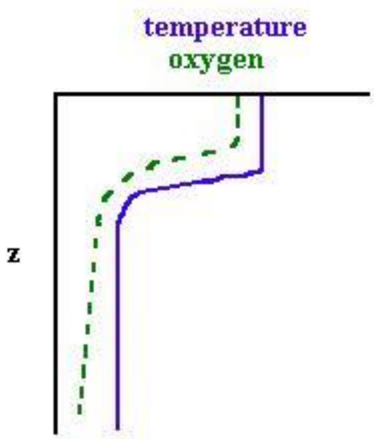
IV. Integration of temperature and oxygen profiles

A. Lake example 1

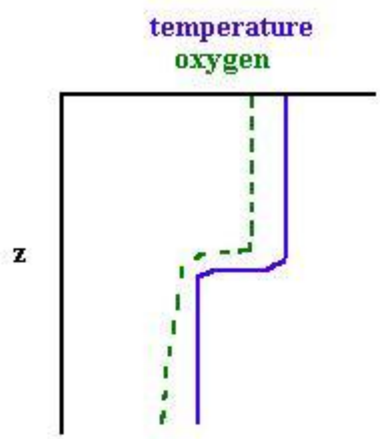
- Summer stratification period
- Same temperature profile
- Sample two lakes of similar morphology during the day and find the following two profiles. Which lake is more productive?



B. Lake example 2
- Lakes 1 and 2 have the same:
    - i. productivity
    - ii. depth
    - iii. transparency/light penetration
- Why are there two different curves?



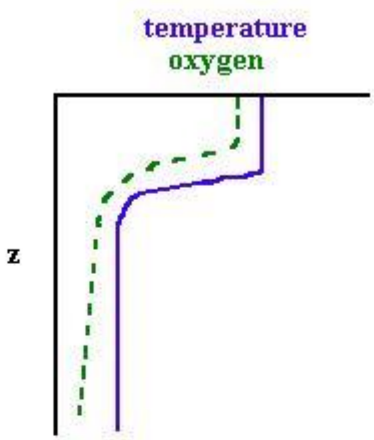
Lake 1



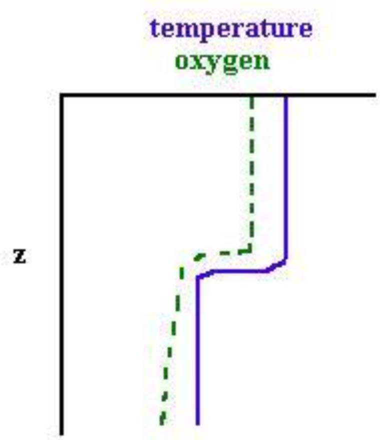
Lake 2

C. Lake example 3

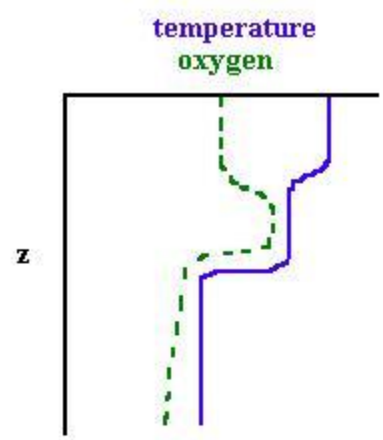
- Three times, each a week apart in summer



Time 1

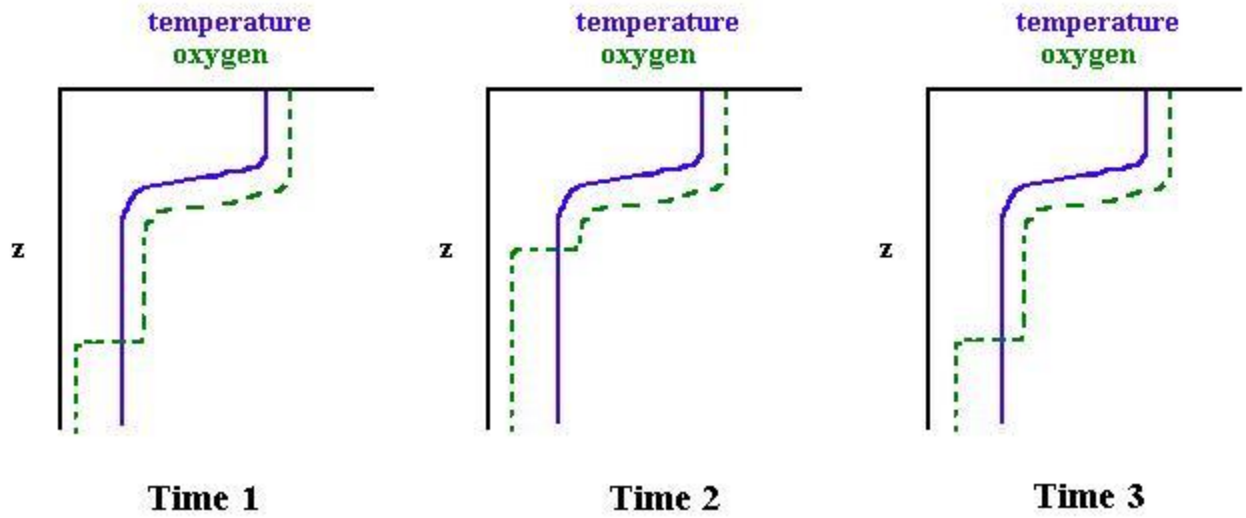


Time 2



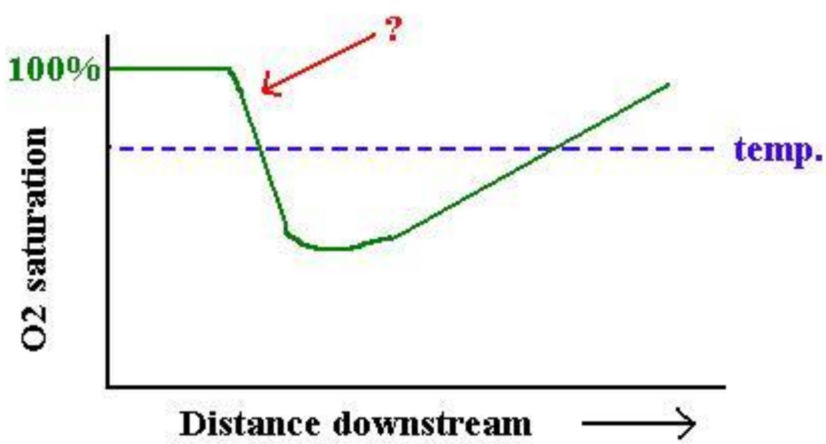
Time 3

D. Lake example 4



- Three times, each a day apart
- Get change in oxygen, not temperature
- What caused this?

E. River example

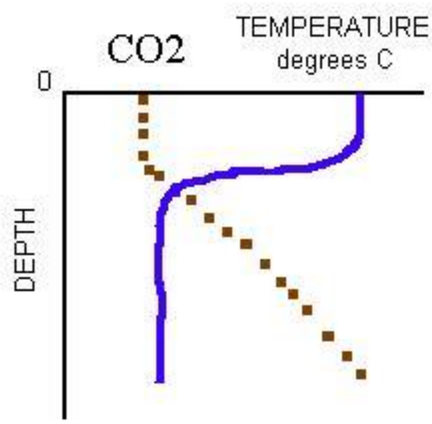


- What caused this pattern?

Inorganic Carbon and pH

I. Controls on CO_2

A. Photosynthesis
B. Respiration
C. Atmosphere
D. Geologic inputs



II. Forms of carbon --

A. Forms and examples of each

	PARTICULATE	DISSOLVED
ORGANIC	Living organisms Dead organic material	Soluble organics: DOC (dissolved organic carbon) Amino acids Sugars
INORGANIC	$CaCO_3$ Carbonates of Mg, K, Na, etc. (minerals)	DIC (dissolved inorganic carbon) CO_2 H_2CO_3 HCO_3^- CO_3^{2-}

B. Carbon cycle – how C moves between these boxes

III. Dissolved inorganic carbon, DIC

Distribution of DIC as a function of pH – See figure 11-1, Wetzel

IV. pH

A. Reactions and definitions

$H_2O \leftrightarrow H^+ + OH^-$

$K_{water} = \frac{[H^+][OH^-]}{[H_2O]} = 10^{-14}$ (dissociation product constant)

by definition concentration of water = 1

$pH = -\log_{10}[H^+]$

if [H+] = 10^{-7} molar, pH = 7

B. Common pH values

1. If distilled water reacts with CO_2, get H_2CO_3 and pH ~5.6
2. Rain with pH less than 5.6 is said to be 'acid rain'
3. Most lakes range in pH from 6-9
4. Low pH lakes
   a. pH < 2; usually due to volcanically produced H_2SO_4 or mine wastes
   b. pH 3.3-4.5 – Sphagnum bogs – exchange of cations for H^+ by the plants
   c. Acid deposition
5. High pH in lakes
   a. Carbonates present (saline lakes, pH>8)
   b. High rates of photosynthesis (decrease CO_2, increase pH)

V. Carbonate buffering system

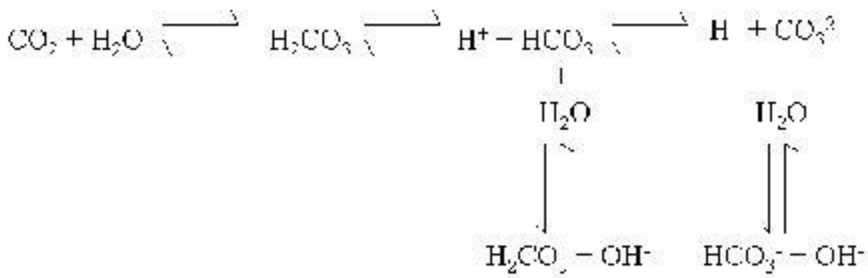
A. Reactions

1. Hydration reaction $CO_{2(aq)} + H_2O \leftrightarrow H_2CO_3$

   $[CO_2]_{aq}$

2. Dissociation reaction $H_2CO_3 \leftrightarrow H^+ + HCO_3^-$

3. Dissociation reaction $HCO_3^- \leftrightarrow H^+ + CO_3^{2-}$



B. Solving equations

1. Basic principles

(a) What is distribution of C species?

(b) What happens when one or more species is changed – when the system is perturbed?

(c) If we know any 2 quantities, then we can determine the others

2. System of equations

a. K_w $$K_{water} = \frac{[H^+][OH^-]}{[H_2O]} = 10^{-14}$$

b. K_1 $$\frac{[H^+][HCO_3^-]}{[CO_2][H_2O]} = 10^{-63}$$

Do not put water in the denominator – is 1

c. K_2 $$\frac{[H^+][CO_3^{2-}]}{[HCO_3^-]} = 10^{-103}$$

d. $K_{sp}(CaCO_3)$ $$K_{sp(CaCO_3)} = \frac{[Ca^{2+}][CO_3^{2-}]}{[CaCO_3]} = 10^{-8.4}$$

solids also are 1

VI. Alkalinity

A. Definition = measure of the buffering capacity of the water; capacity of water to neutralize an acid

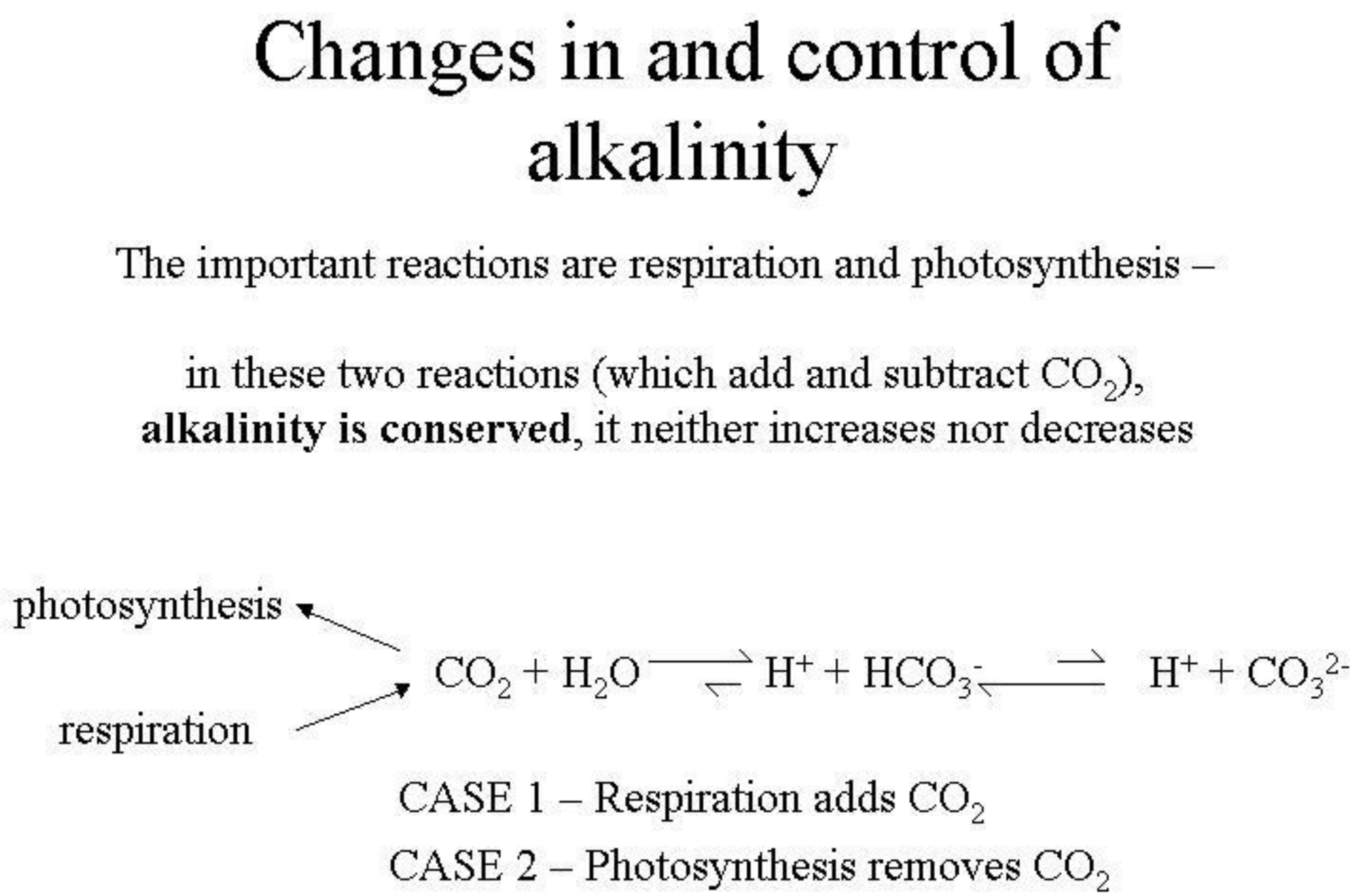
Sum of the anions of weak acids

$$[ALK]_{total} = [HCO_3^-] + 2[CO_3^{2-}] + [OH^-] - [H^+] + borate + silicate...$$

In practice for most lakes: $[ALK]_{total} = [HCO_3^-] + 2[CO_3^{2-}] + [OH^-] - [H^+]$

B. Changes in and control of alkalinity

CLOSED SYSTEMS – ALKALINITY IS CONSERVED

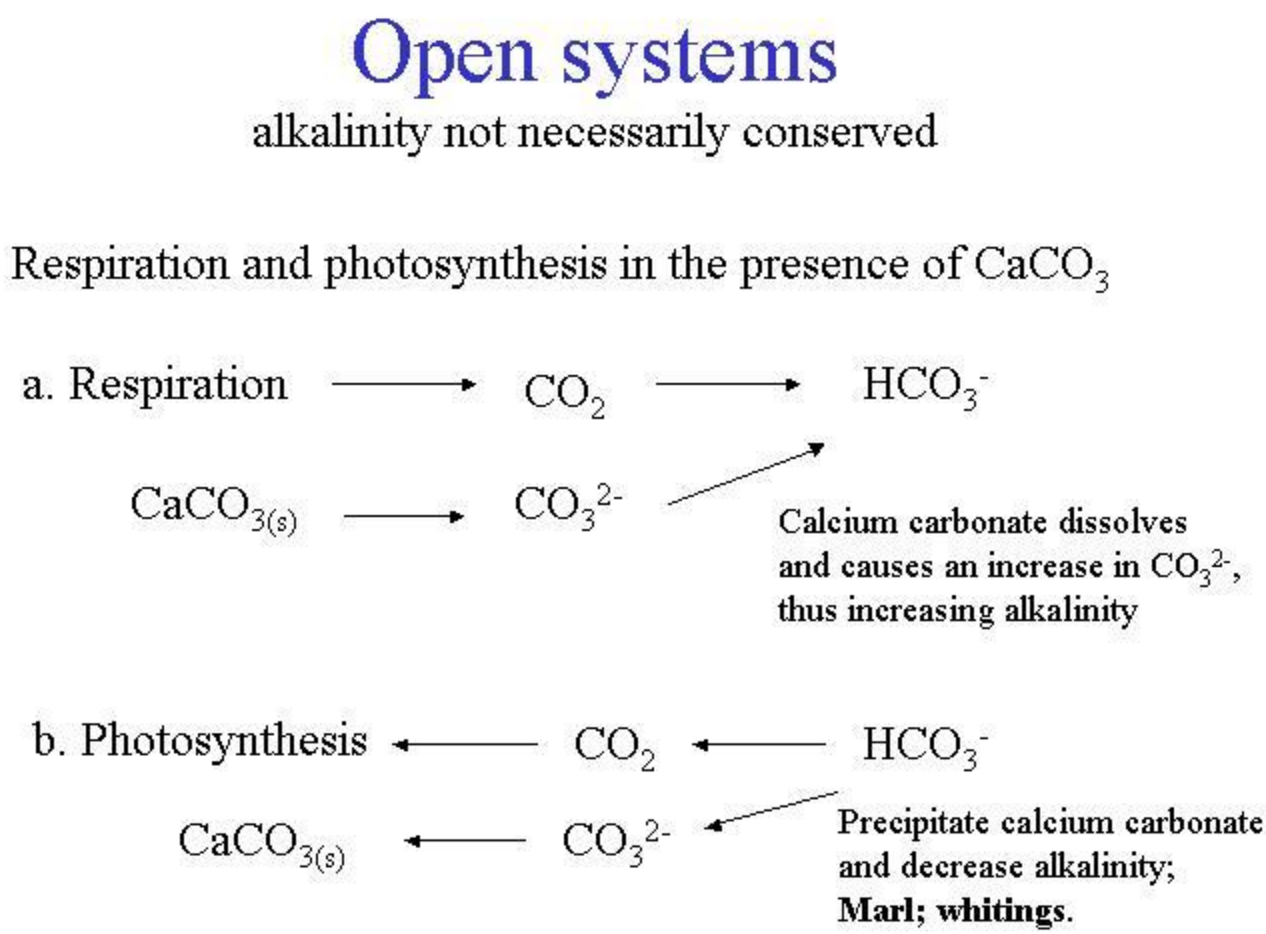


1. CASE 1
   a. respiration adds CO_2

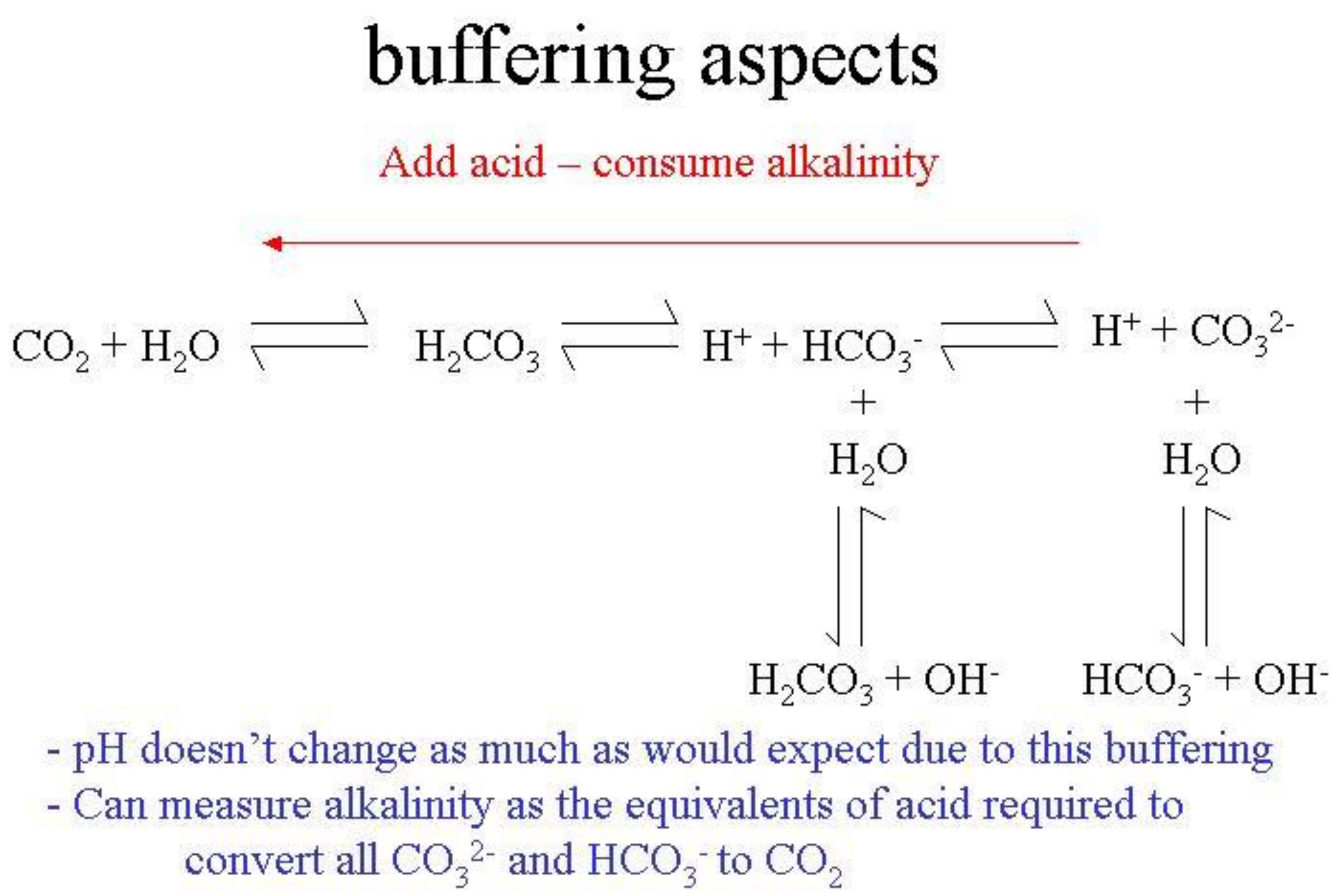
      Remember, $[HCO_3^-] + 2[CO_3^{2-}]$ = constant

2. CASE 2 -- Photosynthesis removes CO_2

Opposite of CO_2 addition case



4. Buffering aspects – What happens when acid or bases are added to the system?



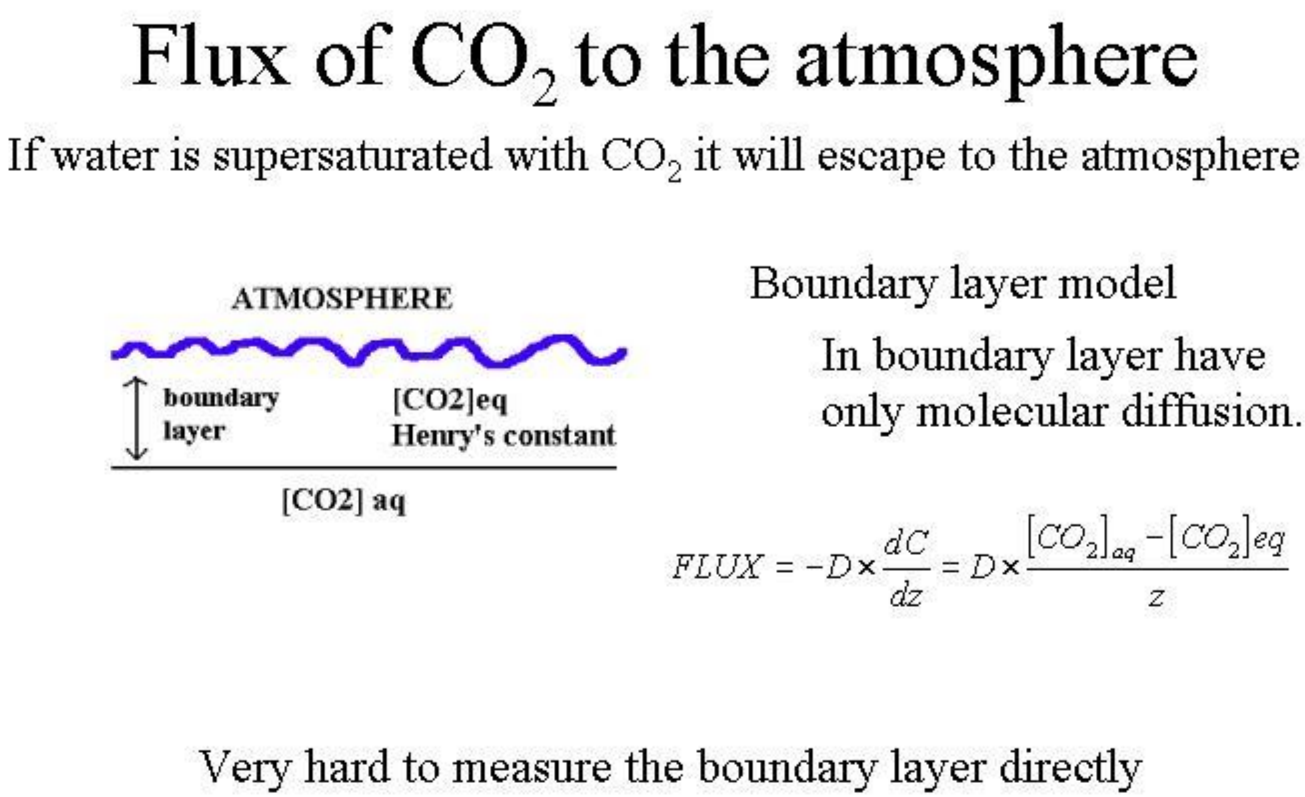
1. add acid – consume alkalinity

2. add base – increase alkalinity and increase pH

3. carbonate system prevents pH from changing as much as expected from amount of acid or base added.

VII. Flux to atmosphere (atmospheric controls)

A. boundary layer model



where z is the thickness of the boundary layer;
related to wind speed

VIII. Questions that have been asked about the Carbon cycle in freshwaters

A. Is carbon a limiting nutrient?

B. Role of lakes, surface waters in the global C cycle

C. Acid rain – areas with few carbonates – little alkalinity or buffering capacity

BACTERIA AND THE MICROBIAL LOOP

I. Characteristics of bacteria

A. Bacterial species; what is in nature?

1. Two major groups
   a) Eubacteria
   b) Archaea (archaebacteria)

2. Small prokaryotic cells – generally 0.2 to 1 υm in length
3. Tolerate a wide range of conditions
4. Generation times: 20 minutes or in viable resting stages for centuries!
5. Locomotion – some have a rotary motor (100 rev/sec)
6. Cyanobacteria – oxygen in atmosphere
7. Bacterial species
   a) Morphology
   b) New molecular techniques

B. Microbial Ecology
1. Enumeration – How many are there?
   a) Underestimates of old plating techniques
   b) Modern epifluorescent techniques
   c) 10^6/ml in natural waters
   d) 10^9/ml in sediments
   e) Some variation with productivity
   f) Mysterious consistency of bacterial values – balance of growth and losses
2. Activity – how fast are they doing things?
   a) Most often measured with radio labeled tracers
   b) Which bacteria are the most active? Specific molecular probes.
   c) 'Ghost cells' can be from 20-90% of total countable cells

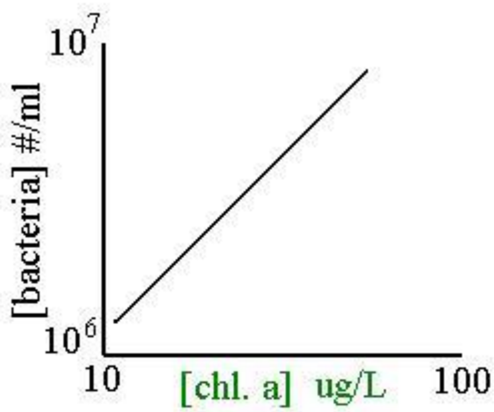
II. Role of bacteria in the lake
A. Potential ways to make a living

Classification	**Energy Source for generating ATP**	**Source of carbon for building cell components**
Photoautotroph	Light	CO_2
Chemoautotroph	Inorganic compounds	CO_2
Photoheterotroph	Light	CO_2, organic matter
Heterotroph	Organic matter	Organic matter

B. Autotrophs produce organic matter
C. Decomposers (mineralizers)
1. DOM often up to 20X more abundant than POM
2. Importance of oxygen

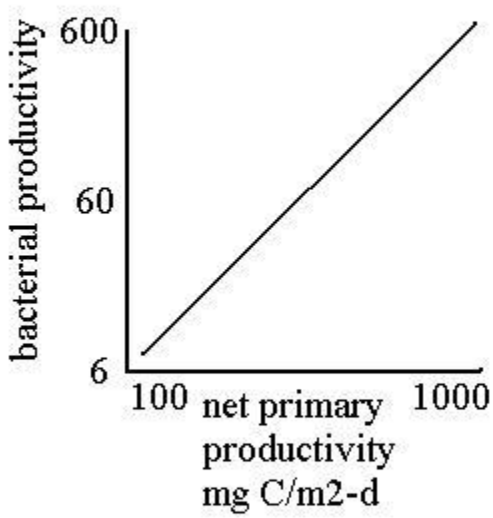
D. Fix nitrogen from atmosphere into useable form
E. Pathogenic

III. Controls of bacterial growth
A. Temperature
B. Acquisition of nutrients
1. types of cellular processes
a) **Assimilative**
b) **Dissimilative**
2. DOM sources (DOC, DON, DOP)
a) C is often limiting
b) Bacteria and algae compete for phosphorus and inorganic nutrients (bacteria are usually better competitors), but
c) There is occasional nutrient limitation -- especially P
d) Best bacterial growth when DOM contains C, N and P
e) 'Quality' of DOC
a. **Labile**
b. **Refractory**
c. UV light can help to break down DOC to more usable forms, but also directly inhibits bacterial growth
f) Sources of DOC - algae, macrophytes, watershed
C. Correlation of bacterial numbers with source of DOM
1. As chlorophyll a increases, bacterial numbers increase



2. Still a small range of bacterial numbers
3. Up to 50% of the C fixed by phytoplankton is exuded and used by bacteria

D. Correlation of bacterial productivity with source of DOM



1. bacterial productivity is often about 25% of net primary productivity
2. bacterial productivity is generally 2X that of zooplankton

IV. Controls of bacterial attrition

A. Grazing – bacteria are fed on by protozoans

1. Protozoans – eukaryotic, heterotrophic, phagotrophic
   a) Amoebas
   b) Ciliates
   c) Flagellates
2. Can ingest 100-1000 bacterial cells per flagellate per day
3. Predator-prey cycles

4. Selective grazing
5. Tests of grazer limitation of bacterial numbers

B. Viruses (Fuhrman, SUNY Stony Brook, Suttle, Univ. British Columbia)

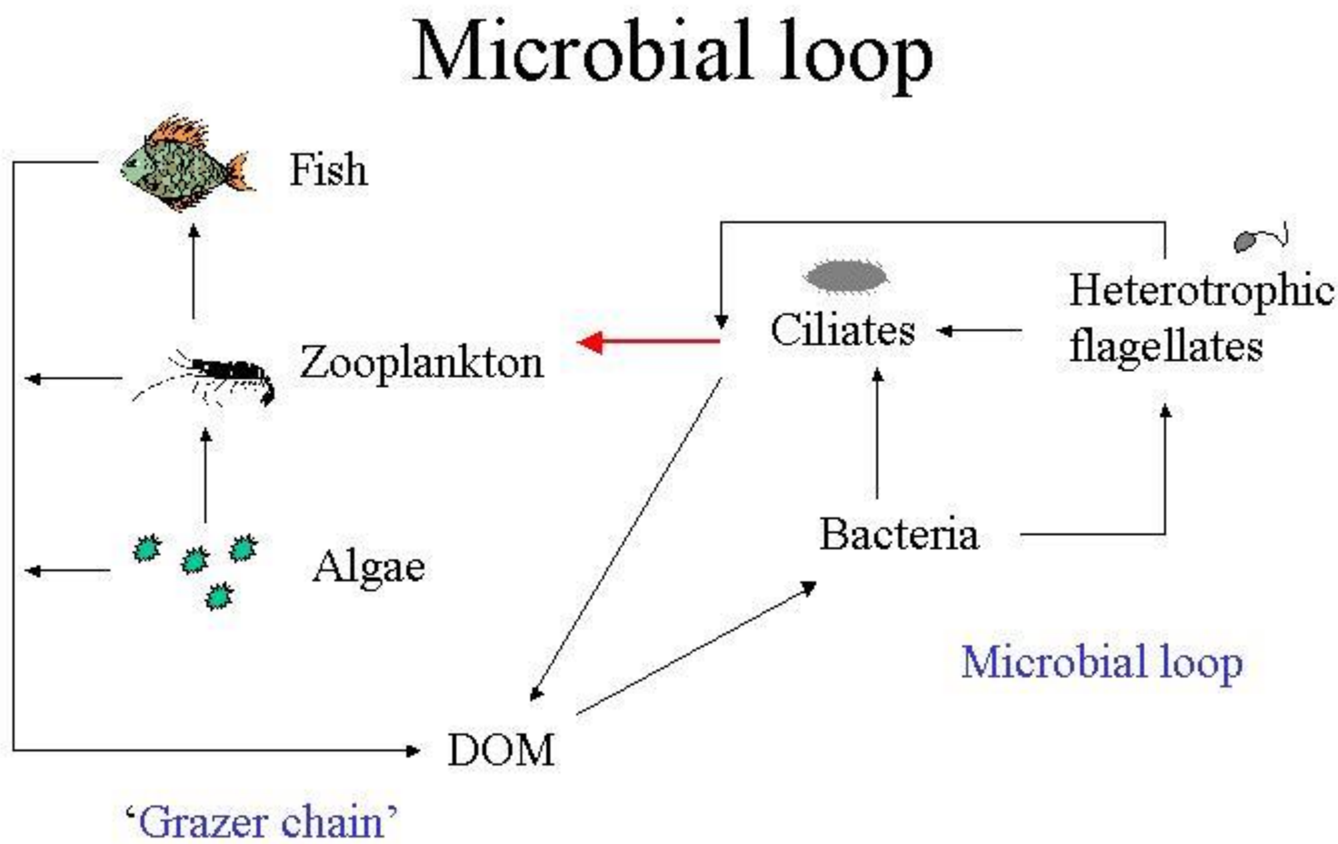
1. Cyanobacteria bloom crashes – historical anecdotal reports; attempted control of blooms
2. Very recent developments in technology
3. 10-100 million viruses per mL
4. diversity of forms
5. may cause half of bacterial mortality; lyse 10-20% of bacteria daily

V. The microbial food web – how important are bacteria to overall lake productivity?

A. Questions

1. Are bacteria food for higher trophic levels?
2. Are bacteria nutrient regenerators or nutrient sinks?

B. **Microbial loop**



C. Experimental evidence

1. First real test - Ducklow (1986) - only 2% of the C taken up by bacteria ended up in higher pools

^{14}C-glucose -> bacteria -> protozoans/larger zooplankton

3. However, these bacteria were only given DOC for growth, with little P or N -- were slow growing
4. The study was repeated with additional nutrients -- higher transfer rates,

but *variable*

D. General current thinking

1. Often a small amount of material from the microbial loop is utilized by higher trophic levels (<20%)

2. Bacteria can *compete* with algae for inorganic nutrients, and thus may actually be a 'sink' rather than a remineralization source

3. Protozoans and viruses may be more important in remineralization

4. Bacteria are very important in mediating chemical reactions and in decomposing organic material

REDOX REACTIONS

I. **Valence** – atoms have different valences (degree of negative or positive charge) determined by whether they have enough protons to balance their electrons. Elements and molecules have tendencies to associate or dissociate with electrons (change valence)

II. **Reduction** – gaining electrons (valence becomes more negative)

A reductant is a compound that donates electrons

III. **Oxidation** – losing electrons (valence becomes more positive)

An oxidant is a compound that accepts electrons

"LEO the lion says GER"

III. **Redox potential**

A. Arbitrary scale – how oxidized or reduced things are compared to a standard

Standard reaction : $H^{+} + e^{-} \leftrightarrow \frac{1}{2} H_{2(g)}$

B. Eh – electron flow relative to the hydrogen standard (**electron potential**)

As Eh decreases, the solution is more reduced (has more electrons to give) and as Eh increases, the solution is more oxidized (will accept electrons).

average in lakes is ~300-500 mV

C. pE – the **electron activity** of a solution

- pE=-log[e-]

- measured at pH=7; =16.9 Eh (so is related to electron potential)
Large and positive in strongly oxidizing solutions (low electron activity)

D. examples: half-reactions

1. Iron in oxygenated waters
2. Sulfate reduction

Redox reactions control the form of elements and the distribution of different forms of elements in lakes

V. Iron

A. Forms of oxygen
1. Fe^{2+} (ferrous) < ~300 mv Eh
2. Fe^{3+} (ferric) > ~300 mv Eh

B. Iron in oxygenated waters

C. Iron in anoxic waters

D. Significance –
1. Fe^{3+} binds with P, element abundances are interrelated
2. as a limiting nutrient

VI. The Redox 'Battlefield' - Most reactions are mediated by bacteria

A. Players in the 'battle'
- One side – PS organisms take light energy and make reduced compounds (local chemical disequilibrium)
- Other side – using these reduced compounds – heterotrophs extracting potential energy and attempting to reestablish equilibrium

B. Who's winning?
- Example: in a lake at pH7, 25 degrees C, and oxygenated, predict that
- C is in CO_2, HCO_3^-, CO_3^{2-}
- N is in NO_3^- (no NH_4^+)
- S is in SO_4^{2-} (no H_2S)
- oxidizers are winning the war
if oxygen is available it will be used as a terminal electron acceptor because it has a large free energy difference

VII. Reactions

A. How does this relate to energy? The free energy depends on the energy difference between the reactants and the products.

B. **Gibbs free energy** of reaction - *Determines which reactions are most energetically favorable*

$$\Delta G^{\circ} = -RT \ln K_{eq}$$

δελταGº = standard free energy of formation
R=gas constant (8.314 J K^{-1} mol^{-1})
K_{eq}=equilibrium constant
T=temperature (K)

$$= -nF\Delta E$$

n=number of electrons involved in the reaction
F=Faraday=23 kcal/mol
δελταE=difference in redox potential in reaction

δελταG°' = Σum (deltaG°'products) - Σum (deltaG°'reactants)

C. Biology behind this

The minimum energy necessary to be useful to organisms is δελταGº=-7kcal/mol – that is what is necessary or ATP formation

Reactions that can sustain life

Strong → Weak

Weak ↓ Strong

		Electron Donors (reductants)						
		H_2	CHO	CH_4	HS^-	NH_4^+	NO_2^-	Fe^{2+}
Electron Acceptors (oxidants)	CHO	+	+					
	CO_2	+	+					
	SO_4^{2-}	+	+	?				
	NO_3^-	+	+	?	+			
	O_2	+	+	+	+	+	+	+

D. Redox reactions

1. Aerobic Respiration (oxidation of organic matter)
   a) reductant CHO, oxidant O_2
   b) Reaction:

$$C_6H_{12}O_6 + 6O_2 \leftrightarrow 6CO_2 + 6H_2O$$

   c) delta G^o = -686 kcal/mol

2. Nitrogen
   a) **NITRATE REDUCTION**
      (i) reductant CHO, oxidant NO_3^-
      (ii) Reaction: **DISSIMILATORY NITRATE REDUCTION**

$$CH_2O + NO_3^- + 2H^+ \leftrightarrow CO_2 + \frac{1}{2}N_2 + 2H_2O$$

(iii) δελτα□G$^{o'}$ = -649 kcal/mol

(iv) This is denitrification, reducing nitrate, NO_3^-, to N_2 gas

b) **<u>Assimilatory nitrate reduction</u>**

(i) Uptake of nitrate by an organism

(ii) Reaction: $NO_3^- + H^+ \rightarrow NH_3 - organic$

c) **<u>Nitrification</u>** – production of nitrate

(i) Reactions:

a) $NH_4^+ + \frac{3}{2}O_2 \leftrightarrow NO_2^- + 2H^+ + H_2O$ δελτα□G^o = -65.7 kcal/mol

b) $NO_2^- + \frac{1}{2}O_2 \leftrightarrow NO_3^-$ δελταG^o = -17.5 kcal/mol

(ii) So δελτα□G^o 1 = -65.7 kcal/mol and delta G^o 2 = -17.5 kcal/mol

(iii) This produces the source material for denitrification

3. <u>Iron</u>

IRON OXIDATION

a) reductant Fe^{2+}, oxidant O_2

b) Reaction:

$$Fe^{2+} + \frac{1}{4}O_2 + H^+ \leftrightarrow Fe^{3+} + \frac{1}{2}H_2O$$

$$Fe^{3+} + 3H_2O \leftrightarrow Fe(OH)_3 + H^+$$

c) δελτα□G^o ' = -10.6 kcal/mol

IRON REDUCTION

a) Reaction: $Fe(OH)_3 + 3H^+ \rightarrow Fe^{2+} + 3H_2O$

b) Can occur with some oxygen present, but not energetically favorable

c) δελτα□G^o ' = -300 kcal/mol

4. <u>Sulfur</u>

SULFATE REDUCTION

a) reductant CHO, oxidant SO_4^{2-}

b) Reaction: $2CHO + SO_4^{2-} + 3H^+ \leftrightarrow 2CO_2 + HS^- + 2H_2O$

c) δελτα□G^o ' = -190 kcal/mol

SULFIDE OXIDATION

a) reductant HS^-, oxidant O_2

b) Reaction: $HS^- + 2O_2 \leftrightarrow SO_4^{2-} + H^+$

c) delta G° ' = -190 kcal/mol

5. <u>Methane</u>

METHANOGENESIS

a) reductant H_2, oxidant CO_2

b) Reaction: $4H_2 + CO_2 \leftrightarrow CH_4 + 2H_2O$

c) delta G° ' = -8.3 kcal/mol

METHANE OXIDATION

a) reductant CH_4, oxidant O_2

b) Reaction: $CH_4 + 2O_2 \leftrightarrow CO_2 + 2H_2O$

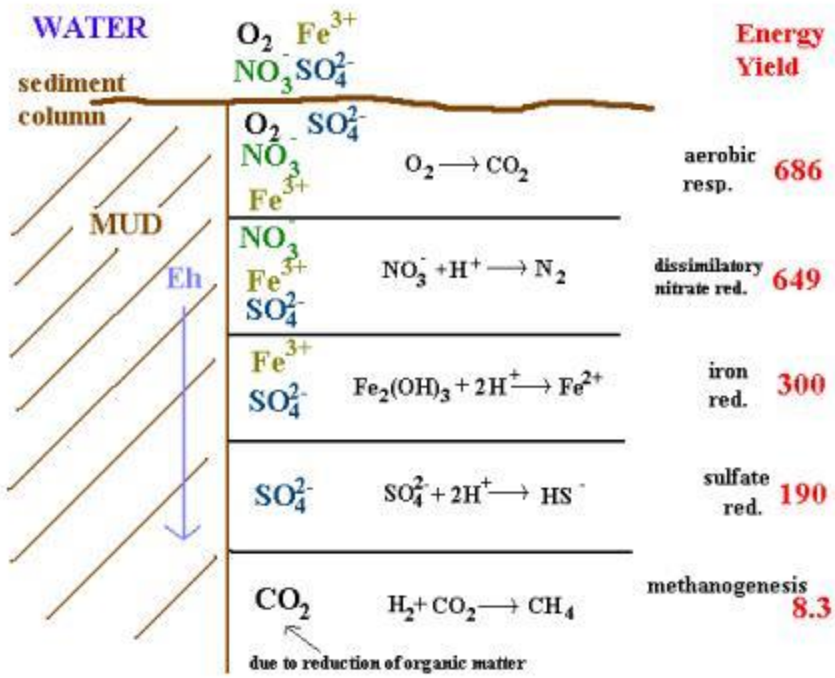
c) δελτα□G° ' = -193.5 kcal/mol

d) Whether methane can be oxidized with either SO_4^{2-} or NO_3^- is disputed

VIII. Oxidation of organic matter

A. Sediments

Oxidation of organic matter



This sequence also occurs in stratified lakes with anoxic hypolimnia

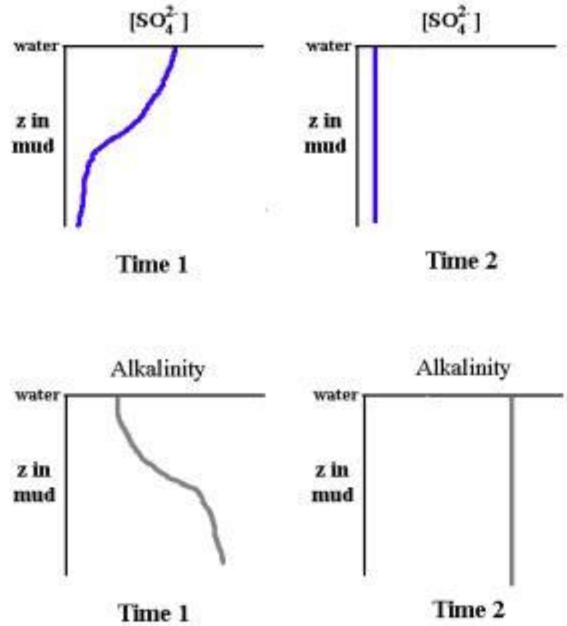
B. Other examples

1. Sediment profile:

   What happened from time 1 to time 2?

Redox Example 1, continued

- Sulfate reduction
- Alkalinity Changes

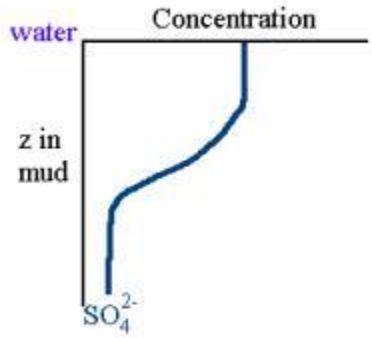


$$2CHO + SO_4^{2-} + 3H^+ \leftrightarrow 2CO_2 + HS^- + 2H_2O$$

2.

Redox Example 2

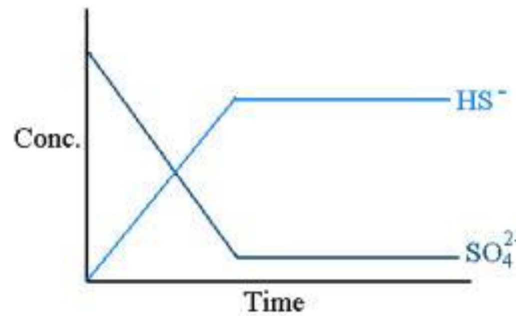
- If sulfate profile is as given, what is the methane profile?



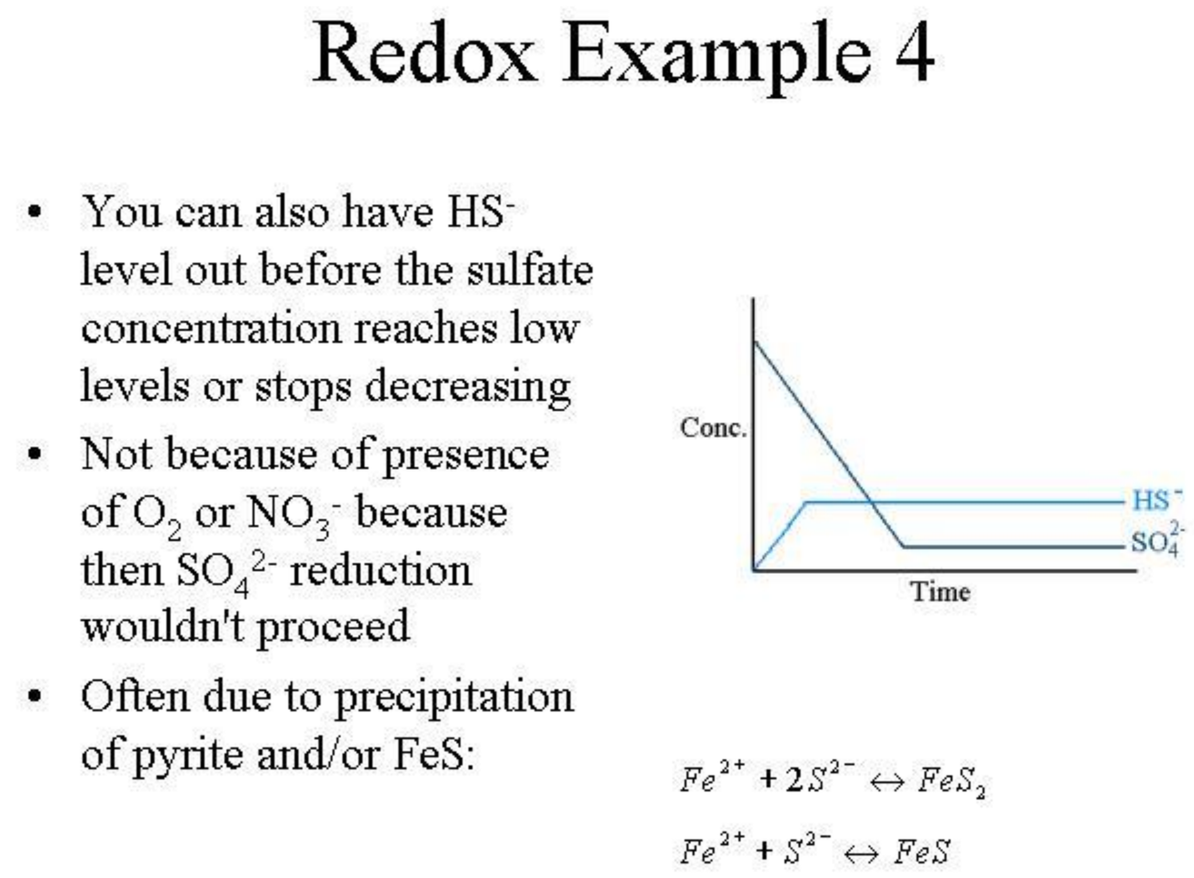
3.

Redox Example 3

- Time course in water column above sediments
- What is happening here?
  - Sulfate reduction
- Why does the curve level off?
  - Ran out of substrate
- What does the alkalinity look like?



4. You can also have the HS- level out before the sulfate concentration reaches low levels and stops decreasing. Why?

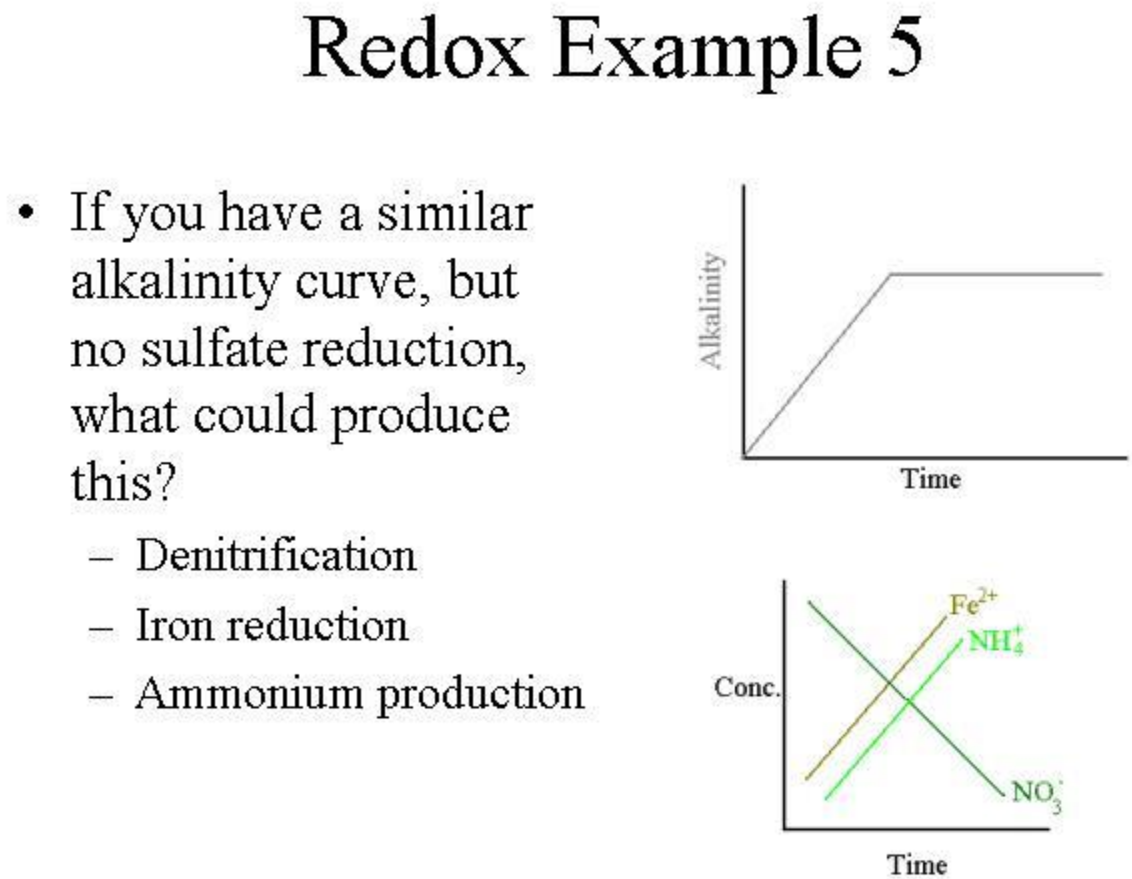


-Not because of presence of O_2 or NO_3^- because then SO_4^{2-} reduction wouldn't proceed

-Often due to precipitation of pyrite: (see above)

for this to occur, there must be a source of Fe^{2+}

5.



NITROGEN CYCLING

I. Background

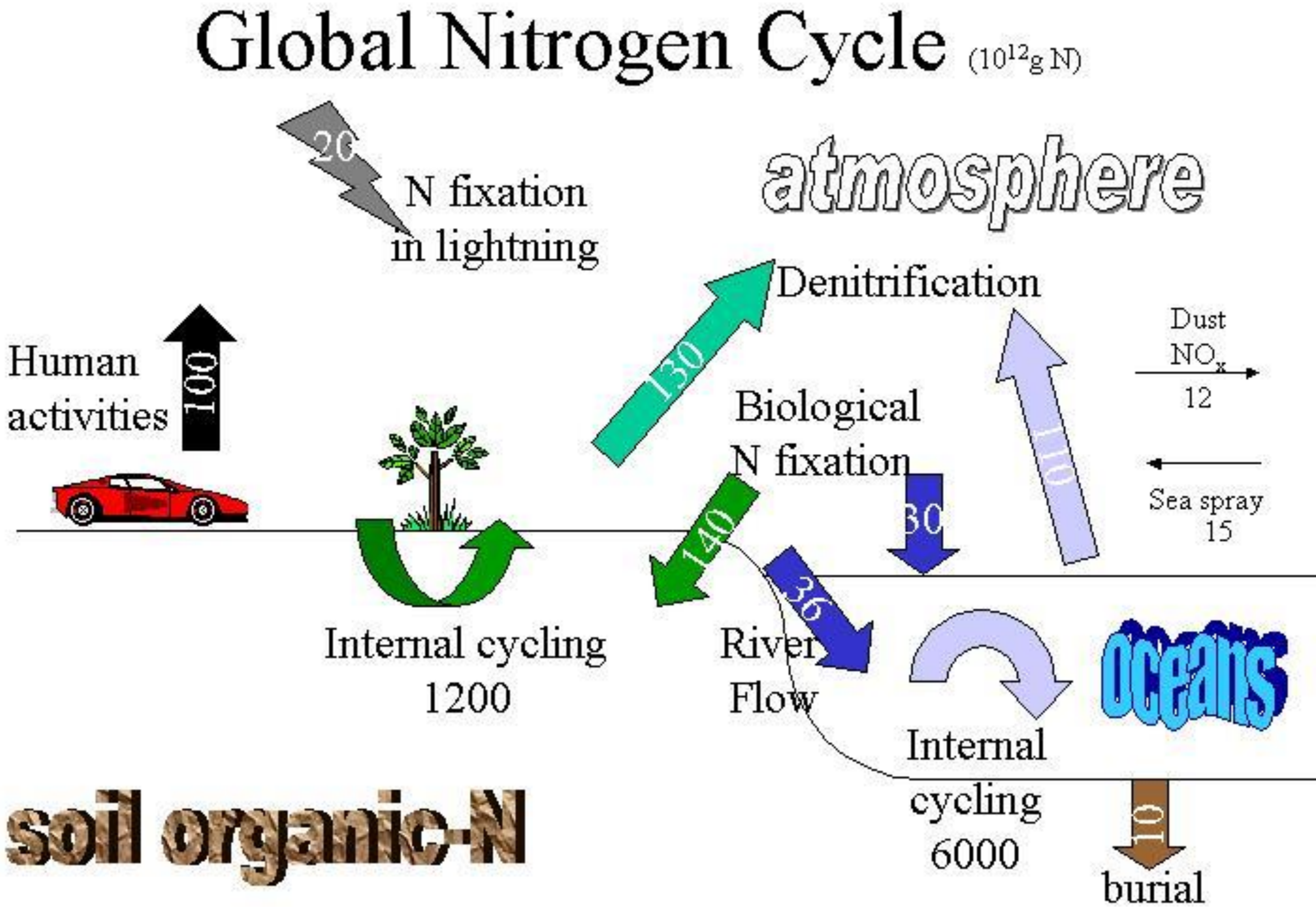
A. N can exist in multiple oxidation states

-3	0	+3	+5
NH_4^+	N_2	NO_2^-	NO_3^-
reduced			oxidized

B. N is a basic component of protoplasm

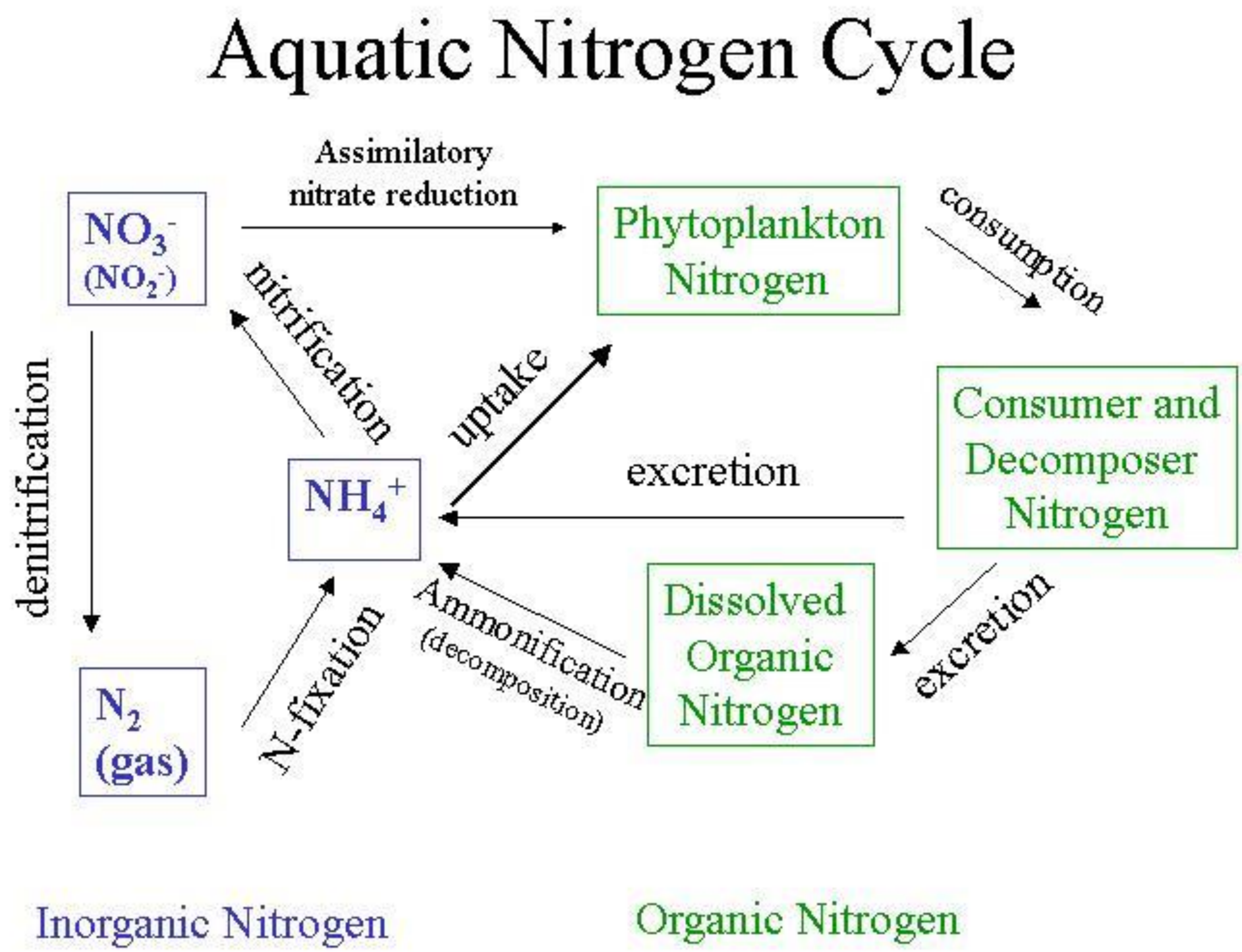
II. Nitrogen cycle

A. Global N cycle



B. Aquatic N cycle

1. Closed cycle



2. Example of inputs and outputs

Lake Mendota, Wisconsin (modified from Wetzel)

3. Human impacts

III. Reactions within the aquatic cycle

A. NH_4^+ uptake by algae: $NH_4^+ \rightarrow organic-N(NH_3)$

B. Ammonificaton -- ammonium production through decomposition of organic matter: $organic-N(NH_3) \rightarrow NH_4^+$

NH_4OH toxic

C. Nitrification -- NH_4^+ conversion to NO_3^- (oxidation; bacterial gain of energy)

$$NH_4^+ + \frac{3}{2}O_2 \leftrightarrow NO_2^- + 2H^+ + H_2O$$

$$NO_2^- + \frac{1}{2}O_2 \leftrightarrow NO_3^-$$

D. NO_3^- uptake by algae (<u>assimilatory nitrate reduction</u>): NO_3^- to organic-N(NH_3)

$$NO_3^- + H^+ \rightarrow NH_3 - organic$$

E. Denitrification -- dissimilatory NO_3^- to N_2 (reduction)

$$CH_2O + NO_3^- + 2H^+ \leftrightarrow CO_2 + \frac{1}{2}N_2 + 2H_2O$$

F. Nitrogen fixation -- N_2 to organic-N(NH_3); cyanobacteria

Is very energy expensive -- 76 kcal/mole N

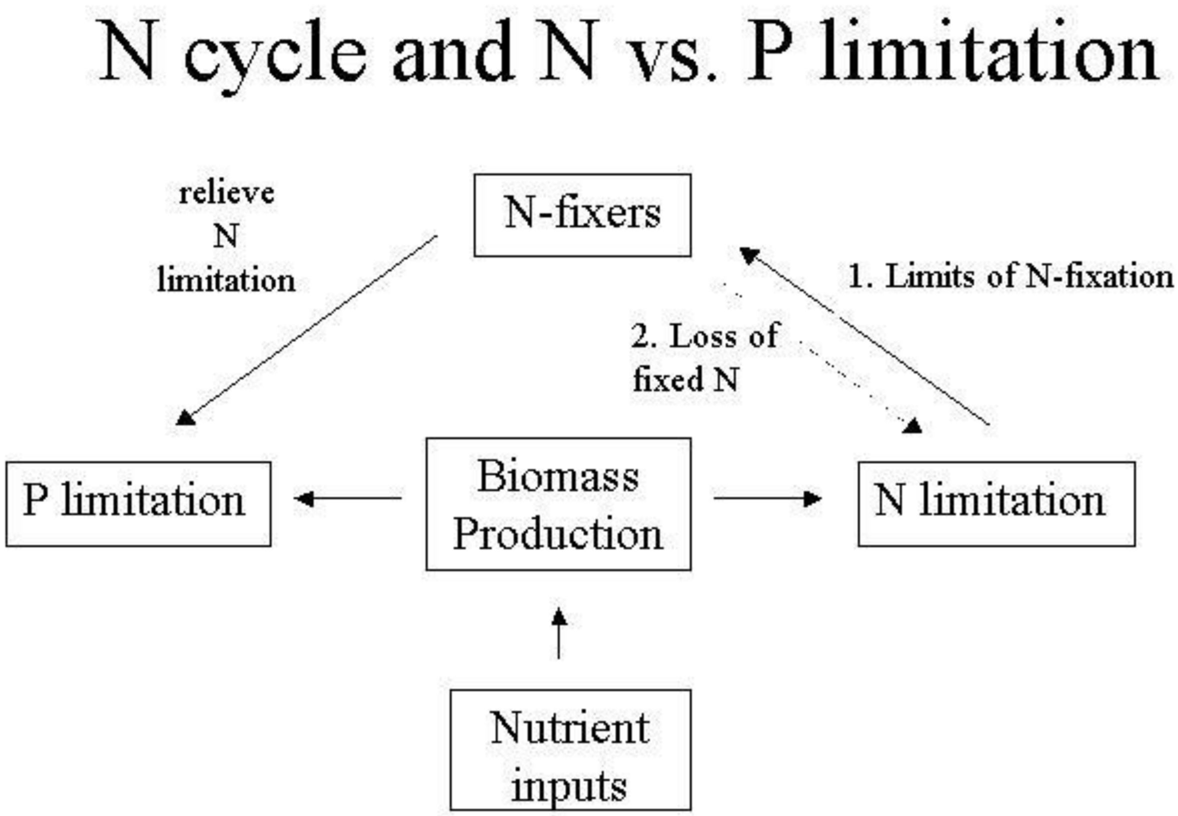
III. Nitrogen cycle and N limitation

A. Patterns

In most cases, P is limiting to algal growth in lakes

N most often limiting to algal growth in oceans and estuaries

B. How can you get N limitation?



1. Loss of fixed N -- denitrification

2. Limits on N fixation

a. light -- the N - N triple bond in atmospheric N_2 is hard to break -- requires lots of light energy.

b. trace elements are limiting -- iron and molybdenum needed to fix N

c. too little phosphorus for N-fixing cyanobacteria to grow

d. CO_2 can be limiting (only on short time scales)

NUTRIENT CYCLING AND PHOSPHORUS

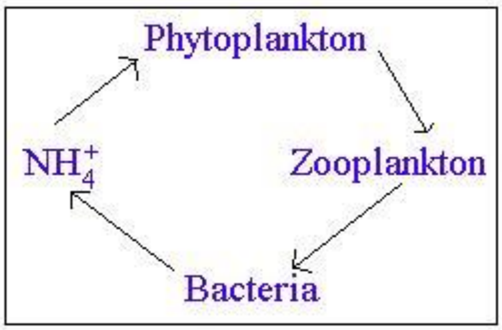
I. General Principles of Nutrient cycling

A. Energy versus nutrients

Energy flows

Nutrients cycle

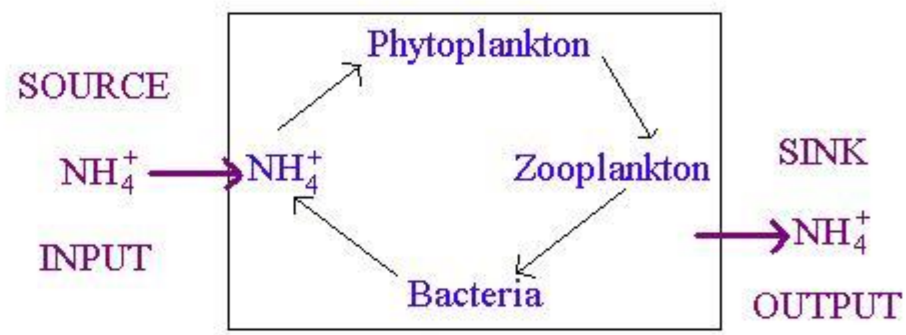
B. Closed system



1. rate = cycles/time
   a. as rate increases, productivity increases
   b. total N or P versus the amount of inorganically available N or P
2. pathways

   - In a closed system all the nutrients cycle within the system

C. **Open system**



- Boundaries

1. rate
2. pathways
3. <u>**residence time**</u> time spent cycling before being lost from the system

- residence time = amount of nutrient in the system/amount in output
- nutrient use depends on recycling rate <u>and</u> residence time
- inputs and outputs do not necessarily balance --

PHOSPHORUS

I. Importance -- Why study P?

A. Biomolecules

ADP and ATP, nucleic acids, phospholipids (membranes), apatite (bones and teeth)

B. Limiting nutrient

1. Theoretically most limiting nutrient

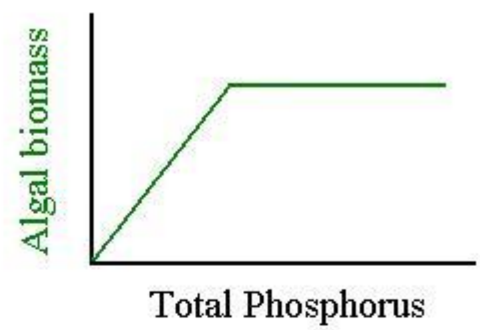
- '***Ecological stoichiometry***' -- Ratio of elements in plankton and other organisms (oceanographer ***Redfield*** in the 1950's)
- Found an average phytoplankton composition of

C	H	O	N	P	S
106	263	110	16	1	0.7

- and compared with available nutrient ratios
- based on these comparisons he considered P to be the most

limiting nutrient even though it is only
~1% organic matter
- BECAUSE the amount of P available to organisms is much less than the *amount required*
relative to these other elements
- in freshwater, P is often 80,000 X less concentrated than the amount required by phytoplankton
- Also implies that if nothing else is limiting, then increasing P can theoretically generate >100X
the weight of added P in algae

2. Algal biomass versus total P



3. Forms and Measurement of P
- Total **P = DIP + DOP + PP**
i. DIP – (<5%) dissolved inorganic phosphorus -- PO_4^{3-} polyphosphates
ii. DOP – dissolved organic phosphorus -- often associations of organic colloids; less quickly available
- Alkaline phosphatase enzyme mediates the release of P from these organic compounds; produced more when P is
limiting and can be an indicator of P limitation
iii. PP – particulate phosphorus -- often largest percentage of P in lakes (>70%) – nucleic acids (decompose slowly),
phosphate sugars, ATP (available more quickly)
- most P is in organic matter -- living or dead organisms;
- some particulate P is mineral P (not as bioavailable)
- phosphate adsorbed onto clays
-Measurement of phosphorus

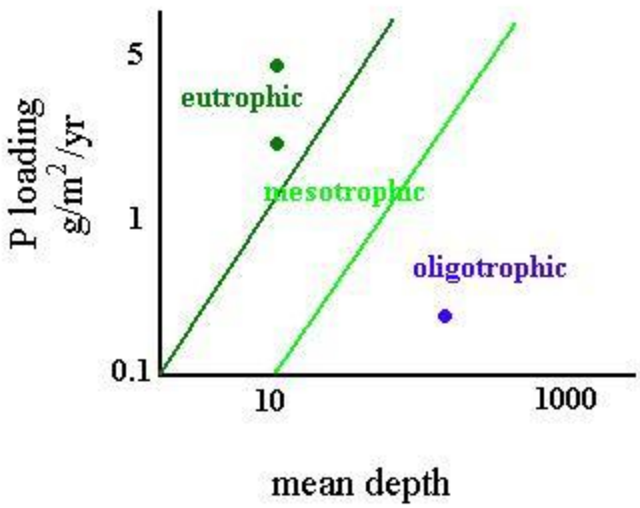
- soluble reactive phosphate (SRP) and scientists long thought this was PO_4^{3-}

- Unreactive phosphate – break down dissolved compounds – thought was organic (SUP) + PO_4^{3-}

- Particulate

- BUT, SRP is not PO_4^{3-}; measurement procedure actually digests some organics

4. P loading versus mean depth -- trophic state classification



Lake Productivity Classification	Total Phosphorus µg/L
Ultra-oligotrophic	<5
Oligotrophic	5-10
Mesotrophic	10-30
Eutrophic	30-100
Hypereutrophic	>100

5. No gas phase

i. phosphine (PH_3) gas may be produced by bacterial action under *strongly* reducing conditions

ii. spontaneously combusts

iii. may be responsible for will-o'-the-wisps, moving lights over swamps and marshes

6. Sources of P

i. weathering of calcium phosphate minerals, especially <u>apatite</u> [$Ca_5(PO_4)_3OH$] – is a slow process

ii. mostly stored in marine deep ocean sediments

iii. anthropogenic P is now often much greater than natural inputs of P in many watersheds -- sewage, urban runoff, agriculture,

"cultural eutrophication”

- ‘**point source**’ – sewage (treated or untreated), industry...
- ‘**nonpoint source**’ – e.g., agriculture – animal waste, fertilizers

7. Modes of Entry of P to aquatic systems

i. Precipitation – dust in air

ii. Groundwater –P adsorbs to soil particles

iii. Surface runoff

8. Decomposition and excretion

i. biota persist due to well-developed, efficient recycling of P

ii. P excreted by animals is rapidly taken up by algae and bacteria

iii. often one major function of decomposition is the liberating of usable P

iv. $organic - P \rightarrow PO_4^{3-}$

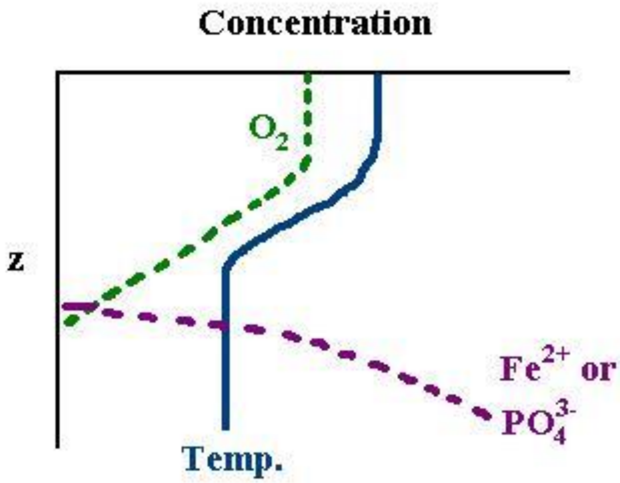
v. Lack of oxygen due to decomposition actually feeds back and affects the availability of PO_4^{3-} through some more redox reactions.

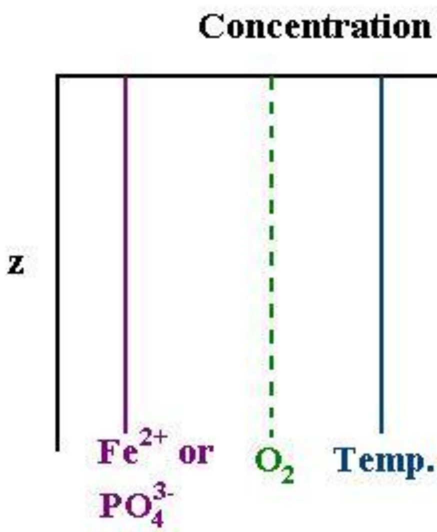
II. Redox reactions

- P doesn't go through redox reactions itself, but it is influenced by the solubility of Fe, which changes due to its redox state

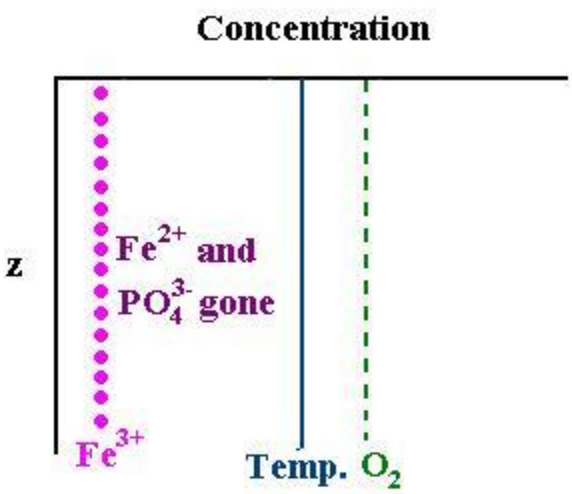
A. **Iron trap for P**

- In oxygenated waters, iron is present as Fe^{3+} (ferric)
- At pH<7 you get $Fe^{3+} + PO_4^{3-} \leftrightarrow FePO_4$ -- vivianite
- At pH> or equal to 7 you get $Fe^{3+} + PO_4^{3-} + OH^- \leftrightarrow Fe_x(OH)_y(PO_4)_z$
- **stratified lake** **day of turnover**


Concentration
z
O_2
Fe^{2+} or
PO_4^{3-}
Temp.

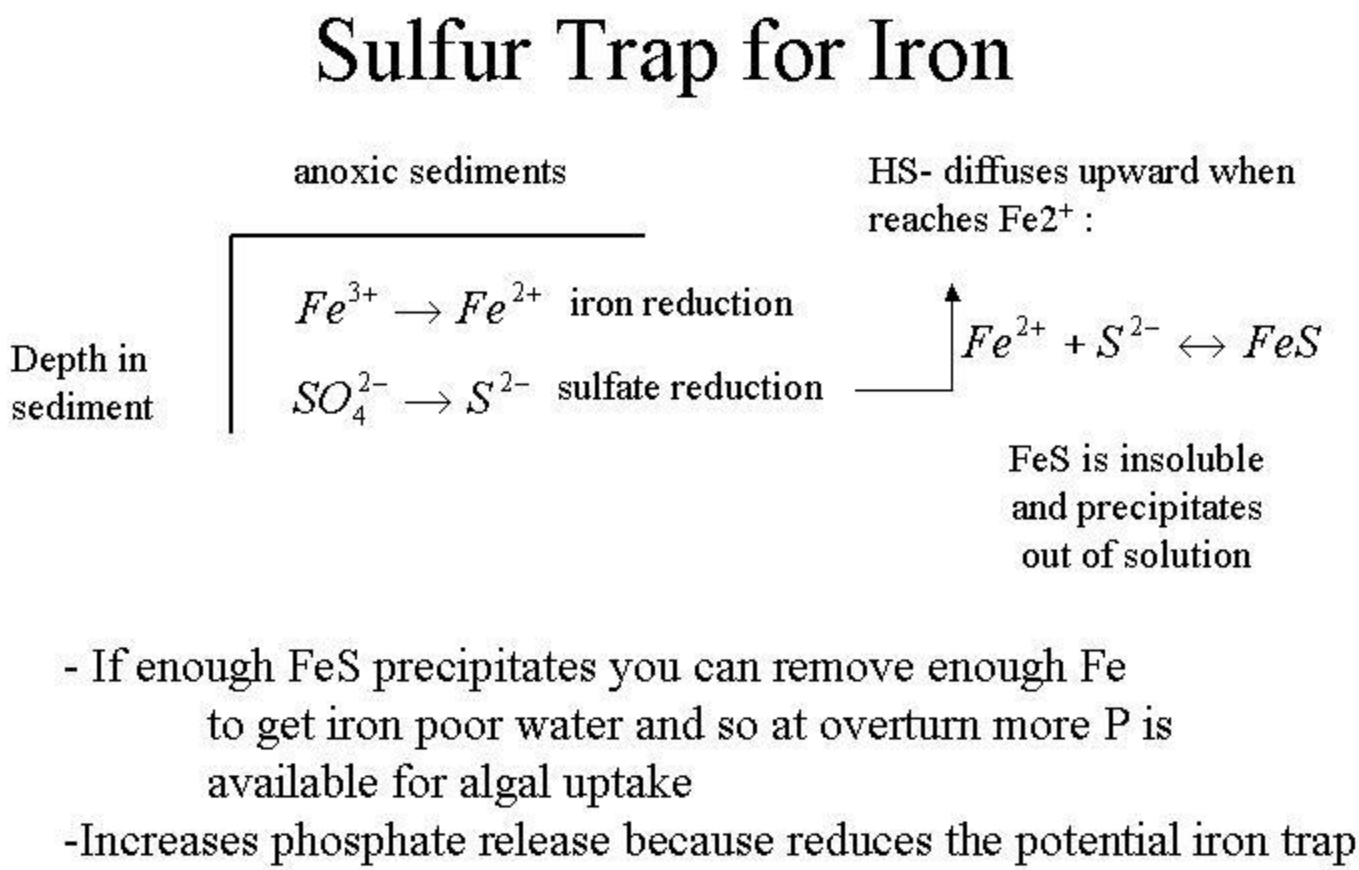

Concentration
z
Fe^{2+} or
PO_4^{3-}
O_2
Temp.

one week later



- What happens?
  i. Fe^{2+} is converted to Fe^{3+} due to presence of oxygen
  ii. Fe^{3+} goes to $Fe_x(OH)_y(PO_4)_z$, FeOH, and $FePO_4$
- "**iron trap for P**", less available for algae
- Can be a *critical point for eutrophication* -- when hypolimnion becomes anoxic, then more P is released and that increases the P recycling and loading from within the lake as well -- contributes to increased eutrophication.
- As long as hypolimnion remains oxic, any phosphate in sediments will be trapped by iron trap as it comes to the sediment surface, even if the sediments are anoxic.

B. **Sulfur trap for iron**



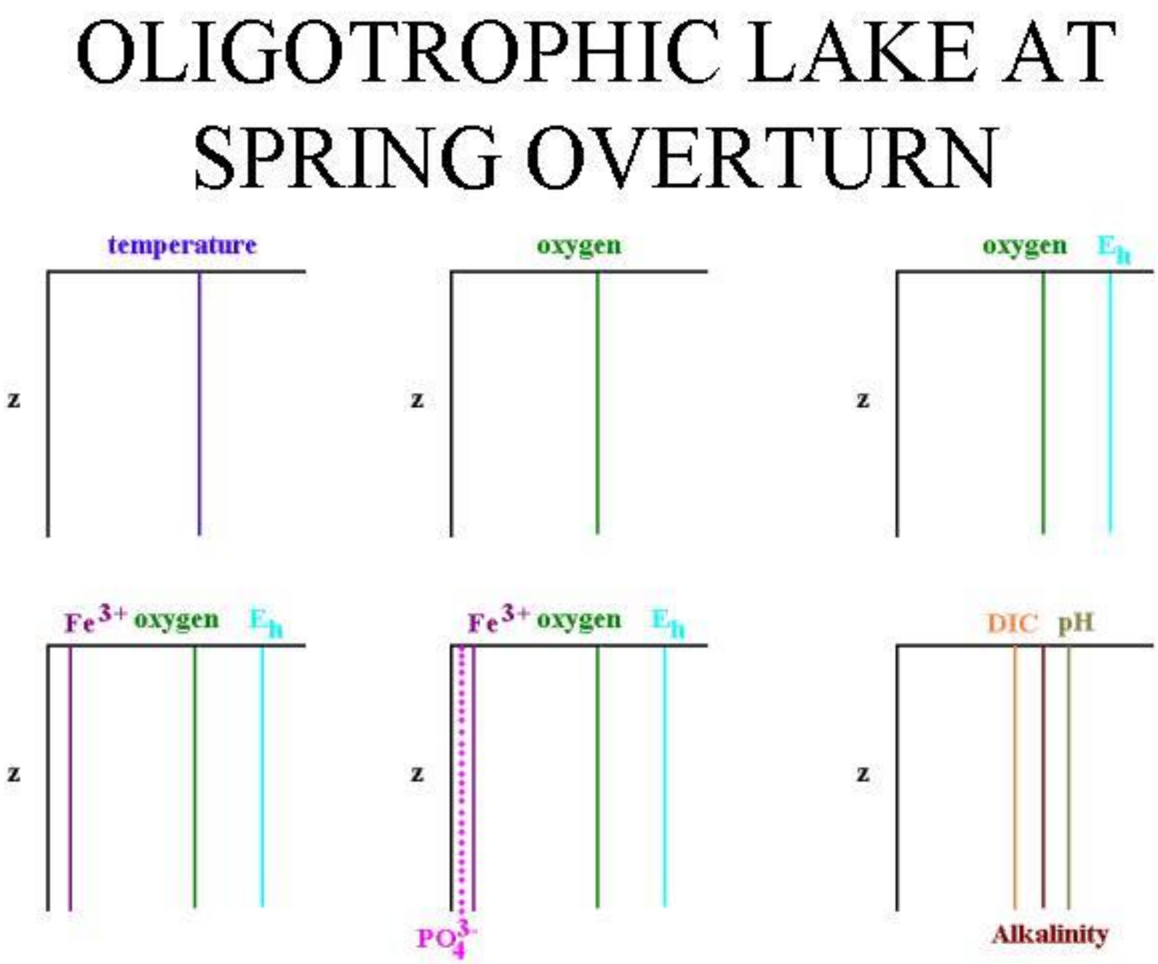
- If enough FeS precipitates you can remove enough Fe to get iron poor water and so at overturn more P is available for algal uptake
  - "<u>Sulfur trap for iron</u>"
  - increases phosphate release, because reduces the potential iron trap

SUMMARY OF REDOX EFFECTS ON PHOSPHATE CONCENTRATIONS:

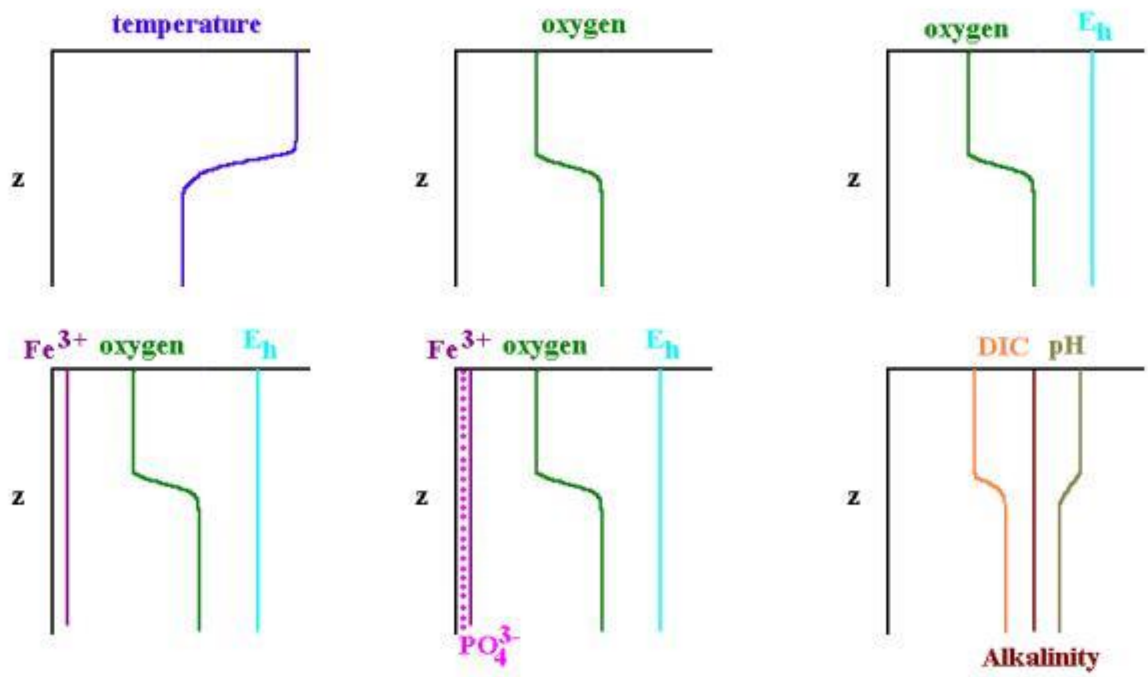
- Fe^{3+} conversion to Fe^{2+} releases PO_4^{3-}
- sulfur trap may lower iron concentrations enough to allow some phosphate to remain at overturn
- All these reactions mediated by bacteria

INTEGRATION OF NUTRIENT CYCLES

Types of Reactions
- A. Dissolved inorganic carbon/alkalinity
  - 1. PS/Resp. cause -/+ CO_2 , +/- pH , +/- O_2
- B. Redox Reactions
  - 1. +/- O_2 cause change in E_h
- C. PO_4 and Fe (solubility)
  - 1. +/- Eh changes Fe solubility and PO_4 co-precipitation

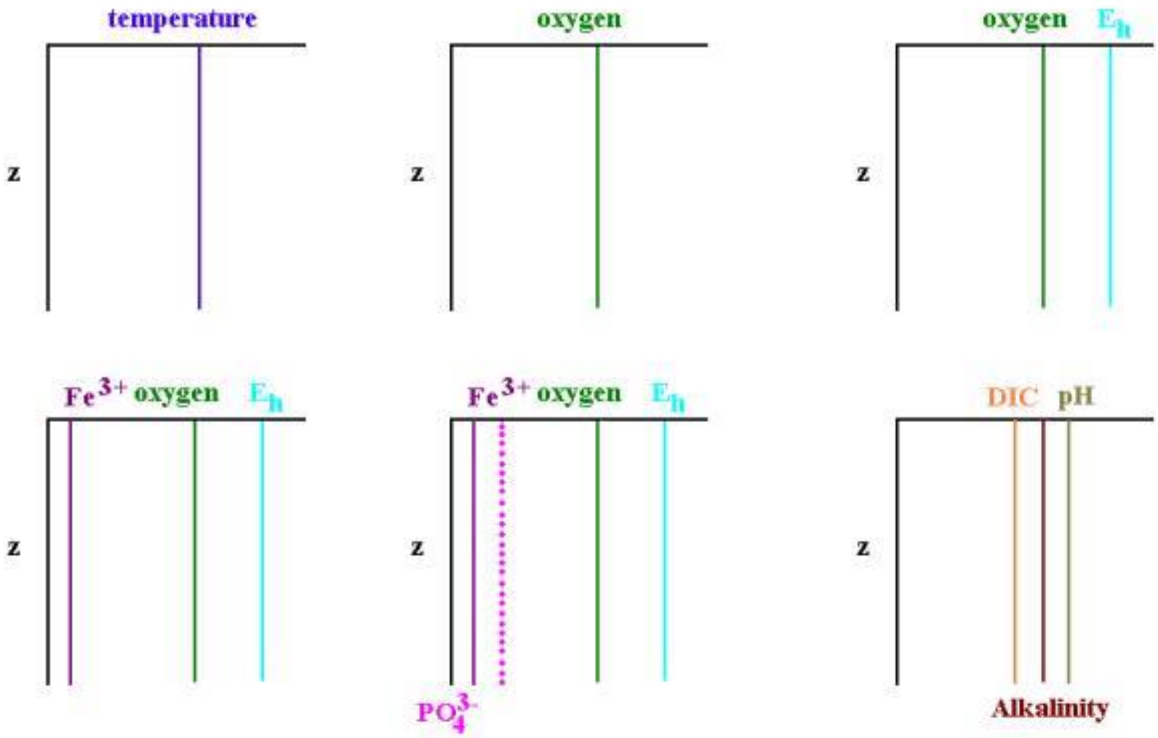


OLIGOTROPHIC LAKE AFTER STRATIFICATION

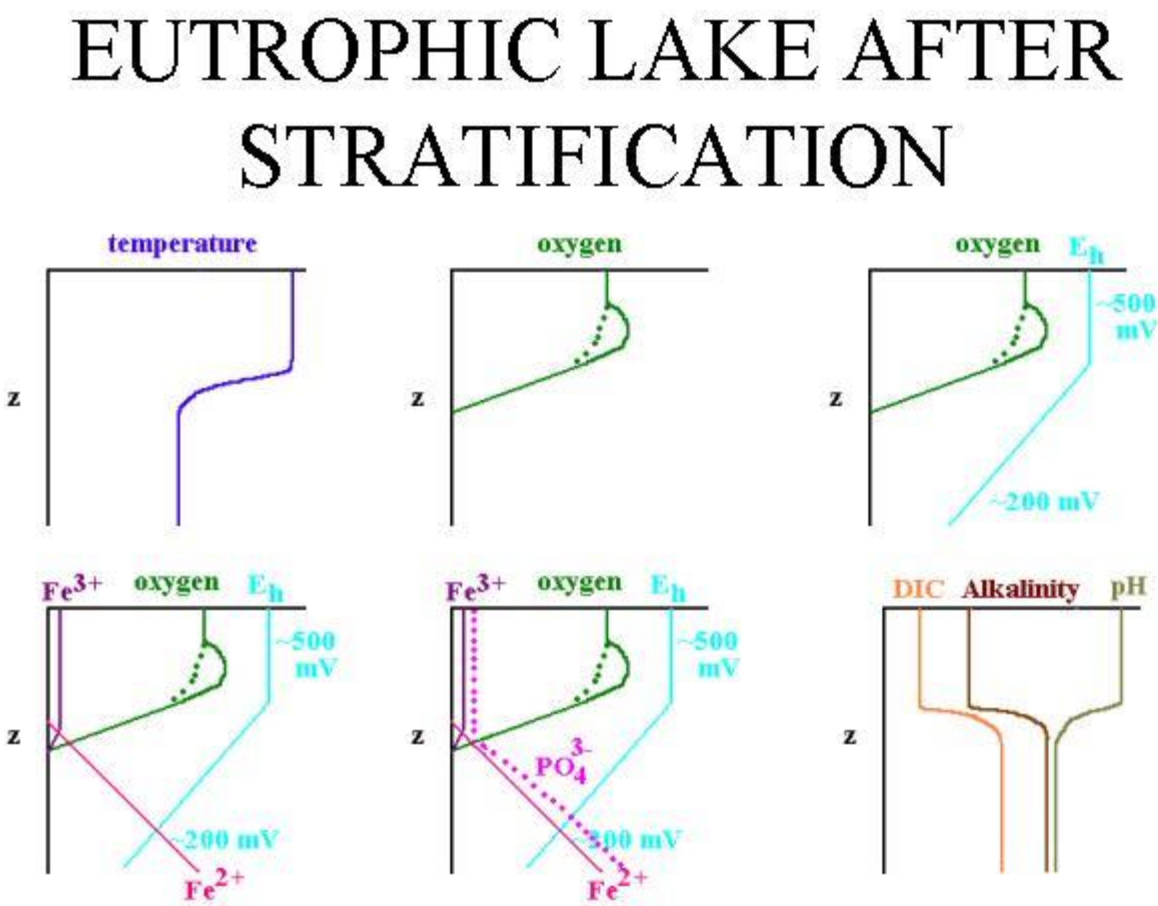


In an oligotrophic lake, the redox sequence of reactions occurs in the sediments

EUTROPHIC LAKE AT SPRING OVERTURN



DAYTIME PATTERNS



In a eutrophic lake, the redox sequence of reactions occurs in the water column

HYPOLIMNETIC VALUES DURING SUMMER STRATIFICATION

LAKE STATUS	**[O2]**	**Eh**	**Fe^{+2}**	**H_2S**	**PO_4^{3-}**
Oligotrophic	High (orthograde)	400-500 mV	Absent	Absent	Very low
Mesotrophic	Much reduced (clinograde)	400-500 mV	Absent	Absent	Low
Eutrophic	Much reduced or absent (clinograde)	~250 mV	High	Absent	High

Hypereutrophic	Absent	<100 mV	Decreasing (formation of FeS)	High	Very high

The Littoral Zone and Wetlands (with emphasis on aquatic macrophytes)

Littoral zone -- from high water area to area with no attached plants; interface between land and water; highly productive

I. **Aquatic Macrophytes --** almost all were originally land plants and are secondarily aquatic.

There are also some ferns, mosses, liverworts and large algae.

NOTE: *You only need to remember (recognize) genus names in **bold** (not others)*

A. Importance of macrophytes

1. Structurally important
   a. Define the littoral zone
   b. Often considered nuisances
   c. Slow currents and increase sedimentation
   d. Habitat for invertebrates and fish
   e. Increased species diversity

2. Functionally important
   a. Very productive
   b. Pump of nutrients from the sediments to the water
   c. High rates of evapotranspiration may decrease lake water levels
   d. Most of carbon fixed by macrophytes goes to the detrital/microbial food web

B. Ecological types of macrophytes – biodiversity of macrophytes

1. Rooted in sediment
   a. **Rooted submersed**
      (1) (Type 1) Long stems and compound leaves. Flexible.
         a) ***Potamogeton* --** pond weed;
            ~80 species in a variety of habitats; variable size and shape; wildlife food
         b) ***Myriophyllum* --** water milfoil
            (*M. spicatum* – Eurasian water milfoil is exotic; native is *M. sibiricum*)
         c) *Najas* -- bushy pond weed;
         d) ***Elodea*** -- water weed (has invaded Europe from N. America)
         e) ***Chara* -- green algae**, stoneworts, ‘musk grass’; precipitate calcium

carbonate
reproduction -- sporangia
f) *Nitella* -- **green algae**; acidic and dilute waters
(2) (Type 2) -- plants with stiff leaves in a close rosette or on short, rigid unbranched stems
a) *Ranunculus* (in part) -- water crowfoot
buttercup family; lodewort; rams foot; sometimes fed to animals
b) *Elatine* -- waterwort
c) *Isoetes* -- quillwort; club moss; often in oligotrophic lakes or deep in water
d) *Eriocaulon* – pipewort, hatpins;
e) ***Vallisneria*** - wild celery; tape grass; eel grass

b. **Rooted floating** (Type 3) - leaves mostly or entirely floating on the surface; lots of wind stress
a) ***Nymphaea*** -- water lily; nearly circular in shape; notched to the center
b) *Brasenia* – watershield; oval and shield shaped leaves. Stalk attached at center of leaf blades;
undersides covered with viscous jelly-like substance
c) *Nuphar* -- yellow water lily; spatterdock; cow lily – heart-shaped leaves
d) ***Potamogeton***
again, pondweeds most totally submersed; some have floating leaves
e) *Trapa* -- "water chestnut"; exotic pest in Central N.Y.

c. **Rooted emergent** – (Type 4) more supportive material, plenty of sunlight; very productive, but often a low species diversity
a) ***Scirpus*** – bulrush
b) *Juncus* – rushes
c) *Pontederia* – pickerelweed
d) ***Typha*** – cattail
e) *Eleocharis* – spikerush
~150 spp.; Some are cultivated as human food; some are major food for birds and other animals

f) *Sagittaria* – arrowhead; edible rhizomes

g) *Carex* – sedge; heavily used by wildlife
h) *Equisetum* -- horsetail/scouring-rush horsetail; consumed by wildlife

2. Unrooted – (can not get nutrients from sediments)
a. **Unrooted submersed**
a) ***Ceratophyllum*** **--** underwater flowers and mobile pollen; leaves are in

whorls on the stem – ‘raccoon’s tail’

b) ***Utricularia*** -- bladderwort; carnivorous

b. **Unrooted floating** (Type 5 – entire plant floating)

a) ***Eichornia*** – water hyacinth; exotic pest in S. U.S., S. America and Africa;

clogs waterways; increases rate of evaporation of water; not many things eat it;

floats into littoral zone and decomposes -- decreases oxygen, hurts fish breeding zones;

can block off light penetration

b) ***Lemna*** – duckweed

c) *Spirodela* - largest of the duckweeds

d) *Salvinia* - water fern; in waters with high organic content; has root-like structures that are actually modified fronds

e) *Pistia* - water lettuce

C. **Zonation** of macrophytes

1. Physical --
   a. Temperature
   b. Light
   c. Pressure -- affects gas transport; limits distribution
   d. Wind and waves
   e. Substrate -- rocks and sand are difficult, do better in soft and organic sediments

2. Biological (not as well studied)
   a. competition -- light, nutrients, space
   b. herbivory -- not as important compared to grazing on terrestrial plants or in the pelagic; << 25% of aboveground biomass

D. Adaptations of macrophytes -- how they deal with mostly physical limitations

1. Water is buoyant -- reduced amount of supportive tissue
2. Reduced light
   a. leaves only a few cells thick
   b. leaves are finely divided -- more surface area per volume
3. CO_2 availability -- diffusion slower than in air
   a. assimilation of HCO_3^-
   b. **lacunae**
   c. finely divided leaves

d. **heterophylly** -- plasticity of shape of plant -- leaves are more finely divided as get lower –

CO_2 concentrations or temperature

4. Nutrient availability
   a. most uptake through roots
   b. increased leaf length increases turbulent flow; then can take up nutrients through leaves as well.
5. Many can reproduce vegetatively -- turions (winter buds) or rhizome sprouting
6. Produce secondary defense compounds to inhibit algae, epiphytes, and grazers

II. Filamentous algae
- concentrated in the littoral zone
- must grow in shallow water where there is adequate light, but can go deeper than macrophytes (no lacunae; extra photosynthetic pigments)
- no roots, no leaves
- nutrients from sediments
- can cause problems/nuisances in small ponds
- often are chlorophytes (green algae; e.g. *Spirogyra*, ***Cladophora***) or cyanobacteria

III. Periphyton – algae (and associated microbes) that live attached to other objects, including macrophytes
- **Aufwuchs --** plants and animals that live attached to something
- can't be moved out of euphotic zone easily

- macrophytes are leaky and release nutrients through stems and leaves; algae take up nutrients from macrophytes

- If periphyton gets dense it will shade the macrophytes -- macrophytes keep growing to try to avoid shading

Wetlands (intermittently to permanently flooded regions)

I. **Peat forming** (accumulate partially decayed plant matter; 'mires')

A. **Bogs --**
- o sphagnum-moss dominated communities
- o only water source is rainwater (**ombrotrophic**)
- o low in nutrients
- o low in primary production
- o form acidic peats (lack of decomposition allows peat to build up)
- o support acidophilic vegetation

B. **Fens**

o Receives nutrients from sources other than precipitation, usually from groundwater

o may range from acidic to non acidic

o can have grasses, sedges, or reeds

o peat can develop due to lack of decomposition in acidic areas, or to high production in non-acidic areas

II. **Non peat forming**

- swamps -- mineral soils rather than peat; ground permanently or seasonally submerged;

vegetation dominated by trees or shrubs (in US common usage)

- marshes – frequently or continually wet areas with herbaceous vegetation adapted to saturated soil conditions

- wet meadows – grasslands with water-logged soil near the surface, but without standing water for most of the year

Wetland and Littoral Management

I. Wetland destruction

- ~1/2 of all wetlands lost in the contiguous U.S. since 1780
- agricultural drainage; health reasons
- loss of birds, mammals and fish

II. Wetland restoration

- resemblance to the original?
- Peatlands

III. During eutrophication littoral plants are often outcompeted by phytoplankton (shading)

IV. Macrophyte control

- Mechanical harvesting
- Herbicides
- Biocontrol – grass carp; insects

Interested in wetlands/macrophytes and wetlands? Two good recent sources are:

Mitsch, W.J. and J.G. Gosselink. 2000. Wetlands. 3rd edition. John Wiley & Sons, Inc. 920 pp.

Naiman, R.J., H. Décamps, and M.E. McClain. 2005. Riparia: Ecology, Conservation and Management of Streamside Communities Elsevier Academic Press. 430 pp.

STREAM BIOTA

Lotic (stream) environment

I. Zones and distributions
A. Physical factors
1. Changes in water levels – seasonal; some unpredictable
2. Changes in temperature – changes oxygen capacity
a. Small streams; unshaded streams
b. Stratification rare except in pools.
3. Oxygen
4. Chemistry – determined by catchment:
"In every respect, the valley rules the stream" (Hynes 1975)

5. Light – if stream has canopy or is turbid, low light may limit primary production in the stream itself
6. Flow
a. Advantages
1. respiration
2. filter feeding
3. transportation (if organisms can control it)
4. chemical communication – water flow increases chemical movements – prey can detect upstream predators

b. Disadvantages –
1. can dislodge organisms
2. shearing action of flowing water transports and deposits material, continually changing the physical environment
B. **Riparian zone** – normally above water line; may be inundated during floods
1. **Allochthonous inputs** – inputs to the system from outside – DOM, leaves, etc.
2. Water and nutrient inputs

Chemical transformation **--** e.g., NH_4^+ to NO_3^-
adsorption of nutrients

C. Shore zone – often bare; colonization difficult – water level often fluctuates
D. Water column
1. **Potamoplankton** – river plankton; usually algae
2. **'tychoplankton'** – don't belong there but are washed in
3. **drift** – mostly aquatic insects – organisms being carried downstream; may

include zooplankton in large rivers

4. fish

E. Benthos - – attached or free-living on bottom

1. **Aufwuchs** – fungi, algae, bacteria, protozoans and some organisms feeding on them

a. Epipelic

b. Epilithic

c. Epiphytic

2. rooted plants

3. animals: aquatic insects, mollusks, fish

F. **Hyporheic** – "below current"

II. Adaptations

A. Algae

1. firmly attached to hard substrates

2. motile

3. body form

a. flattened – trying to remain in boundary layer where there is little current

b. trailing filaments – increase exposure to nutrients

B. Higher plants (angiosperms, liverworts, mosses)

1. attached to rocks

2. rooted in substrate – tough yet flexible stems

C. Potamoplankton

1. River size – there are more potamoplankton as go downstream with increased size of stream and often get decreased velocity areas (pools)

2. No special adaptations

3. Seasonal changes due to export from nearby quieter waters

III. Benthic Invertebrates – most adaptations, wide phylogenetic diversity

1. **Mollusca** (Gastropoda, Bivalvia);

2. Turbellaria (flatworms)

3. **Crustacea** (**crayfish, amphipods**, isopods),

4. Oligochaetes, **Hirudinea** (leeches)

5. Acari (water mites), **Porifera** (sponges)

6. **Cnidaria** (hydra)

7. **Nematoda** (roundworms)

8. Major orders of stream insects

a. **Plecoptera -** stone flies; mostly in temperate regions; rare in tropics; cool, clean streams of low orders; sensitive to low oxygen; tolerant of low pH; adults are poor fliers

b. **Trichoptera** - caddis flies; worldwide distribution; both free-living case-building species

c. **Ephemeroptera** – mayflies; world-wide distribution; gills for respiration; sensitive to low pH; adult lifespan short and do not feed as adults.

d. **Odonata** - dragonflies and damselflies; occur worldwide predators; stalk their prey; can eat vertebrates as well

e. **Diptera** (true flies)- midges(Chironomidae - nonbiting midges); black flies (Simuliidae)

f. **Coleoptera** (beetles) aquatic beetles tend to live in water both as larvae and as adults

Stream Ecology, Part II

D. Benthic Invertebrates – most adaptations, wide phylogenetic diversity

1. Morphology
   a. Flattened and streamlined - decrease resistance to flow; but is also an adaptation for living under rocks
   b. Suckers and hooks - allows to grasp rocks; hooks (tarsal claws)
   c. Tubes -- Chironomid larvae, sticky silk, attached to rock
   d. Ballast - help them to remain on bottom

4. Behavioral responses to stream flow
   a. Current avoidance
   b. **Drift** (both a noun and a verb)
      mostly at night
   c. There is also some movement upstream, but this is relatively slow
   d. Why drift?
      1) **Proximate cause** (cues) - light

      2) **Ultimate or adaptive cause**
         a) None - Accidental -

            - *but* this is counter to periodicity;
            - there **is** some low level continuous accidental displacement

         b) None - Catastrophic drift -- pulsed high density movements resulting from major physical and chemical disturbances
         c) Dispersal - behavioral drift
            i. critical density of organisms that is too high

ii. lack of food
iii. avoid pollutants
iv. some individuals are genetically more predisposed to drift than others

d) Avoid Risks (greatest when moving in the water column) predation by fish

e. Compensation for drift -- why aren't all the insects in the ocean? Why are there any left in the streams?

(1) Colonization cycle – upstream flight

Adults fly upstream; not tested until recently
-Arctic stream insects were labeled with $^{15}NH_4^+$ by introducing it into the stream
-Collected adults upstream later in season when emerging
-Any insects above the $^{15}NH_4^+$ emergence point with ^{15}N had to have come from downstream
Average distance of flight upstream ~2 km
Average distance of downstream drift ~2 km
Therefore upstream flight of adults *can* compensate for drift

(2) Excess production hypothesis

Even if many drift, there are still a lot left
Better success of eggs deposited upstream – less competition
Difficult to assess because it is difficult to measure upstream production and combine these measurements with downstream movement

II. Stream ecology

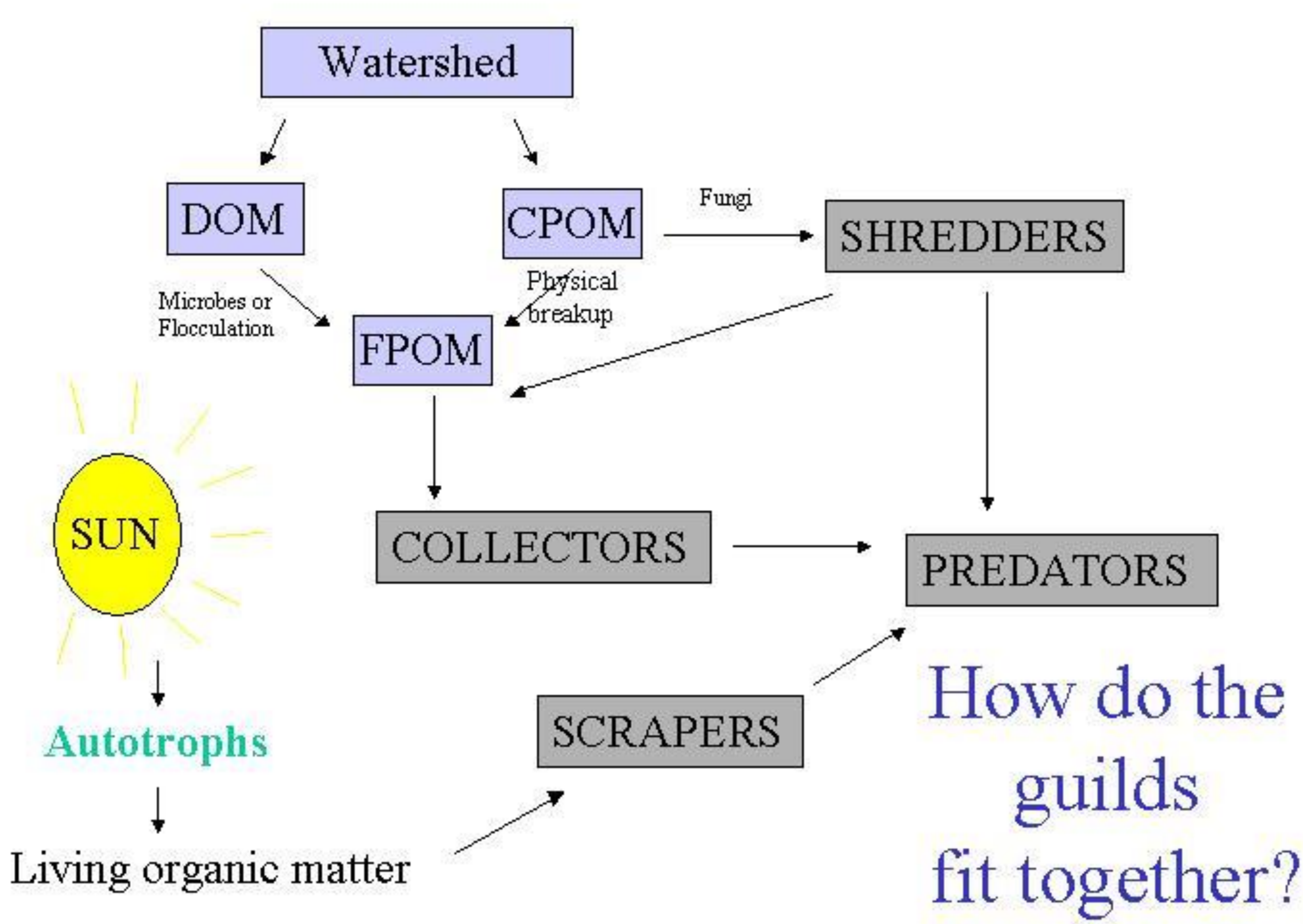
A. Feeding – ***functional group concept*** – 'guilds'

1. **shredders -** biters and chewers; take large food and produce small foods; herbivorous or detritivorous (leaves and microfauna)
2. **scrapers -** feed on aufwuchs (on substrates); specialized mouth parts to scrape material on substrates
3. **collectors -** spin nets or use setae to collect organic matter; feed on fine particulate organic matter;
filter with nets, hairs; cephalic fans (black flies)
4. **predators -** carnivorous; swallow prey whole or bite pieces or suck out contents

B. detrital material - much of the food web in a stream is detrital; this detritus is broken up into categories by size

1. CPOM - coarse particulate organic matter; >1 mm; leaves, wood, litter
2. FPOM - fine particulate organic matter; 50 µm-1mm
3. DOM - <~0.45 µm

C. How do the guilds fit together?



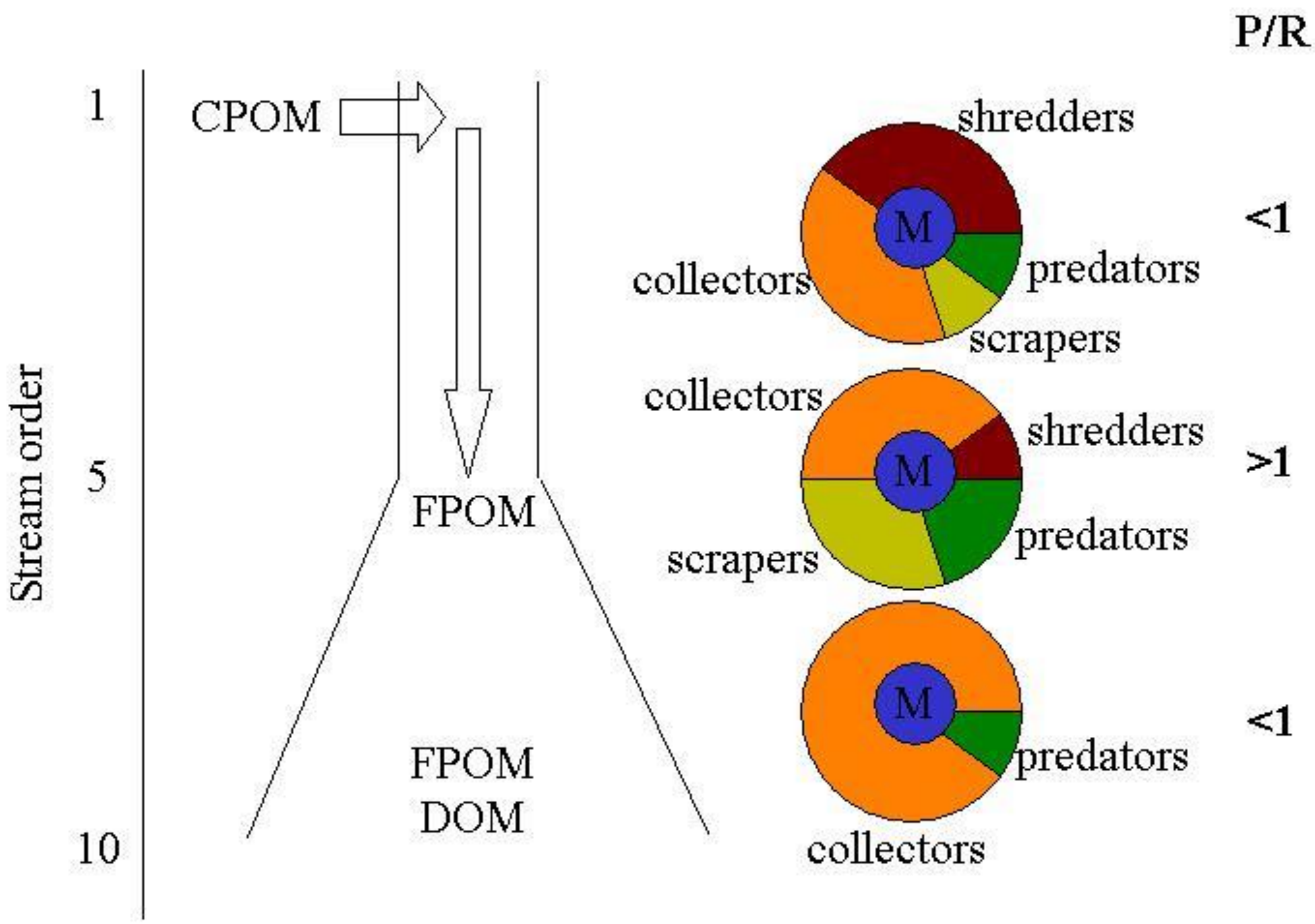
D. **River continuum concept** (Vannote et al. 1980)

- Streams change as you go from the headwaters to the high order rivers
  1. predictable physical features and gradients
     - stream velocity, suspended particulate load, width and depth of stream

2. predictable biological features --

- structure of community and function;
- P/R (production/respiration)

3. correlation of 1 and 2



-Why P<R at 1st order? --

- lots CPOM input to stream and it is being decomposed
- low production due to light limitation (stream is shaded)

-In the middle order

- less CPOM; more collectors and scrapers (fewer shredders);

- more light leads to more production

-Higher order streams

- more FPOM, no scrapers because fewer algae;
- light-limited due to suspended sediments

4. criticisms -
   i. oversimplified;
   ii. mostly holds for pristine rivers
   iii. relates only to macroinvertebrates
   iv. if low order streams are devoid of forest then they aren't shaded and don't have high CPOM loads

E. **Resource spiraling concept** (Newbold et al. 1982)
1. closed system (no inputs or outputs; have rate and pathways)
2. open system (inputs, outputs; rates, pathways, residence time)
3. open system with spiraling (downstream transport)
   a. rate
   b. pathway
   c. residence time
   d. downhill transport 'spiral length' :

   - uptake length - downstream distance a released atom is transported until it is captured again;
   - turnover length- downstream distance moved while in organisms

Slow water, rapid turnover, short spirals
Fast water, slow turnover, long spirals
Often as productivity increases, spiral length decreases

Important for looking at distubances and the responses to disturbances because they propagate downstream

F. Controls on lotic community structure -- What controls the biosystem?
1. **density dependent** = 'biotic interactions'; function of how many organisms are around
   a. competition - for space
   b. predation
   c. parasitism
2. **density independent** = 'abiotic factors'

a. floods
b. changes in substrate
c. changes in temperature (e.g. freezing)

3. Which mechanism dominates? Evidence for both
   a. Abiotic factors have clear influences
   b. Correlational evidence -- density dependent correlations of 1 species with another.
   c. Experiments
      1) Have shown clear effects of grazers feeding on periphyton
      2) Manipulation of insect predators in cages have demonstrated biotic density dependent control
      3) Manipulations of fish predators in cages -- small biotic effects (when you change fish abundance, the *abundance* of insects doesn't change much), although big behavioral effects

   d. Conclusions
      1) Evidence favors strong abiotic controls
      2) Importance of time scale, large abiotic factors (flood/freeze) reset the system frequently so that you don't get enough time/high enough densities for important biotic effects in many streams
      3) In more stable conditions you get lots of biotic interactions
      3) Really not settled yet
         a) continuum of regulation -- Peckarsky
         b) long-term records -- to see how often resetting occurs
         c) density dependent effects -- often subtle; behavioral

GOOD GENERAL STREAM ECOLOGY TEXT BOOKS

Allan, J.D. 1995. Stream ecology: structure and function of running waters. Chapman & Hall.
Cushing, C. and J.D. Allan. 2001. Streams: Their Ecology and Life. Academic Press.
Giller and Malmqvist. 1998. The biology of streams and rivers. Oxford University Press.

ZOOPLANKTON DIVERSITY

Most zooplankton are derived from marine ancestors (not aquatic spiders, mites, insects, pulmonate gastropods, rotifers

and perhaps cladocera)
Freshwater plankton don't bioluminesce

I. **Kingdom Protista** (microzooplankton) – single celled eukaryotic organisms
   A. Taxonomic groups
      1. **Subphylum Mastigophora** (flagellates)

      2. **Subphylum Sarcodina** (amoeboid forms)
         1) ***Amoeba***
         2) ***Difflugia***
            a) makes a hard case called a **test** of sand grains
            b) migrates vertically by regulating density by altering lipid content
            c) often get large *Difflugia* blooms in the great lakes in the spring
         3) Heliozoans
      3. **Phylum Ciliophora** (ciliates)
         Paramecium

   B. Miscellaneous
      1. Less work done on the ecology of individual microzooplankton protists than other zooplankton
      2. Many tolerate low oxygen concentrations
   C. Life history
      1. Reproduction by conjugation
      2. Some can reproduce asexually by fision
      3. Many forms can produce resistant protective cysts induced by drying, excessive heat or cold, lack of food
         (some viable for over 40 years)
   D. Feeding
      1. Mastigophora consume small algae, bacteria and detritus
      2. Ciliophora and Sarcodina can also consume mastigophora
      3. Cilia and flagella are used both for motility and to set up food currents
      4. Sarcodina have pseudopodia that engulf food
      5. Are themselves eaten by other zooplankton

Kingdom Animalia (metazoans)

II. **Phylum Cnidaria** (Coelenterata)
   A. Taxonomic Groups
      1. medusa
         Craspedacusta
   B. Miscellaneous
      1. Medusa forms are fairly rare, poor swimmers

2. Radially symmetrical

C. Life history –

1. Medusas have a polyp stage

2. The benthic cnidarian, *Hydra,* has lost medusa stage – when reproduce sexually they make eggs that when fertilized by sperm produce new polyps

D. Feeding –

1. Eat zooplankton and sometimes small larval fish

2. Have stinging cells (**cnidoblasts/nematocysts**) for catching prey – shoot out a sticky thread; some have neurotoxins

III. Phylum **Platyhelminthes (flatworms), Class Turbellaria**

A. Taxonomy

1. **Rhabdocoels** (order)

B. Miscellaneous

1. Move by cilia and muscular undulation

2. Gut opening in the center of body

C. Life History

1. Are hermaphrodites with internal fertilization

2. Direct development

D. Feeding

1. Predators and scavengers

2. Rise up from lake bottom at night and eat other zooplankton

(Case et al. 1979. Flatworms control density of mosquito larvae in rice paddies)

IV. Phylum **Mollusca**

A. Taxonomic Groups – adult mollusks are benthic, but some bivalves have planktonic larvae

B. Miscellaneous

1. **Glochidium** (larval form) found in the plankton

a. Most glochidia are parasitic and attach to fish

b. Later encyst

c. Metamorphose into mussels and sink to the bottom

3. **Veliger** larva of zebra and quagga mussels live in the plankton (disperse)

C. Life history

1. adult unionid mussels (native) release large numbers of small glochidia larvae

2. zebra mussel (exotic) veligers live in the plankton for ~10 days

D. Feeding

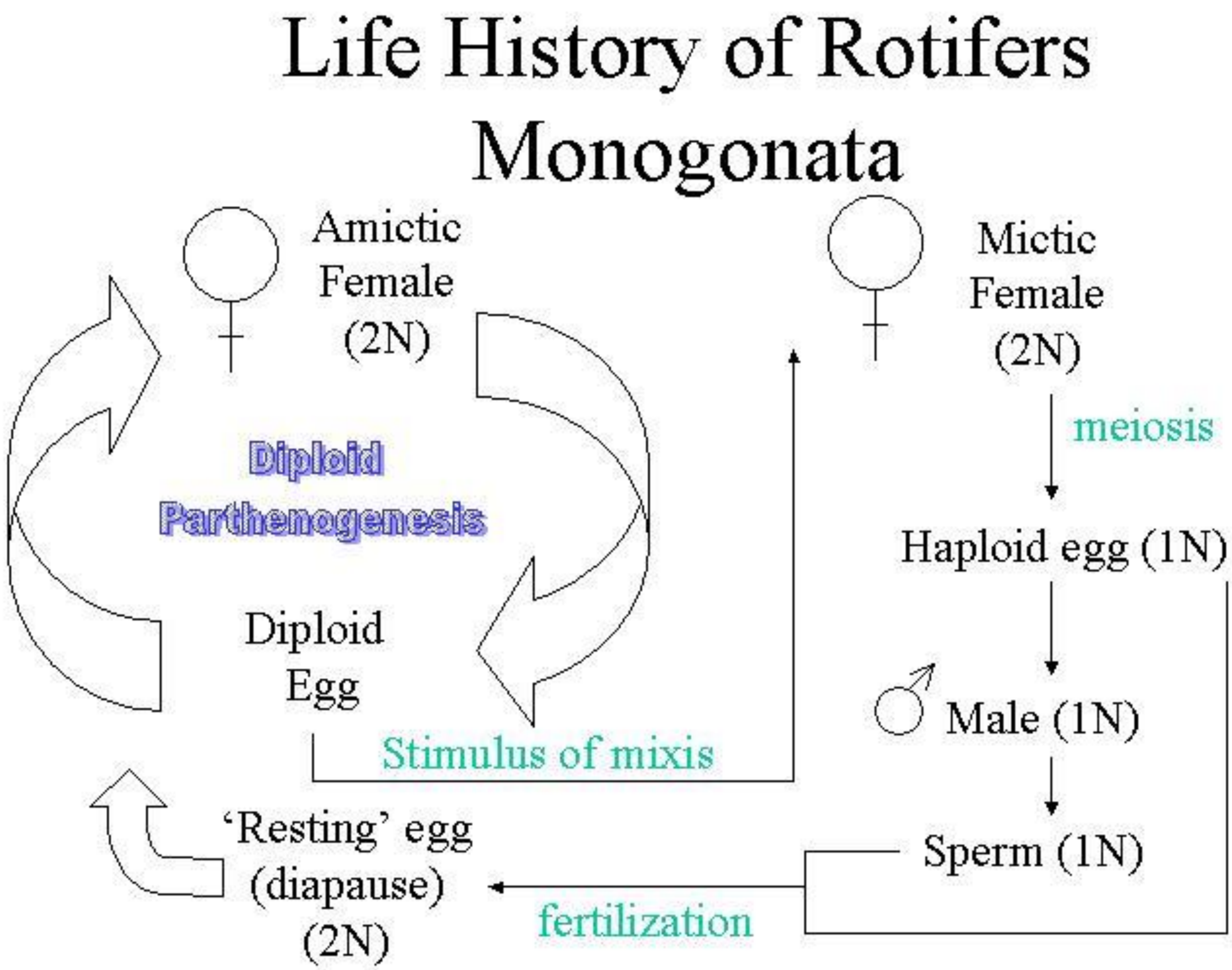
1. veligers consume algae (adults filter algae, microzooplankton and detritus from the water)

V. **Phylum Rotifera** (Rotatoria)

A. Taxonomy
1. Class **Bdellioda**
   a.~200 species; very difficult to tell apart
   b. ID them by their **trophi** (jaws)
2. Class **Monogonata**
   a. 90% of the species
   b. representative genera
      i. ***Keratella***
      ii. *Brachionus*
      iii. *Conochilus*
      iv. ***Asplanchna***

B. Miscellaneous
1. small: 30 μm (include the smallest metazoan) in tropics to 1 mm
2. most morphologically diverse group of freshwater plankton
3. some species are sessile (attached), but many are purely planktonic
4. most abundant in freshwater; evolved in freshwater
5. can have a hard case called a **lorica** (same name as for some algae);
6. have eutely – cell constancy – no cell division in any somatic cells
7. cilia band is known as a **corona**
8. jaws are called **trophi** and are made of chitin
9. often fairly abundant (200-300/L up to 5000/L)

C. Life History
1. Bdelloid males are never seen (no sex for 40 million years)
2. Monogonata are cyclical parthenogens



1. fast generation times – a few days to 2 weeks/generation
2. some species are viviparous
3. most lay 1 egg at a time and then carry it for 1-3 days
4. male production
   a. males are haploid (produced by meiosis)
   b. stimulus for male production -- sometimes diet shift, sometimes crowding
   c. resting eggs
      (1). Monogonata
      (2). Bdelloids never have males and don't have resting eggs; the adults can withstand desiccation

D. Feeding
   a. the rotifers use their cilia to create currents around their anterior ends
   b. some are predatory; some eat algae; some eat protozoans
   c. Trophi (jaws):

(1) malleate – designed to mash food; algae eaters
(2) virgate – designed to suck in food or puncture tissue and suck up contents
(3) forcipate – designed to extend out of mouth

VI. **Phylum Arthropoda, Class Crustacea, Order Branchiopoda**

A. Taxonomy

1. **Cladocera**

a) ***Daphnia*** – water flea
b) ***Bosmina***
c) ***Leptodora***
d) ***Cercopagis***

B. Miscellaneous

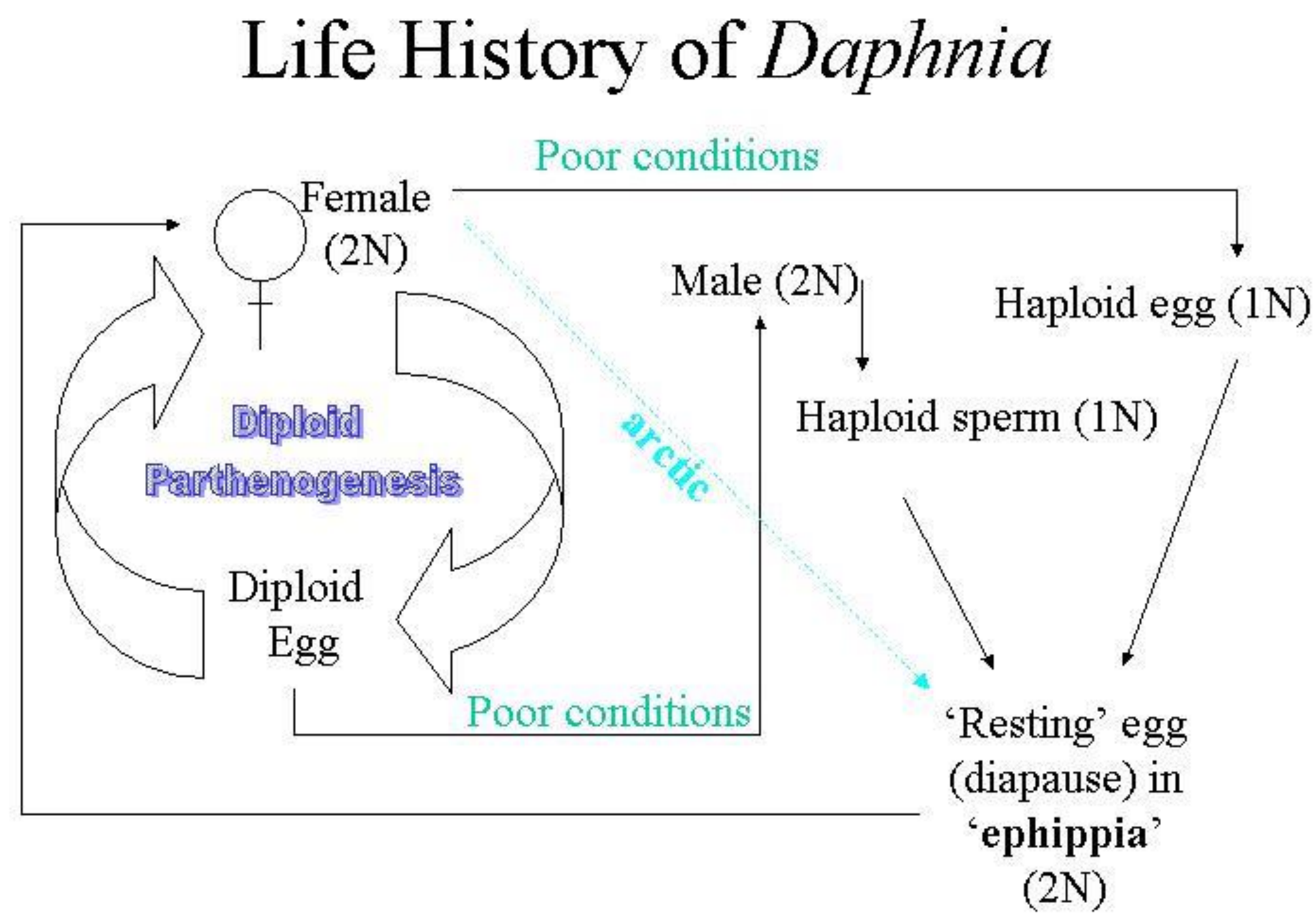
1. 300 μm to 1 cm long
2. Have a bivalve carapace with a gap
3. Herbivorous cladocera have paddle-shaped legs and draw water currents into carapace

C. Life History

1. rapid life cycles – 1 to 2 weeks per generation
2. most often are parthenogenic – cyclical parthenogens
3. direct development **--** no distinctive change in morphology associated with each instar
4. clutch size variable

a. related to age (body size), instar, food levels
b. eggs produced after each adult molt

5. cues for male and haploid egg production – crowding (excretion products), decreased food, light decreases, temperature decreases
6. Sexual reproduction results in diapause eggs **-- ephippia** (saddle)
7. arctic daphnids can often produce resting eggs without males (asexually)
8. Some daphnid species and clones never make resting eggs
9. some cladocera overwinter as adults in the lake



D. Feeding
1. most are herbivorous
2. some predaceous (*Leptodora*, *Polyphemus*, *Bythotrephes*)
3. some can feed on bacteria

VII. **Phylum Arthropoda, Class Crustacea, Order Copepoda**
A. Taxonomy
1. **Suborder Cyclopoida** – short antennae

2. **Suborder Calanoida** – long antennae
a. ***Diaptomus***

3. Suborder Harpacticoida -- mostly littoral and benthic; some parasitic

B. Miscellaneous
1. widely distributed in all freshwaters

a. from tropical to arctic regions
b. from low ionic strength to salty
2. Will accumulate different lipids if are in cold versus in warm environments
3. Body size -- 300 μm to 5 mm

C. Life History
1. Sexual reproduction only – males and females
2. Indirect development –
a) juvenile – **nauplius**
b) **copepodid** stage – metamorphosis to this stage
3. Cyclopoida
a. eggs are carried by the females in egg sacs
b. mating behavior
i. male make spermatophores (packages of nonflagellated sperm)
ii. males must give spermatophores to the females (mating pheromones and behavior)
iii. males have 'geniculate' antennae that are used to deposit spermatophore on female (true for calanoids as well)
c. relatively short generation time, several per year
1) 1-2 months per generation
2) generation time affected strongly by temperature
d. resting stages
1) in some species the eggs can be dried and hatch when wet
2) **diapause** in copepodite IV stage, not as a resting egg
3) encyst in sediments in fall and undergo stasis for the winter
4) diapause is broken by temperature or light in the spring
2. Calanoida
a. relatively long generation time, 1 to 2 per year
b. most carry eggs in a sac or deposit them into water
c. no diapause stage as a copepodite
d. production of morphologically distinct **resting eggs**
1) normal hatching eggs have a thin shell and the nauplii develop (rate proportional to temperature)
2) diapause (resting) eggs have a thicker shell and can withstand desiccation.
3) one type has a 2-layer integument or shell, mostly in Northern populations (arctic), some temperate, not tropical
4) cues for hatching related to temperature and light

D. Feeding
1. Cyclopoida
a. predaceous/omnivorous

(1) can feed on algae or other animals
(2) nauplii (juveniles) are generally herbivorous and there is an **ontogenetic** (developmental) switch from herbivory to predation as they metamorphose to adult copepods

b. no elaborate modifications for feeding

2. Calanoida
   a. set up feeding currents and remove particles – can select their food
   b. mostly herbivorous; large forms like *Epischura* are sometimes predaceous (but are herbivorous as nauplii)
   c. mouthparts of some modified for filter feeding
3. how do they find food?
   i. Mechanoreception – setae on antennae
   ii. Chemoreception
4. Harpacticoids
   a. mouthparts adapted for seizing and scraping particles from the sediments and macrovegetation
   b. parasitic on fish

VIII. **Phylum Arthropoda, Class Crustacea, Order Malacostraca**

A. Taxonomy

i. **Mysidacea - mysids**
(1) Glacial relicts
(2) Long lived
(3) omnivores

ii. **Amphipoda**

- Life history – two sexes; long lived
- Feeding - omnivores

IX. **Phylum Arthropoda, Class Crustacea, Eubranchiopoda**

In temporary bodies of water without fish
Eat algae, bacteria, protozoans, rotifers, detritus
Have resting eggs

A. **Anostraca - Fairy shrimp**
Swim on backs (‘like tiny walruses’)

B. Notostraca – tadpole shrimp (*Triops*)
Notostraca will also eat dead animals or are sometimes predaceous

X. **Phylum Arthropoda, Class Crustacea, Order Ostracoda**

Mostly benthic
Herbivorous
Resting eggs
Sexual or asexual reproduction

XI. **Phylum Arthropoda, Class Insecta**

A. Taxonomy

1. Dipteran (true fly) larvae

a) ***Chaoborus*** – voracious predator

2. Predators

3. Larval stage of flies

Integrated Plankton Ecology

I. Plankton distribution

A. Regional –

Biogeography

- cosmopolitan – many rotifers

- Some species (many cladocera and copepods) not distributed worldwide – good study organisms for questions of biogeography

Understudied in general for plankton vs. other organisms

1. tropics vs. arctic

2. flowing versus still water -- negative correlation of plankton size, diversity and numbers with water velocity

3. lake size

4. endemism

Baikal

5. chemistry – look at lake districts of crater lakes (reduce differences in lake morphometry)

a. Lake District	% similarity of rotifers among lakes
Cameroon	22
Bali	34
Germany/France	63 (most

similar chemistry)

Australia 13 (greatest differences in

Arizona/Mexico 17 chemistry – saline to FW)

b. Changing chemistry over time

Grand Coulee Dam

Year	Lake Lenore	Soap Lake
1945	16.9 g/L TDS	37.1
1961	3.1	18.9
1945	*Diaptomus sicilus*	*Moina*
	Diaptomus nevadensis	*Hexarthra*
1961	*Daphnia*	*Moina*
	rotifers	*Diaptomus sicilus*

c. conductivity

At conductivity >400 µS, start to lose zooplankton species

d. Specific Ions –

1. e.g., Changes in [Fl^-] in East Africa; copepods
2. calcium

e. Acidity

6. geography
   a. mountain ranges – may prohibit movement of species
   b. events not now apparent
      i. plate tectonics
      ii. climate events
         1. *Daphnia* in the lakes of Cameroon (40 crater lakes)
            alternative hypotheses

         2. glacial relict species
            a. *Mysis relicta* (opossum shrimp)
            b. *Limnocalanus*
7. other abiotic factors
   a. temperature
   b. lake morphology – variability in habitat
8. biotic controls
   a competition
   b. predation

B. Local

1. horizontal

a. pelagic versus littoral -- 'avoidance of shore'
b. patchiness – random, uniform, clumped
(1) uniform – spacing effect of territories
(2) clumped or random – currents, clumped resources, predators, seiches…
(3) scales of patchiness
a. large scale >1km (e.g., windward vs. leeward)
b. small scale, wind induced circulation; Langmuir circ.
c. swarms (biotic)

2. vertical – zooplankton can adjust their depth
a. patterns
(1) increased lake transparency – increased vertical migration
(2) increased organism body size – increased migration
(3) migration related to life history
(4) seasonal patterns
b. types -- **diel vertical migration**
(1) nocturnal
(2) twilight
(3) reversed
c. causal evaluation
(1) proximate cue is light
(2) ultimate or adaptive (plankton towers at Plon)
(a) metabolic boost hypothesis
(b) protection from damaging light
(c) protection from predation
vertebrate predators are visual predators
why come up ever? Food – production is at surface

II. Role of predation

A. Size structuring of fish – large bodied versus small bodied zooplankton

-Hrbacek, 1962, reservoirs in Poland and Czechoslovakia; fish species were correlated with zooplankton species

-Brooks and Dodson, – *Alosa* (blue-backed herring) efficient predator on zooplankton:

lakes with *Alosa* – *Bosmina*, small *Cyclops* and *Tropocyclops* – small zooplankton;

lakes without *Alosa* – large *Daphnia*, *Diaptomus*, *Epischura*, *Leptodora* – large zooplankton – correlational evidence

-1941 Crystal Lake – no *Alosa*, large bodied zooplankton

-1950's *Alosa* added to the lake

-1964 Crystal lake resampled – found small bodied zooplankton

-arctic – depth of the lake determines the presence/absence of fish <2 m freeze to the bottom, so no fish –

fish lakes have small bodied zooplankton, fishless lakes have large bodied zooplankton

-are exceptions – lakes with lots of piscivorous fish – effect of an extra trophic level

-better to be small in the face of vertebrate predation **- size selective predation**

WHY AREN'T ALL ZOOPLANKTON SMALL?

B. **Size-efficiency hypothesis** –

- Brooks and Dodson – large zooplankton are competitively superior
- can take a larger size range of food
- allometric (changes with body size) respiration function – lower respiration rate at larger size
- works sometimes, but not always (e.g., between cladocera and rotifers)
- other things going on – INVERTEBRATE PREDATION

Integrated Plankton Ecology, continued

II. Role of Predation, continued

C. **Cyclomorphosis** – changes in body form/shape over seasons – development of spines and changes in body shape – WHY?

1. resistance to sinking?

2. temperature?

3. predation?

a. vertebrate – Tom Zaret; Lake Gatun (Isthmus of Panama); 2 forms of *Ceriodaphnia cornuta* – *Melaniris* fish

b. invertebrate

- may set a minimum size
- invertebrate predators choose small or medium size prey – opposite to vertebrate predation
- example: Kerfoot - *Bosmina* and *Epischura*

So, why have a short form? greater reproductive output

- *Epischura* versus sticklebacks

D. Developmental polymorphisms

1. **inducible defenses**

a. chemical signals – morphogen chemicals

- Gilbert:
    - *Brachionus* (loricate rotifer); predator *Asplanchna* releases a chemical ('Asplanchnin') that induces *Brachionus* to become spined;
    - spines induced only with the water from an *Asplanchna* culture;
    - inducibility only in early developmental stages
- *Daphnia* with a *Chaoborus* predator

b. density

- *Asplanchna* (cannibalistic at high densities) – 3 forms – sacchate, campanulate, cruciform (large, resistant to predation by campanulate form)

-SO, TO AVOID INVERTEBRATE PREDATORS – CHANGE SHAPE TO MAKE PREDATION MORE DIFFICULT
-TO AVOID VERTEBRATE PREDATORS -- REDUCE VISIBILITY

2. pigmentation and light

a. high altitude or saline lakes without fish – copepods are often pigmented bright red

i. carotenoid pigment, astaxanthin;
ii. when exposed to blue/uv light, clear copepodsl die
iii. red pigment absorbs this light

b. high altitude or saline lakes with fish – no pigmentation because makes them visible; remain deeper in the water column

III. Summary of effects of invertebrate and vertebrate predators

Zooplankton community size
Phytoplankton that can be grazed

IV. Plankton in rivers, reservoirs and natural lakes

	Rivers	Reservoirs	Natural Lakes
Phytoplankton Diversity	Low in low order streams; increases in high order rivers	Low in riverine zone; increases in lacustrine zone	High diversity in oligotrophic, and mesotrophic lakes, decreasing in eutrophic

			lakes
Zooplankton Diversity	Small forms; rapid life cycles or mostly benthic life cycle	Small forms in riverine zone; lake forms in lacustrine zone	Micro and Macro-zooplankton
PhytoplanktonBiomass	Low in low order streams; increases in medium order rivers	High in nutrient-rich riverine zone; lower in lacustrine zone	Highly variable in temperate lakes (5 orders of magnitude); less variable in tropical lakes
Zooplankton Biomass	Low; inputs from lakes and floodplain pools; higher in higher order rivers	Most in transition zone; high degree of horizontal patchiness	High; vertical and seasonal gradients
PhytoplanktonProductivity	Low in low order streams and high order streams; limited by light and flow	High in transition zone; limited by light in riverine zone and nutrients in lacustrine zone	Increases with nutrient loading (until reach light limitation). Pelagic productivity often less than littoral
Zooplankton Growth/Productivity	Low; higher in medium and high order rivers;eat detritus as well as algae	Moderate; most in transition zone; variable; some consumption of detritus	Moderate to high; extreme fluctuations due to resources and predation

High Conductivity Limnology – Estuaries and Saline Lakes

Estuaries

I. What are estuaries?

A. Definitions

1. Where freshwater drainages meet the sea
2. Semi-enclosed coastal bays in which fresh water derived from land drainage and sea water from the ocean mix
3. Classifications

· **salt wedge**

· patterns of salt and freshwater (stratified/partially mixed/mixed)

B. Very productive systems

1. Allochthonous from rivers and land – detritus is very important
2. Autochthonous
   a. Phytoplankton
   b. Sea grasses and macroalgae

II. Physical Characteristics of Estuaries

A. Salinity

1. single most important characteristic; nowhere is variation in salinity more pronounced than in estuaries
2. variability is horizontal, vertical and seasonal
3. causes of variability
   a. amount of freshwater input
   b. evaporation
   c. vertical variability (density differences)
   d. tides are periodic events

B. Substrate

1. soft mud
2. terrestrial and marine derived materials
3. gradient of sediment size that depends on current strength
4. storms and floods can reshape estuaries

C. Wave Action and Currents

1. currents from combination of tidal and river flows
2. **flushing time**

D. Turbidity --

1. often high due to resuspension of particles
2. lowest at mouth of estuary and highest inland and when river flow is large
3. decreases light penetration -- reduces primary production

E. Oxygen

1. generally high due to mixing
2. will vary in salt and freshwater layers (salinity; temperature, stratification...)
3. can be anoxic conditions
4. depleted in the muddy substrates

III. Interesting organisms and their adaptations in estuaries

A. Number of estuarine species is less than in adjacent marine and freshwater habitats

B. Faunal composition

1. Marine and freshwater biota
   a. **stenohaline** – very narrow salinity tolerance
   b. **euryhaline** – broad salinity tolerance
      (1)osmotic regulation

(a) **osmoconformers** – osmotic concentration of their internal fluids fluctuates with the external environment

(b) **osmoregulators** –

(c) some may osmoregulate at low salinities and osmoconform at high salinities

c. Plankton

(1) reduced number of species

(2) composition and biomass depends on turbulence, turbidity and flushing rate

d. Benthos --often are lots of anoxic sediments

(1) get tolerant organisms and organisms that aerate their burrows

(2) oyster beds

(3) seagrasses in lower areas

(4) macroalgae

(5) benthic algae -- diatoms; filamentous cyanobacteria

2. **brackish water**/estuarine species -- adapted to life in intermediate salinities; not in freshwater or seawater (5-18 psu)

3. some species are transitional – passing in and out of the estuary during some of its lifecycle;

a. migratory fish

b. some shrimps

c. breeding and feeding grounds for many birds, fishes

IV. Human impacts on estuaries

A. Have historically been treated as wastelands that should be reclaimed for human use --

housing developments, marinas, seaports, industrial parks, cities, garbage dumps…

1. Dikes and drainages; fill

2. 1/3 of all estuaries in the US are completely gone

3. dredging of navigation channels

B. Rivers input modifications

1. damming and diversion often reduces freshwater flow from rivers and affects salinity of estuaries

2. carry pollutants -

3. carry extra nutrients leading to eutrophication (more later in course!)

C. Exotic species – ports and ballast water (more later in course!)

D. Overharvesting (fish, shellfish)

E. Aquaculture

Salt Lakes

I. Distribution
 A. half of the water volume in the world's lakes is fresh and half is saline
 B. global distribution
  1. generally restricted to semiarid and arid regions

  2. some in other regions if near underground salt sources or a salt mine
 C. Interesting facts: saline lakes include
  1. the largest (Caspian)
  2. highest (Nan Tso, Tibetan Plateau 4,718 m.a.s.l.)
  3. and lowest (Dead Sea, 400 m.b.s.l.) lakes of the world
 D. less studied

II. Characteristics
 A. salinity
  1. Definition of saline lakes **--** salinity greater than or equal to 3,000 mg/L = 3 ppt
   a. often a breakpoint for biota
   b. a point at which certain chemical equilibria change
   c. subsaline lakes >0.5 ppt (500 mg/L) but <3
   d. freshwater <0.5 ppt
  2. Subcategories of saline lakes
   a. ***hyposaline*** – 3-20 ppt
   b. ***mesosaline*** – 20-50 ppt (oceans are ~33 ppt)
   c. ***hypersaline*** **-** > 50 ppt
  3. records
 B. Freezing point depression
 C. Sometimes high pH
 D. Variety of chemical composition
 E. Extremely high nutrient levels
 F. High, potentially toxic levels of trace metals
 G. Low oxygen

III. Unique fauna and flora
 A. Almost all species in saline lakes are derived from freshwater, not marine species
 B. Decreasing numbers of species phytoplankton, zooplankton and benthos as salinity increases

C. Species are often cosmopolitan
D. The few species present are often in high densities and very productive
E. Some specific organisms and food webs
1. some tilapias (fish) can live in moderately saline lakes and wetlands
2. brine shrimp, ***Artemia*** - occurs world wide in fishless saline lakes and tolerates high salinities (>300 ppt).

3. Lake Nakuru (Kenya) - flamingo population
4. Lake Werowrap, Australia – even simpler food web

IV. Human impacts on salt lakes
A. Mining of minerals – salt, uranium, lithium, borax, potassium, nitrates, sodium carbonates
B. Harvesting of phytoplankton -- *Spirulina*
C. Harvesting of animals – brine shrimp; sometimes spread to other lakes
D. Global warming
E. Case studies -- under threat from diversion of water from rivers for irrigation of crops in the semiarid zone (like Aral Sea)
1. Great Salt Lake
2. Dead Sea
3. Mono Lake, CA – tufa; brine shrimp and brine fly; waterfowl;
ecosystem, lake level and water management model interact with politics of water management in the Western U.S.

Food Chains and Webs

I. Food chains
A. Background -- Ray Lindeman; Cedar Bog Lake
B. Conceptual:
light + nutrients
primary producers (phytoplankton) first trophic level
primary consumers (herbivorous zooplankton) second trophic level
secondary consumers (carnivorous zooplankton or planktivorous fish) third trophic level
tertiary consumers (piscivorous fish) fourth trophic level

1. **trophic levels** – contain functionally similar organisms that utilize similar food resources

2. **trophic dynamics** – transfer of energy from one part of the ecosystem to another

C. Currency –

1. calories – 1 mg C ~= 10 cal (energy)
2. C or N (conservation of mass within the system)
3. dry mass (as a proxy for C and N; C ~ 50 % dry weight)
4. ash-free dry weight -- parts of a sample that aren't organic (minerals) are excluded; good for diatoms or for mussels
5. limitations of currency measures – vitamins, nutrients, lignin

D. Ecological efficiency – efficiency at each link

change in energy content of trophic level N= energy income from N-1 minus losses (metabolism/respiratory)

Increased efficiency of transfer as you move up the food chain

E. Length of food chains – food webs usually are short – 4-5 levels – why?

1. **Energetic Hypothesis** – length limited by inefficiency

2. **Dynamical stability** – long food chains are less stable

3. **Ecosystem size** - more habitat? More stable habitats...Do tend to find longer food chains in larger lakes

F. Body size –

1. Often organisms at each successive level in aquatic systems are larger than those at the previous level
2. This is not often true in terrestrial systems

II. Food webs

A. Food chain transformed into a web due to:

1. **omnivory** – feeding on several trophic levels at once
   a. finding that this is more and more common
   b. ***mixotrophy*** – both a primary producer and a heterotroph
   c. Or a predator like cyclopoid copepods, that will also sometimes consume flagellated algae (acts as an herbivore).
   d. Omnivory is thought to be more common in aquatic systems

2. **ontogeny** – may change the food level an organism feeds on

3. temporal shifts in diet

B. Microbial loop

- Inadequate attention is often paid to decomposers (althought their importance was recognized by Lindeman)
- Most of the carbon in aquatic systems is in detrital form – in the particulate detritus, DOC, or the microbial loop
- "microbial loop" starts with dissolved organic matter

C. Mathematical descriptions of food webs – can allow us to make comparisons between different food webs

1. **stability** –

2. **connectance** – draw lines between species in food webs – connections between different trophic levels and species,

and examine how many of the potential lines are filled in

actual interations/possible interactions

As you decrease the number of species you increase connectance

Aquatic predators generally are connected to 2.5-3 prey items

3. diversity

D. **Stable Isotopes** and Food Webs (see attached sheet)

Extra neutron doesn't usually affect the chemical properties (doesn't change outer electron shell)

In some reactions it makes it harder to get activation energy because it is heavy – isotope discrimination

If a reaction proceeds to completion then there is small fractionation (C4 plants have less fractionation than C3 plants)

For carbon you are what you eat

For nitrogen you are what you eat plus 3 $^{0}/_{00}$

Can determine potential versus realized food webs

Can separate terrestrial and aquatic sources

Whole lake experiments feasible

Fractional trophic levels

III. Major paradigms of what controls the organisms in an ecosystem

A. **Bottom-up control** – nutrient regulate

Nutrients -> 1 producers -> 1 consumers -> 2 cons (sm. fish) ->3 cons. (lg. fish)
increase increase increase increase increase

B. **Top-down control** –

1. 'odd-even link paradigm'/'saw tooth paradigm', cascading trophic interactions

Increase pred -> decrease sm. fish -> increase zooplankton -> decrease phytoplankton

2. **keystone species** (Paine)
3. **biomanipulation** (Shapiro) – controlling of algal blooms – get more **big** zooplankton by increasing piscivorous fish
'biomanipulation' – main idea to decrease small fish so increase large zooplankton so decrease algae
4. **trophic cascade hypothesis** (Carpenter and Kitchell)

C. What is evidence for each?

1. Bottom Up

2. Top down
Add big fish, almost always decrease small fish, usually get larger zooplankton (but not necessarily more zooplankton),
but not always, rarely get algal decreases or nutrient effects.

D. Where and why do these controls break down in food web?

1. need to take into account ontogeny – often piscivorous fish are planktivorous when young and will themselves eat zooplankton
2. predator-prey cycles – periodic releases from predation
3. rearrangement of trophic structure during perturbation – may have species changes
   i. smaller zooplankton are less good grazers and don't often reduce phytoplankton
   ii. may get shifts to inedible algae (e.g., blue-greens)
4. variability of diet, plasticity in feeding

E. Effectiveness of biocontrol often depends on trophic condition

1. oligotrophic lakes – small responses of biotic release (top-down) –
there are so few zooplankton that they can't graze down the phytoplankton

2. mesotrophic lakes – greatest response of biomanipulation and greatest overlap of top-down and bottom up controls

3. eutrophic – fewer species at high and low end – less opportunity for these effects; more inedible algae -- but this is where they hoped it would work

F. Synthesis –

1. Both types of control operate most strongly closest to where they are initiated (piscivores to planktivores; nutrients to phytoplankton)

2. Both operate at some time in almost all ecosystems

3. There are also other physical and chemical controls imposed on food webs

Mixing resets the system

Oxygen limitation of fish

Temperature

Stable Isotopes Lecture note supplement

Not all atoms of the same element have identical masses. For some elements, such as carbon and nitrogen a small percentage of atoms is enriched with extra neutrons, making them heavier. Atoms with the same number of protons, but different numbers of neutrons are known as isotopes. Some isotopes are unstable or radioactive, and decay over time (e.g., ^{14}C). Other isotopes are stable and the atoms do not decay. Most of the atoms of carbon and nitrogen exist as ^{12}C and ^{14}N. A small percentage of each element exists as a stable isotope, ^{13}C and ^{15}N, known as heavy isotopes due to the extra mass of their additional neutrons. In nature, materials, including the tissues of organisms, contain some mixture of light and heavy isotopes. Stable isotopes can be used to solve many problems in ecology, among them the understanding of feeding relationships.

The isotopic composition of materials can be measured very precisely with a mass spectrometer. This isotopic composition is generally expressed as a ratio of heavy to light isotope in a sample relative to that in a standard; these relative ratios are δ values, given in units of parts per thousand (‰). Increases in δ values indicate increases in the relative amount of heavy isotopes in a sample. Decreases in the δ values indicate decreases in the heavy isotope content (and a corresponding increase in the light isotope content).

The magnitude of these ratios in an organism reflects the isotopic ratios of the food or elements that were used to build the tissue.

1. **The rule for carbon and sulfur is that you are what you eat.** In other words, the isotopic ratio in your tissue is the same as the isotopic ratio of the food metabolized to make the

tissue. Different food sources (e.g., C_3 versus C_4 plants, terrestrial versus aquatic detritus, near shore versus offshore material) often have characteristic isotopic compositions. The isotopic composition of the consumer will reflect the source of its food.

2. **The rule for nitrogen is that you are what you eat +3 ‰ heavier**. In other words, your tissues will be enriched by 3 per mil over the ratio in your food. This results from the fact that the lighter isotope (^{14}N) takes part in more biochemical reactions during protein breakdown and is excreted at a higher rate than the heavier isotope (^{15}N). This leaves the remaining protein and tissue enriched in the heavier isotope. Typically consumers are +2 ‰ to +5 ‰ (average ~ +3‰) heavier (or enriched in ^{15}N) than their diet. At each successive trophic link, the consumer's diet contains prey that are more isotopically enriched in ^{15}N, so that $\delta^{15}N$ values of different organisms in a food chain reflect their relative trophic position.

3. Acid Deposition

4. (Acid Rain; pH<5.6)

5.

I. Sources

A. Natural and burning of fossil fuels

(man made emissions well over 10X natural emissions in most regions)

B. Strong acids of N (NO_x) and S

1. **wet deposition** (H_2SO_4, HNO_3)
2. **dry deposition** – aerosols, gases, deposited on surfaces
3. current controls on S emissions; N from automobiles is harder to control

(NO_x has increased 12-20X in Eastern U.S. since 1900)

C. History

1. first noticed in 1660's
2. by the 1700's scientists realized that S was in coal/fossil fuel emissions
3. 1850 - sulfuric acid first discovered
4. 1900-1980 -- S emissions doubled in N. America and Europe
5. 1920's began using S in crop fertilizer
6. 1920-1960 – found that precipitation inputs can affect bogs
7. 1950's – 2000 people died in one episode of acid fumes in a city; solved with higher smokestacks -- made this a regional issue
8. 1960 – fish kills observed in Norway and attributed to acidic deposition
9. 1967 – concept of regional precipitation – link between emissions in England and pollution in Scandinavia – became a political issue
10. 1972 (US) Clean air act
11. early 1970's Gene Likens – regional precipitation in the US – Hubbard Brook Forest – record of precipitation chemistry since 1967; coined the term 'acid rain'

D. Average pH of precipitation in central NY in early 1990's: 4.3

6. II. Catchment effects (what happens when acid hits the ground)
   A. Weathering reactions
      1. CO_2 in water weathers rock minerals to produce of HCO_3^- to neutralize acids (alkalinity; acid neutralizing capacity)
      2. Ca^{2+} and Mg^{2+} are also weathered out
      3. loss of H^+ in cation exchange; (Al^{3+}) is also released
      4. sulfate is not well absorbed and runs through to lake in ground water
      5. some nitrate is taken up by vegetation
   B. Cation exchange for H^+
      1. H^+ comes in and displaces other cations in soil
      2. eventually the soil runs out of cations to exchange, and then there is no more buffering
         (decreasing pH decreases cation exchange capacity, decreases base saturation, decreases the
            pH of groundwater runoff)
      3. extent of reaction related to base saturation of soils and to time
      4. most lakes get much of their water from the catchment
      5. Cation exchange effects on drinking water – acidic water can leach copper and lead from pipes.
         Aluminum can be leached from soil into drinking water
   C. Base saturation of soils related to rock type and to elevation
   D. pH and alkalinity of lakes and streams decreases with increasing elevation
   E. Sensitive areas found in crystalline bedrock (granite, gneiss), old soils
7. III. Biological effects
   A. Strongly related to pH
      1. Not necessarily H^+, but can be related to low pH
      2. Increased aluminum concentrations (increased solubility of aluminum at low pH);
         increases gill mucus production and clogs gills; affects respiration efficiency
      3. Increased concentration of other heavy metals (lead, cadmium, iron, copper, zinc, nickel); solubility
         increases with decreasing pH (vanadium and mercury become less soluble with low pH)
      4. Increased water transparency (changes thermal regime and UV penetration)
8. B. Effects are species dependent
      1. Initial effects of acidification – encroachment by benthic algae (clearing and loss of benthic invertebrates);
         invasion by sphagnum

2. 6.0 lose some mollusks (calcium carbonate shells)
3. 5.5 lose some fish, amphipods, crayfish
4. Between 5-6, algal species diversity decreases considerably – blue green algae and diatoms are the most susceptible; become dominated by dinoflagellates, chrysophytes
5. some fish (perch, pike) and some mayflies can remain until pH slightly below 5 (although reproduction may be impaired)
6. Daphnids are severely affected, while *Bosmina* are not
7. 4.0 lose all fish; often left with large calanoid copepods, some rotifers (*Keratella* and *Polyarthra*), some insect larvae (*Chaoborus* and Corixids)

C. Effects are dependent on life stage – embryos and fry of trout (both rainbow and brook) are less resistant to pH change; adults can sometimes survive to pH 4.5, but their eggs can not develop

9. IV. In-lake biogeochemical reactions

A. Hard rocks – crystalline, igneous – slow weathering
1. tend to find oligotrophic lakes in these geological substrates
2. effect of catchment is small -- little neutralization of acid
3. acid brought into surface waters consumes alkalinity

B. Soft rocks – sedimentary or carbonates
1. tend to find mesotrophic and eutrophic lakes in these geological substrates
2. effect of catchment is large
a. neutralizes acid
b. NO_3^- and SO_4^{2-} brought into surface waters, accompanied by major cations
3. fate of NO_3^- and SO_4^{2-}
a. NO_3^- uptake (assimilatory reduction) consumes acid
b. SO_4^{2-} reduction consumes acid – confined to lakes with sufficient organic matter and low Eh (redox)
1) One idea for natural remediation – will sulfate redution produce alkalinity and negate the H^+ coming in?
2) Problem: high potential at lake turnover for oxidation of sulfides and production of acid
3) Must bury solid phase sulfide or lose sulfur gas to make the gain in alkalinity permanent
4. Water renewal time important – then in lake reactions are less important and catchment reactions are more important
5. More exposure to hypolimnetic sediments (redox reactions), then more

importance of in lake processes

C. Effects on DOC – breaks down DOC and reduces color in water (also precipitates with aluminum)

D. Effects on production – aluminum causes precipiation of phosphorus

10. V. Remediation efforts

A. Regulation – slow natural recovery

B. Liming – add calcium carbonate

1. expensive
2. rapid increases in pH and alkalinity
3. reduction in transparency
4. reduction in metal concentration
5. increase in species diversity and biomass – not as good a recovery as hoped;

>10 years for zooplankton; more for fish if not re-stocked

6. only a temporary solution if acid rain continues

C. Sometimes add NaOH

D. Regulation of emissions

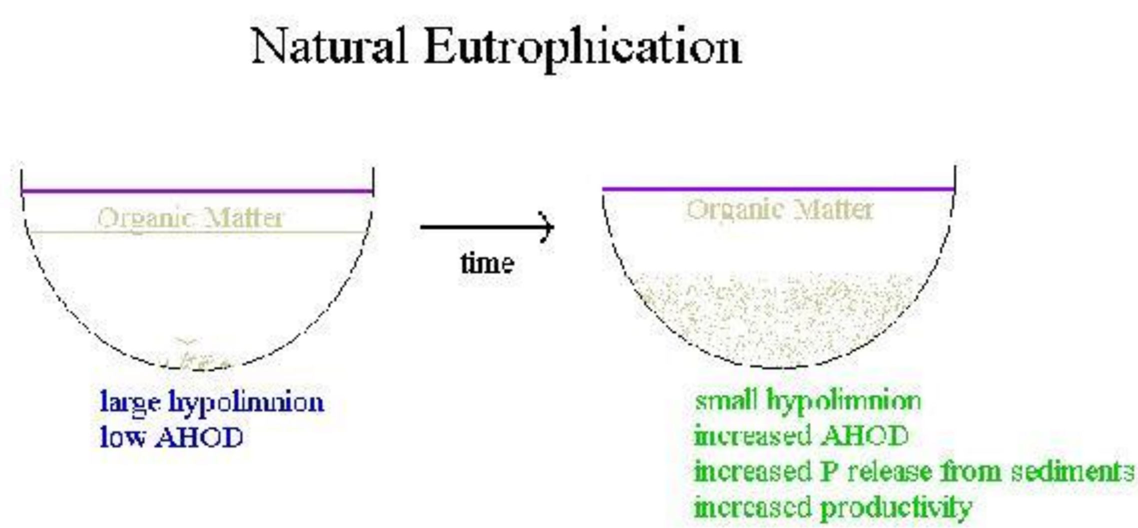
1. Decreased loading
2. Recovery of pH is slow
3. Recovery of communities is slow even when pH recovers

11. Cultural Eutrophication and Pollution

12.

I. Trophic Equilibrium

A. Natural eutrophication



13.

14.

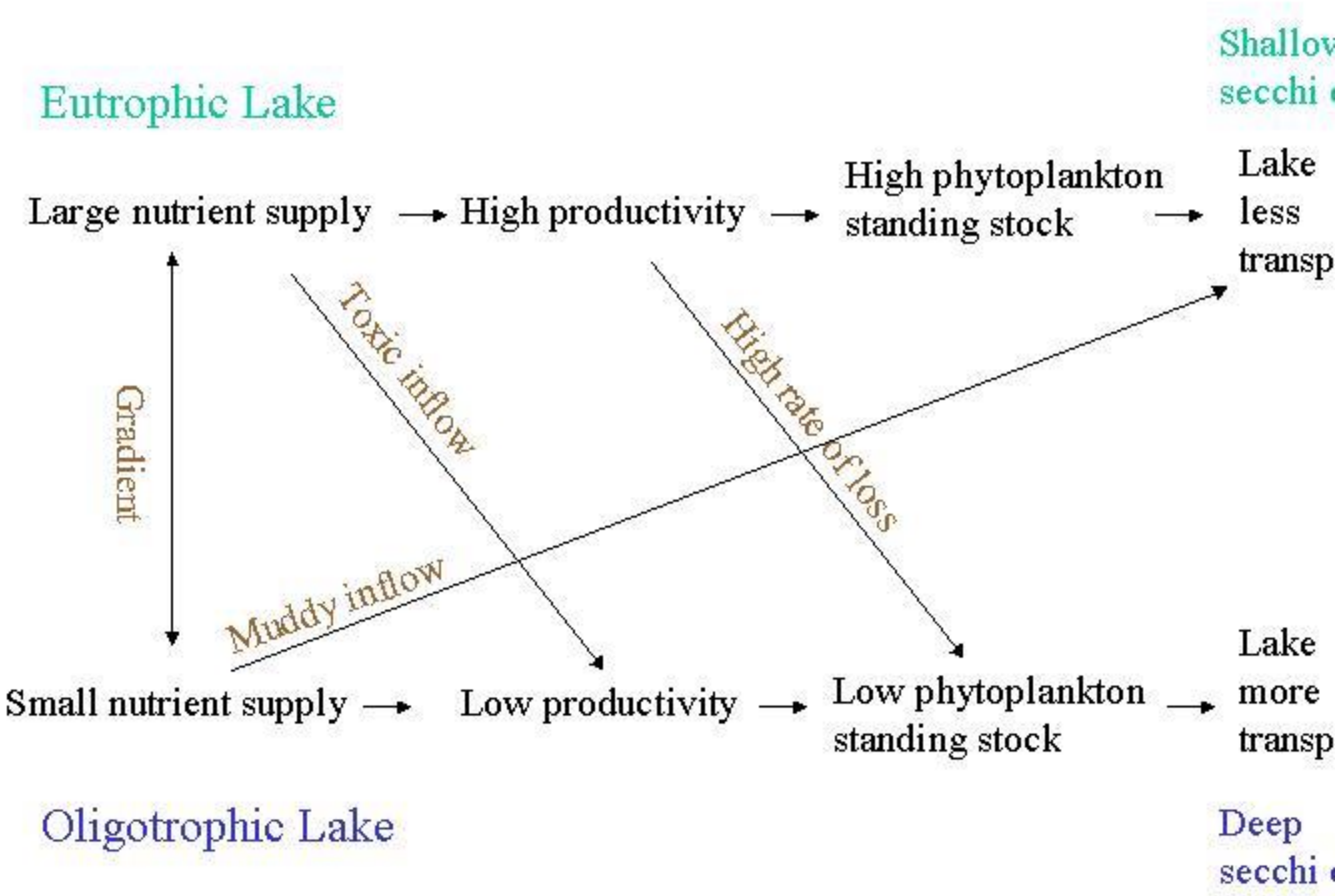
15. 1. Changes over time with the filling in of lakes – the epilimnion volume doesn't change as fast as the hypolimnion – the mixing depth is set by the SA of the lake, the fetch and the wind speed

2. Increased **AHOD** – aerial hypolimnetic oxygen deficit

3. Decreased volume of hypolimnion

B. Artificial Eutrophication

1. altered watershed conditions
    a. fire (changes evapotranspiration, water budgets, runoff)
    b. clearcutting – changes runoff
    c. agriculture
2. addition of nutrients
    a. fertilizers
    b. waste treatment plants
        1) ***primary treatment*** – settling
        2) ***secondary treatment*** – digest organic matter;
        3) ***tertiary treatment*** – any additional treatment of secondary effluent to improve its quality; for example, alum to remove P (expensive)



16.

17. II. Case Studies of Cultural Eutrophication

A. Lake Zurich – two basins – Zurichsee and Obersee

whitefish

1898 first record of ***Oscillatoria*** *rubescens* (an indicator of eutrophication);

clarity decreased; oxygen consumption increased; whitefish decreased (Coregonids sensitive to low oxygen);

all this was mainly in the Zurichsee

1918 whitefish disappeared (need cold water and high oxygen)

Obersee stayed relatively pristine due to fewer people and lower nutrient input

1940's -- Obersee followed the same course

Calculated that 54% of the P in the lake was from sewage inputs.

18. B. Madison Lakes, Wisconsin

Mendota, Monona, Waubesa, Keyonsa, Yahara River

Early 1900's – settlement, clearcutting, agriculture

1912 – Monona and Mendota eutrophied; to kill algae added $CuSO_4$

1930's -- Monona was still so bad that they were diverting sewage to Waubesa

1962 – so bad that diverted sewage into the Yahara River

For these lakes 88% of the P and 75% of the N had come from sewage

19. C. **Lake Washington**

1933 – oligotrophic lake; 65 m deep

Lake Washington is a monomictic lake in Seattle, with a residence time of ~3 years

Seattle population in 1865 – 300; 1965 – 1.2 million

In the 1950's, the secchi depth was >3 m; lake was dominated by diatoms

1955 *Oscillatoria* was found in the lake

Early 1960's – "Lake Stinko"

T. Edmondson at the U. Washington

At the maximum of eutrophication, Lake Washington was receiving 20 million gallons of secondary effluent each day

Sewage diversion was started in 1963 and was completed in 1968, with no more effluent entering after that year.

In 1962, 72% of the phosphorus was brought in by sewage; in 1966 it was 62%, and in 1967 it was 26%

1962-1964 were even worse algal blooms

1965-1966 dramatic algal production decline and increase in transparency;

Food web effects:

Early on in eutrophication, *Daphnia* were replaced by *Diaptomus* (because*Oscillatoria* clogs the filtering apparatus)

In the mid-1970's *Daphnia* returns; secchi depth increased to record levels – 12 meters – due to *Daphnia* grazing

20. D. Arctic Lake Example: Lake N2 – divided lake in the arctic, Fe binding of P, delayed effects of fertilization

E. Tropical Lake Example: **Lake Victoria**

Year	Secchi	Chl. a (μg/L)	Prim. Prod. ($g\ O_2/m^2/day$)	Reference
1960	7 m	3	1	Talling
1990	1-2 m	15	4	Hecky

21. Lake had become eutrophied and no one knew what had happened. The algal species had changed from diatoms to blue-green algae. There were many changes in the system.

1. *Addition of nutrients* from basin – now in Lake Victoria there is constant N limitation, especially inshore; there have been increases in P loading; N fixation is not enough to relieve N limitation. 30 years ago the bottom waters were rarely anoxic, today they are often anoxic – 70% less space for the fish to live in.
2. *Food web changes* – introduction of Nile Perch (*Lates*); introduced in the early 1960's; haplochromines, the cichlid fishes, included many guilds and trophic specialists; many of the 300 endemic species have been eaten by the Nile Perch.
3. *Climate changes* causing different mixing – in the past 50 years the climate has warmed, causing changes in mixing and the strength of stratification; affects light, nutrients, oxygen (blue greens need more light and have an advantage at shallow mixing depth)

22. F. Practice of moving sewage outflows to rivers has improved the nutrient condition of lakes, but caused many problems in estuaries and nearshore ocean environments -- lots of **Nitrogen** loading leads to **dead zones**

23. III. **Oligotrophication** – concern about too low phosphorus levels in the Laurentian Great Lakes – are we actually decreasing fish production?

24. Proposals to start fertilizing lakes in a balanced N:P ratio to increase fisheries production levels. Some fisheries managers see the issue as a choice between productive 'greener' lakes and streams and unproductive aesthetically clear waters.

25. IV. Other Pollution

26. A. Types

1. Thermal Pollution – power plants; industry
2. Radioactivity

3. Toxic contaminants

a. Types

1) **POPs – persistant organic pollutants --** Pesticides and organic toxins – dioxins, furans, benzopyrene,

DDT/DDE, dieldrin/aldrin, hexachlorobenzene, alkylated lead, mirex, mercury, PCB's, toxaphene,

heptachlor, chlordane, endrin

i. Nearly 80,000 synthetic organic chemicals are in daily use

ii. Endocrine disrupters

2) Metals – cadmium, mercury, arsenic, lead

b. Characteristics

1) Toxicity

i. **Acute** – quick death

ii. **Sublethal/chronic** – impairment of growth, reproduction..

iii. **Carcinogenicity** – impairment of function, death

iv. **Mutagenicity/teratogenicity** – effects on future generations

2) **Bioaccumulation**

i. Capacity to enter the food chain

ii. **Biomagnification**

3) Persistence – resist degradation in the environment

4) Volatility – easily evaporated and *transported in the atmosphere*

BIOLOGICAL INVASIONS

homogenizing of the world's flora and fauna
'*biological pollutants*'.

I. Invasive species in general

A. Rule of tens

1. 10% of imported plants escape to become introduced
2. 10% of **introduced** organisms
(found in the wild, released, but not yet breeding successfully) species become **established**
(have a self-sustaining natural population)
3. 10% of those established become **pests**

B. Pattern of establishment and spread of exotic species

1. **LAG** phase, before growth occurs (small numbers, adaptation).
2. During this lag is the best opportunity for control.
3. Then there is a rapid expansion of range.

4. Expansion decreases when all of the suitable habitat is colonized, or when there are barriers to expansion.

C. Is invasion success predictable?

1. Attributes of invaders – (not universal)
(resting stages, fast reproducers, generalists, related to other successful invaders...)
2. Community vulnerability
-‘vacant niches’/community species richness
-escape from biotic constraints
-disturbance
3.Propagule Pressure

D. Theory predicts that there will be species extinction (based on species-area curves)

E. Deliberate versus accidental invasions

II. Notorious Aquatic Invaders

A. **Nutria** (*Myocastor coypus*)

1. Introduced from South America in the 1940's; fur industry
2. Relatively large herbivorous rodent that lives in marsh habitats.
3. Has increased marsh loss along the tidal, emergent marsh habitats.

B. Brazilian pepper – *Schinus terebinithifolius*

Everglades

C. Water Hyacinth, ***Eichornia***

1. Pest to people in many areas of Southern U.S., S. America, and Africa
2. Clogs waterways
3. Increases evapotranspiration
4. Floats into littoral zone and decomposes -- decreases oxygen, hurts fish breeding zones;
5. Blocks light penetration

D. Eurasian watermilfoil (***Myriophyllum*** *spicatum*)

1. Accidentally introduced to North America from Europe
2. Can interfere with water recreation.
3. Can also crowd out important native water plants
4. Fragments clinging to boats and trailers can spread the plant from lake to lake.

E. Hydrilla (*Hydrilla verticillata*)

F. **Purple loosestrife** (*Lythrum salicaria*),

1. Native of Eurasia first introduced into the northeastern U.S. and Canada in the early 1800's for ornamental and medicinal uses
2. Subsequently spread W and S through most of temperate North America.
3. Crowds out native wetlands and vegetation, forming extensive monospecific stands; affects some federally endangered orchids, and reduces habitat for waterfowl.
4. Alters flow

III. Some consequences of intentional invasions

A. Fish

1. **Nile perch** (*Lates nilatica*) - effects on native cichlid fish

2. 1991 study -- 44 species of fish in the US were endangered by the introduction of non-native fishes.
3. Of the 40 fish species that have gone extinct since 1890, 27 were negatively affected by the introduction of non-native fishes [Wilcove and Bean 1994])

B. ***Mysis*** in Flathead Lake (Spencer et al. 1991)

- Tremendous food web effects
- Did not overlap spatially with its intended prey, kokanee salmon (introduced)
- Actually competed with the kokanee by eating many of the zooplankton
- Kokanee population crashed
- Eagles no longer stopped at the spawning site in the fall migration
- Grizzly bears declined in the area

IV. Invasions in the Laurentian Great Lakes

A. Importance of the Great Lakes

20% of the freshwater in the world

important fishery, historically a commercial fishery, now more important sport fishery

lots of shipping

B. Historically many intentional fish introductions

C. Unintentional introductions -- Spread via canals and shipping

example – Sea Lamprey, *Petromyzon marinus*

1. First found in Lake Ontario in 1835, and then spread after the extension of shipping channels to the other Great Lakes
2. Parasite that attaches to deepwater fish, especially lake trout and chubs.
3. Lake trout, burbot and whitefish populations were devastated by lamprey predation by the early 1940s.
4. Today the lampreys are less abundant in the Great Lakes, but this is only due to expensive continued control

D. Unintentional transport by ballast water
1. European ruffe

Are we turning the Great Lake into the Caspian Sea?
1. **Zebra mussel** *Dreissena polymorpha*
   a. Filter much of the algae out of the lake, leaving less food for zooplankton, and potentially for fish
   b. Clear the water by reducing phytoplankton abundance, and transfer energy to the benthos
   c. Have harmed many native clams and crustaceans by settling on them and covering them
   d. Large cleanup costs at water intakes for industry and drinking water
2. **Goby**, *Neogobius melanostomus*,
   a. Presumably introduced via ballast water
   b. Spread to lakes Erie, Michigan and Superior and to many rivers including the Mississippi watershed.
   c. This fish is an aggressive, voracious feeder and takes over spawning sites used by native species.
3. Spiny waterflea, *Bythotrephes cederstroemi*
   a. Not much known in its native habitat
   b. Like *Mysis*, but unlike most invertebrate predators, it eats large zooplankton; responsible for local extinction of two daphnids in Lake Michigan
   c. Voracious
   d. Competes with juvenile fish
   e. Tailspine protects it from predation by small fish
   f. Less energy going up the food web because it is more inefficient than are small fish
4. *Cercopagis pengoi* -- fish hook flea

Potential food webs effects?

Problems with preventing spread -- resting eggs

5. *Daphnia lumholzi*

a. Native of tropical and subtropical lakes in east Africa, east Australia, and India was first found in Texas in 1990

b. Aquaculture introduction? It is suspected that *Daphnia lumholzi* may have been transported with shipments of Nile perch or tilapia

c. Very spiny

d. Invaded many southern lakes; reached Lake Erie in 2001

7. Bacteria and viruses

a. Ballast is dispersing human pathogens

b. *Vibrio cholerae* – causes cholera – found in 93% of ships tested

V. Management of invasions

A. Economic costs

Loss in potential economic output

Cost of combating the invasion

Effects to human health – disease, vectors of disease (mosquitoes that carry disease), parasites

US estimate -- $138 billion/year

Cost-benefit analysis

B. Management of Invasions

1. Preventing entry

2. Eradication

3. Maintenance control

-Chemical control – resistance, cost, health hazards for humans and other species

-Mechanical control

-Biological control

C. What can be done?

1. Scientists

Get better at predicting invaders and systems at risk

Document effects

2. Technology

Cheaper/quicker methods for preventing and controlling invasive species

3. Ultimately a policy question

Publicize to make people aware of the problem

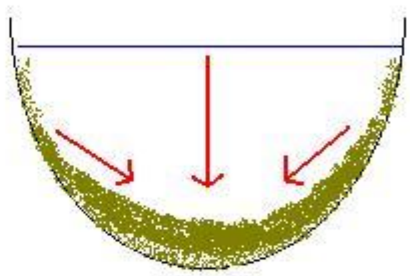
Evaluate the current human dispersal rate compared with historic rate
Determine costs/benefits of preventing/controlling invasions

VI. CONCLUSIONS
Unexpected effects of invasions
1. some because animal not well known
2. some because no predators/enemies/disease in the new habitat
3. not coevolved with new prey/ competitors
4. propagated effects through the food web
Need for increased predictability
Importance of overlooked small invaders
Importance of preventing future introductions

Paleolimnology

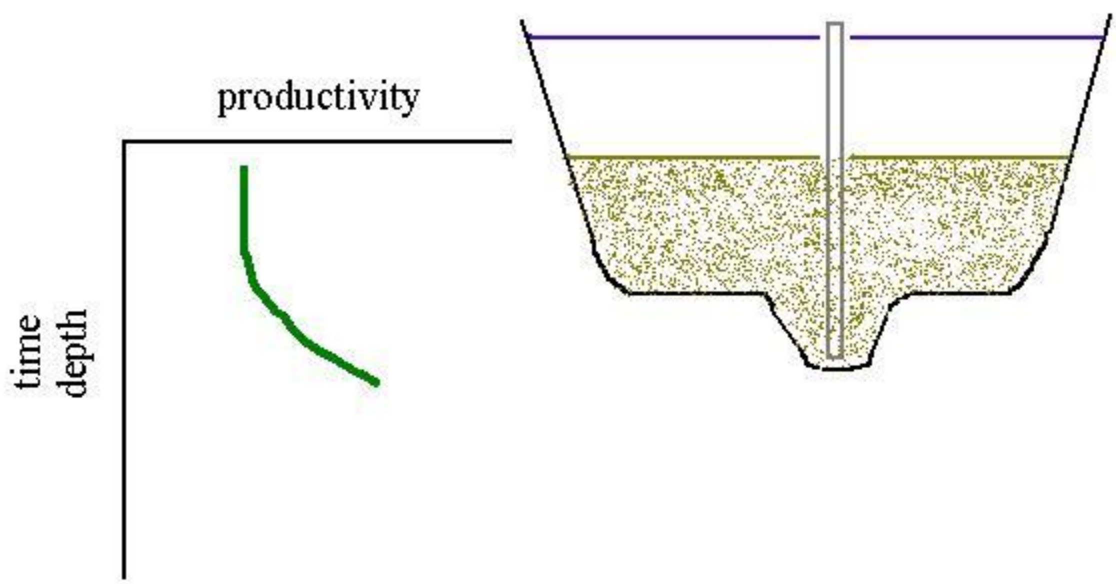
I. Rationale
A. Academic – scientific curiosity
1. lake typology
2. evolution of lake ecosystems
3. biogeography and evolution of organisms
B. Anthropogenic changes to lakes
1. baseline for restoration
2. confirming time course and extent of changes
C. Climate – understanding past climates so that you can predict future trends/responses

II. Problems
A. Selective destruction
B. Spatial averaging – mixing spatially separate communities



sediment focusing

1. sediment focusing
2. apparent changes in productivity over time



The bottom levels integrate the whole lake's productivity into a smaller area – can result in an apparent change in productivity, even if constant over time

C. Mixing and bioturbation

III. Tools

A. Fossils – these indicators can be proxies not only for what lived in the lake or around the lake, but also for other conditions (habitats for organisms) when we can't measure those conditions directly

1. diatoms, chrysomonads
   a. the siliceous frustules are preserved
   b. dissolution if Si is undersaturated in the sediments
   c. different diatom species can have very different tolerances for conditions (acidity, salinity, eutrophication…)
2. cysts, resting stages
   a. crysophytes, dinoflagellates
   b. zooplankton
3. pollen, spores
   a. some from macrophytes
   b. lots of pollen falls on the lake from the surrounding area
   c. local versus regional effects
4. crustaceans
   a. ostracods (benthic); have different requirements
   b. water column crustaceans – mostly cladoceran carapaces; copepods not as well preserved
5. chironomids
   a. again, different species have different tolerances
   b. especially good for oxygen tolerances
6. mollusca
   a. again, looking at preferences
   b. can look at isotopes in shells to find out temperature when formed
   c. must be a calcareous environment or the shells will dissolve
7. fish
   a. bones or scales
   b. fairly rare
8. sponges
   a. siliceous structures – spicules
   b. hard to interpret
9. macrofossils
   a. fruits, seeds, pieces of wood

b. rare, but very distinctive and informative
c. from catchment; not blown from long distances
10. grass cuticles
a. have siliceous structures that can be distinguished to family
b. from catchment area
B. Other indicators
1. Pigments
a. Distinctive to different algae
b. Degradation products of chlorophylls
c. Accessory pigments unique to specific algal groups
d. Need to correct for degradation
2. Organic matter – chemistry of C and N
a. Bulk form, bulk amount, chemical characteristics…
b. Originate in algae and/or land plants (are biochemical differences – structural compounds; C:N is higher in land plants)
c. Alkanes and alkenes
(1) Higher plants versus algae
(2) Stable isotopes for CO_2
3. Minerals, elements – N, P, S
a. Cations, nutrients, inorganic precipitates can be used to infer water chemistry
b. E.g., Gypsum deposits – must have been lots of sulfate (SO_4^{2-})
4. Grain size – large versus small; how turbulent the environment was
5. Paleothermometers

Stable isotopes (O, H)
In diffusion the lighter isotope is enriched at the endpoint
As temperature increases this difference between fractionation of light and heavy isotopes decreases
(fractionation greater at low temperatures)
C. Dating – needed to resolve depth with respect to time
1. varves – annual laminations in the sediments
2. 0-150 years
a. ^{210}Pb
b. ^{137}Cs
c. Pb rise from the use of automobiles
d. Ragweed pollen (*Ambrosia*) rise with human settlement; this pollen can mark human arrival in an area
3. 150-75,000 years (often only used until 40,000 years ago)
a. ^{14}C – 5,568 years is the half life
b. for every ^{14}C atom there are 10^{12}, ^{12}C atoms

c. bomb produced ^{14}C can also be used from 0-40 years

i. 1950 – 100% modern (defined)

ii. 1975 – 140%

iii. 1995 – 117% modern (the extra 17% is all due to bomb testings)

4. >75,000 years

a. other isotopes with longer half-lifes

i. K/Ar – half life of 1.31 x 10^9 years

ii. Uranium series – ^{238}U half life of 4.51 x 10^9 years

iii. Half lives in billions of years – not precise for tens of thousands of years

b. Thermoluminescence

c. Paleomagnetism

i. Remnant magnetism (e.g., hematite, Fe_2O_3)

ii. Pole reversal

iii. The last reversal was 730,000 years ago

iv. Iron in the sediments is aligned with the poles

d. Tephrachronology -- Volcanic ash