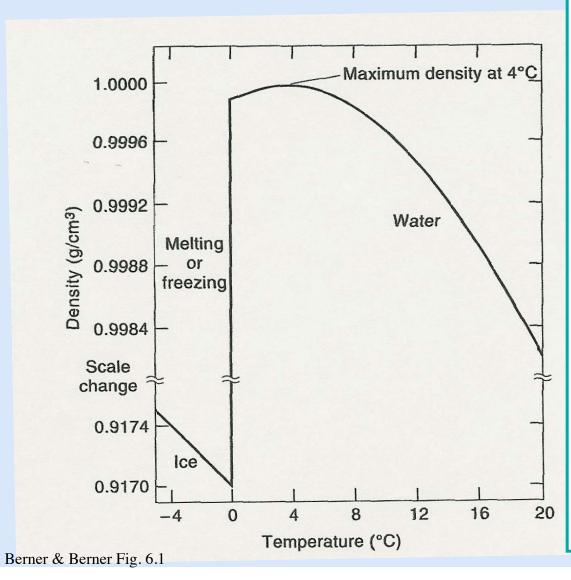
Lakes: Primary Production, Budgets and Cycling

Reading: Schlesinger, Chapter 8

Lecture Outline

- 1. Seasonal cycle of lake stratification
 - Temperature / density relationship of water
 - Lake classification according to stratification/mixing patterns
- 2. Primary Production and Nutrient Cycling in Lakes
- 3. Lake Budgets (C, N, P)
- 4. Lake classification according to trophic state
- 5. Alkalinity and Acid Rain

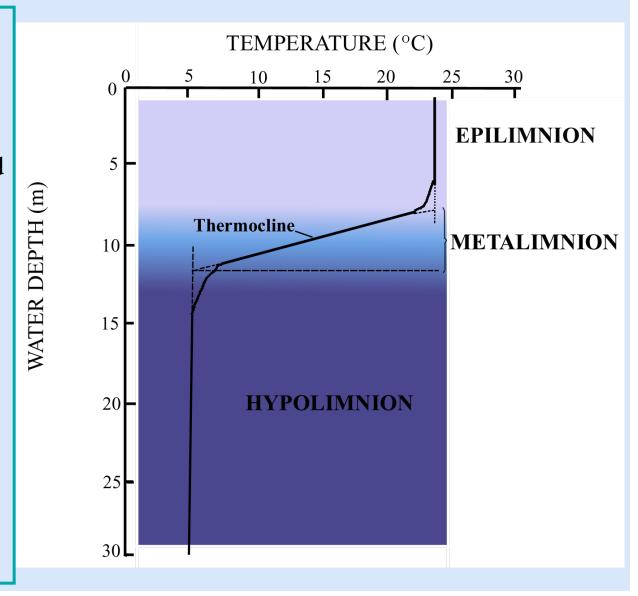
Physical Properties of Water: The Temperature-Density Relationship



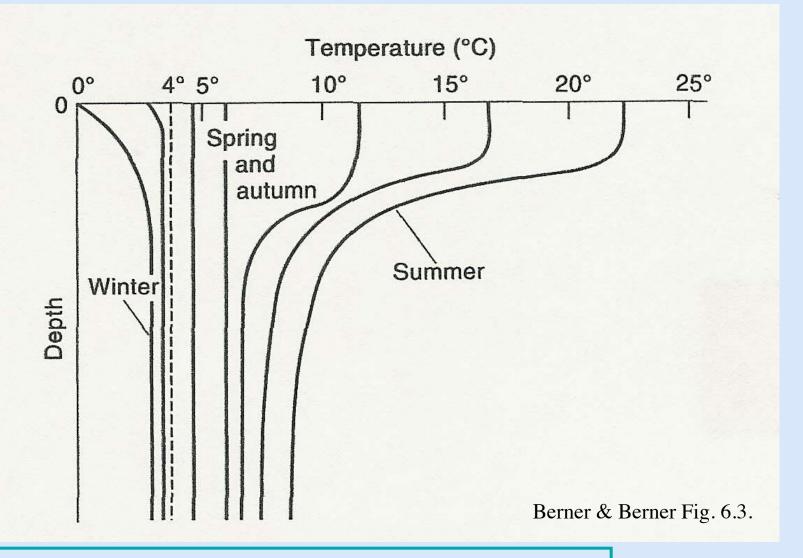
- Water maximum density at 4 °C
- Both ice and warmer water are less dense
- Important implication: ice floats!
- If less dense water is overlain by more dense water *lake overturn* occurs
- If denser water is overlain by less dense water, *stable stratification* occurs
- Lake chemistry and biology are affected by these physical processes.

Temperature structure for a typical temperate freshwater lake in summer

- Epilimnion: warm surface waters; light energy rapidly attenuates with depth
- Metalimnion: zone of rapid temperature change, or thermocline
- Hypolimnion: cooler, deep waters
- Many tropical lakes are permanently stratified
- Temperate lakes show seasonal break-down of temperature stratification & can mix from top to bottom.



The Seasonal Cycle of Lake Stratification



- Annual temperature profiles for a typical temperate lake
- Dashed line represents maximum density at 4°C

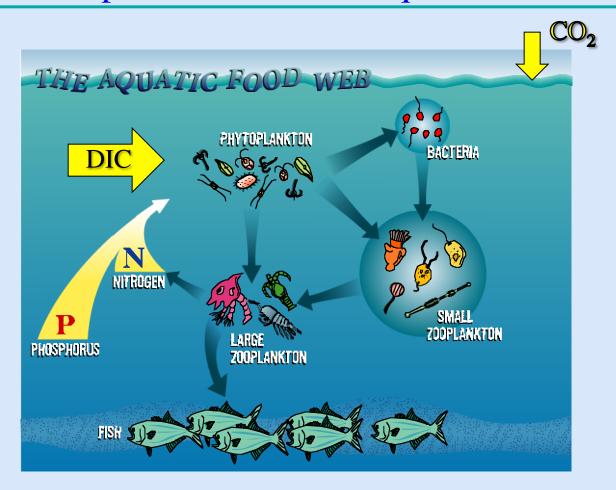
Freshwater Lake Classification

Type	Mixing Pattern	Example
1. Holomictic	Hypolimnion & Epilimnion mix	
1a) Dimictic	Mixes 2x/yr	Temperate
1b) Monomictic	Mixes 1x/yr	
- Warm monomictic		Mediterranean
- Cold monomictic		Alpine
1c) Oligomictic	Mixes irregularly	Tropical
1d) Shallow lakes	Continuous mixing	
1e) Very deep lakes	Mixes only upper portion of hypolimnion	Baikal (depth = 1623 m)
2. Meromictic	No mixing between hypolimnion and epilimnion	Saline lakes

Berner & Berner Table 6.2

During stratification, deep waters are isolated from the atmosphere and can evolve geochemically to be quite distinct from surface waters, with implications for water quality.

Nutrient uptake in Lakes & Aquatic Food Webs

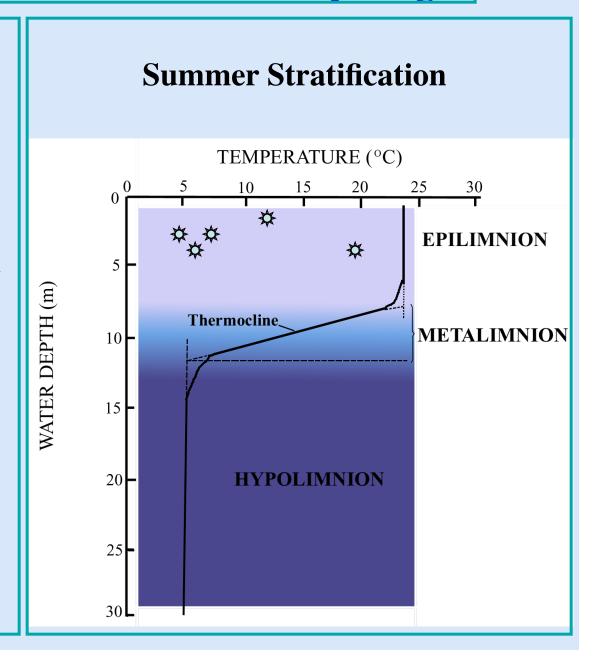


- P and N can be limiting nutrients in lakes, similar to terrestrial systems.
- Unlike terrestrial systems, C can also be limiting, because it must equilibrate over a relatively small, finite surface area, according to reactions of the CO₂ system:

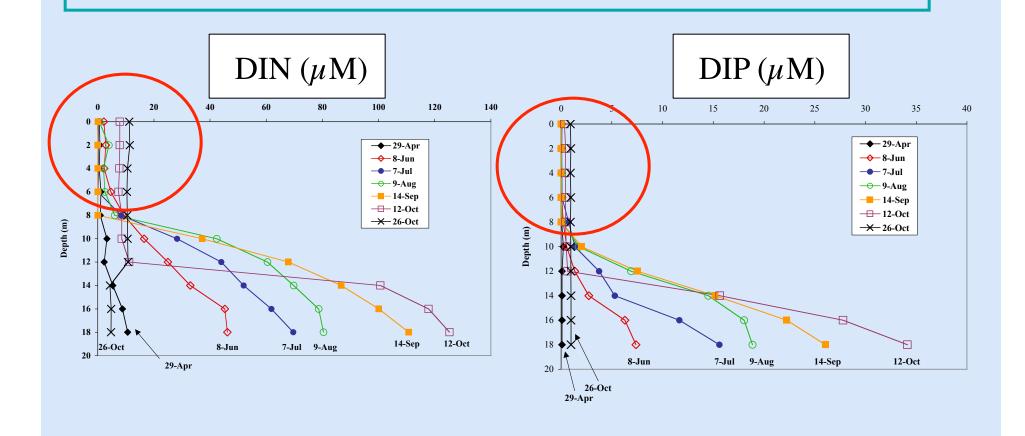
$$CO_2 + H_2O \iff H_2CO_3 \iff H^+ + HCO_3^- \iff 2H^+ + CO_3^{2-}$$

Primary Production and Nutrient Cycling

- Phytoplankton (free-floating algae)
 - contribute most of the net primary production
 - are confined to surface waters due to light limitation
- NPP depends on external nutrient inputs to epilimnion and regeneration/recycling
- Epilimnion is oxic, so organic matter decomposes rapidly by aerobic respiration
- Low levels of nutrients are found in surface waters due to efficient phytoplankton uptake



Seasonal Evolution of DIN ($NO_3^-+NO_2^-+NH_4^+$) and DIP (PO_4^{3-}) in the Epilimnion of a temperate Massachusetts lake



Ruttenberg and Haupert (unpubl.)

Measuring Primary Production

- Collect water samples
- Incubate water samples in clear & dark bottles
- Two methods for quantifying PP:
 - Measure change in dissolved oxygen (O₂), or
 - Measure production of ¹⁴C-labeled POC (from ¹⁴C-HCO₃ additions)

Looking at PP and R in terms of Reactions

- Water incubated in clear bottles:
 - Oxygen evolution (photosynthetic O₂ production)

$$CO_2 + H_2O \rightarrow O_2 + CH_2O$$
 (eqn. 5.2)

- ¹⁴C-labeled POC (C-uptake)

$$^{14}\text{CO}_2 + \text{H}_2\text{O} \rightarrow \text{O}_2 + ^{14}\text{CH}_2\text{O}$$

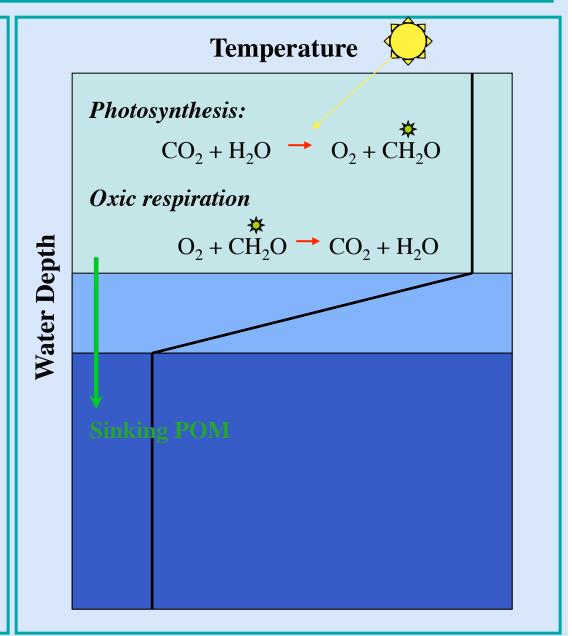
- Calculate results via O₂-evolution method:
 - Dark bottle: Respiration (drop in O_2 is a measure of net respiration):

$$O_2 + CH_2O \rightarrow CO_2 + H_2O$$

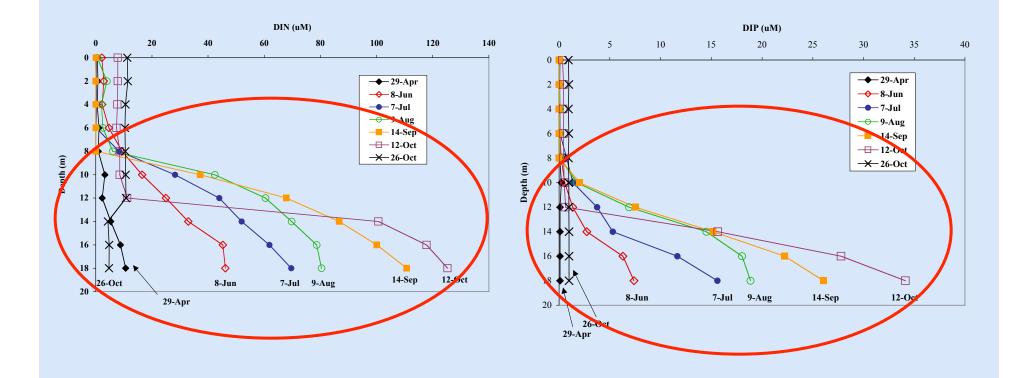
- Clear bottle: <u>Net</u> Primary Production (NPP):
 - increase in O_2 is a measure of NPP, photosynthesis in excess of respiration: NPP = P-R
- GPP = NPP R (e.g., the sum of changes in light & dark bottles)

Fate of Primary Production (photosynthetic POM)

- Dead organic matter sinks into the hypolimnion where it is decomposed by microbial respiration.
- Decay within hypolimnion consumes O₂ (low redox potential develops);
 - isolated from the atmosphere
 - no re-oxygenation.
- As a result of hypolimnion isolation, and of continual supply and respiration of POM:
 - O₂ is consumed
 - nutrients build up



Seasonal Evolution of DIN and DIP in the Hypolimnion of a temperate Massachusetts lake



Ruttenberg and Haupert (unpubl.)

Export of POM from the Epilimnion

- Export ratio = percentage of PP that sinks to the hypolimnion.
- Export ratio is 10-50% of NPP in 12 US lakes.
- Greater fractional export in lower productivity lakes.
- High P in hypolimnion is returned to the surface during seasonal mixing.
- P-Turnover is incomplete, some P is lost to sediments.

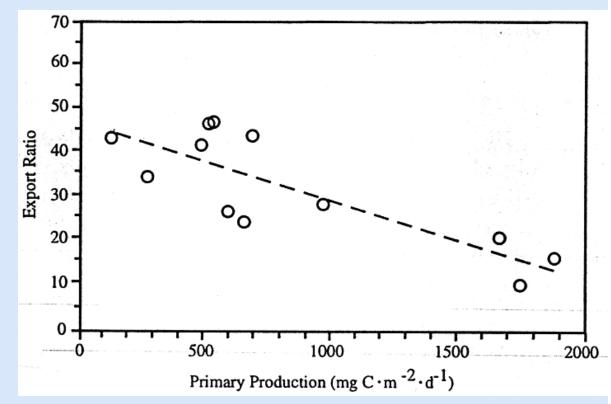
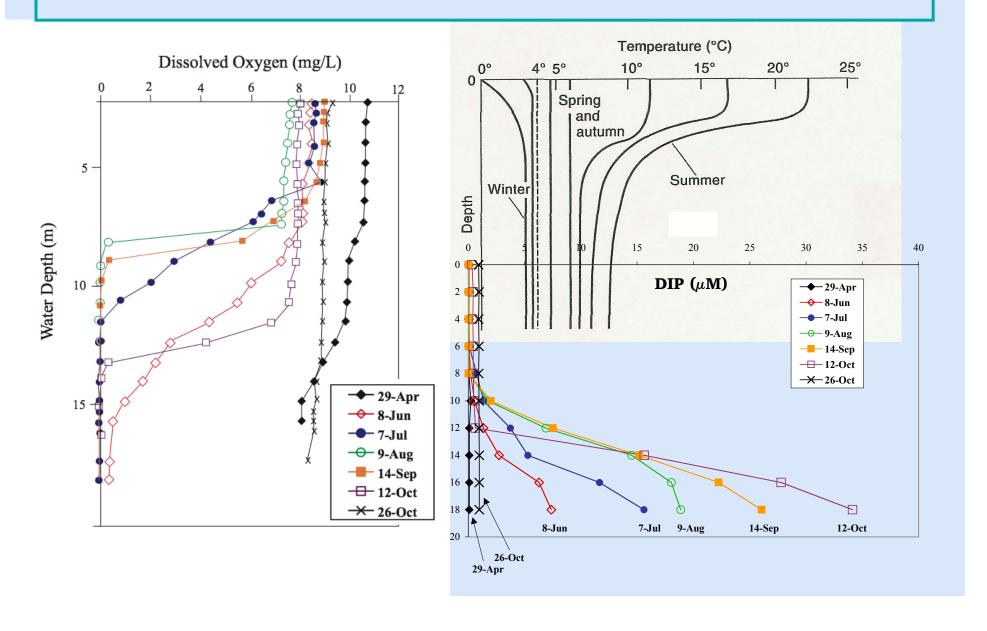


Fig. 8.17 % of phytoplankton PP that sinks to hypolimnion (export ratio) as a function of lake net primary productivity; after Baines and Pace 1994).

Consequence of POM Export: Nutrient build-up and O₂ draw-down in Hypolimnion



Lake Productivity is Linked to Nutrient Concentration

Comparison of world lakes:

- Most lakes appear to be *P-limited*.
- Other factors can be important (e.g., other nutrients, sunlight).
- More recent studies suggest co-limitation

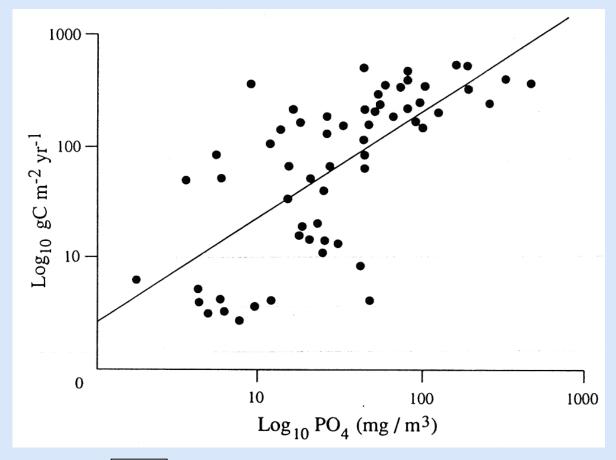


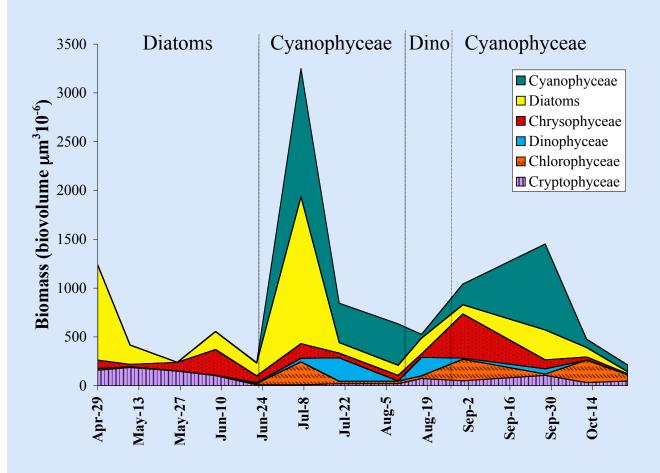
Fig. 8.13 Relationship between NPP and phosphate concentration of lakes of the world (Shindler 1978).

Nutrient Cycling in Lakes

- Natural P inputs to lakes is small.
 - Retention in terrestrial watersheds: vegetation and soil
 - P associated with soil minerals not bioavailable
- Large proportion of P is in plankton biomass; small proportion is "available" (dissolved in lake water).
- P-recycling in the epilimnion is dominated by bacterial decomposition of organic matter (internal recycling)
 - Production of POM and DOM (DOC, DON, DOP)
- Phytoplankton and bacteria excrete enzymes to convert DOP to bioavailable PO_4^{3-} .
- When N is limiting, shift to N_2 -fixing algae, e.g., from green to blue-green algae (cyanobacteria)

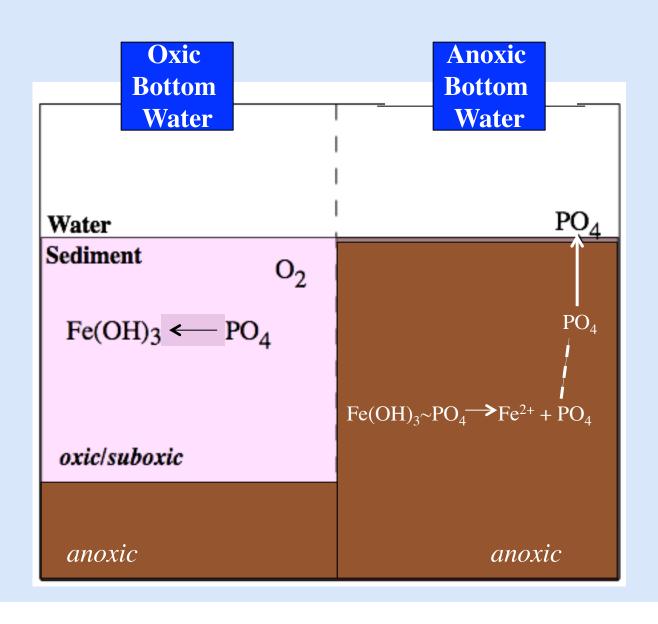
Role of N-Fixation in Epilimnion





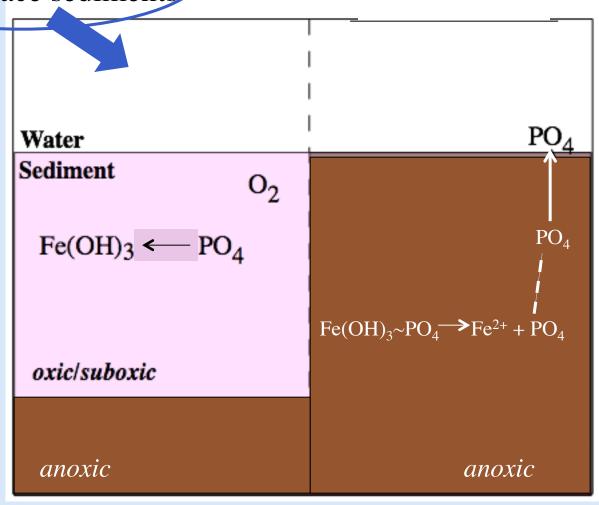
- Both P & N are depleted in epilimnion.
- Encourages bluegreen algal growth, because they are Nfixers.
- Pollutant P
 encourages blue green algal growth,
 can account for
 >80% of N-input to
 phytoplankton.
- N-input via N-fix'n maintains Plimitation

Role of Sediments in P-Cycling



Role of Sediments in P-Cycling

Oxic hypolimnion
Oxic surface sediments



Role of Sediments in P-Cycling

 O_2



Water

Sediment

oxic/suboxic

anoxic

 $Fe(OH)_3 \leftarrow PO_4$

Reducing sediments PO_4 PO_4 $Fe(OH)_3 \sim PO_4 \longrightarrow Fe^{2+} + PO_4$ anoxic

Lake Carbon Budgets

- Identify and quantify carbon sources / inputs
- Identify and quantify carbon **sinks / exports**
- Evaluate whether system is in balance: steady state
- Identify particular characteristics of system

Table 8.3 Origins	and Fates of C	Organic Carbon in	Lawrence Lake	, Michigan"

	$g C m^{-2} yr^{-1}$	%	% (total)
Net primary productivity (NPP)			
POC			
Phytoplankton	43.3	25.4%	
Epiphytic algae	37.9	22.1%	
Epipelic algae	2.0	1.2%	
Macrophytes	87.9	51.3%	
Total	171.2	100.0%	
DOC			
Littoral	5.5		,
Pelagic	14.7		
Total	20.2		
Total NPP	191.4		88.4%
Imports			
POC	4.1	16.3%	
DOC	21.0	83.7%	
Total imports	25.1	100%	11.6%
Total available organic inputs	216.5		100.0%
Respiration	TO SAN SOLIT COME SHARE AN ARRANGE AND ARR		
Benthic	117.5	73.6%	
Water column	42.2	26.4%	
Total respiration	159.7	100.0%	74.2%
Sedimentation	16.8		7.8%
Exports			
POC	2.8	7.3%	
DOC	35.8	92.7%	
Total exports	38.6	100.0%	18.0%
Total removal of carbon	215.1		100.0%

[&]quot;From Rich and Wetzel (1978).

Autochthonus vs. Allocthonous Carbon

- NPP within the lake is "autochthonous" production.
- Note importance of macrophytes (i.e., rooted plants), which reflects the extent of shallow water.
- Organic carbon from outside the lake is "allochthonous"
 production.

	g C m ⁻² yr ⁻¹	%	% (total)
Net primary productivity (NPP)			
POC			
Phytoplankton	43.3	25.4%	
Epiphytic algae	37.9	22.1%	
Epipelic algae	2.0	1.2%	
Macrophytes	→ 87.9	51.3%	
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Total exports	38.6	100.0%	18.0%
Total removal of carbon	215.1		100.0%

[&]quot;From Rich and Wetzel (1978).

The Balance between Photosynthesis & Respiration

- In lakes with lower chlorophyll (i.e., lower productivity), respiration exceeds production.
- This reflects the increased importance of allochthonous carbon inputs.
- Lake waters are often supersaturated with respect to CO₂ relative to the atmosphere.

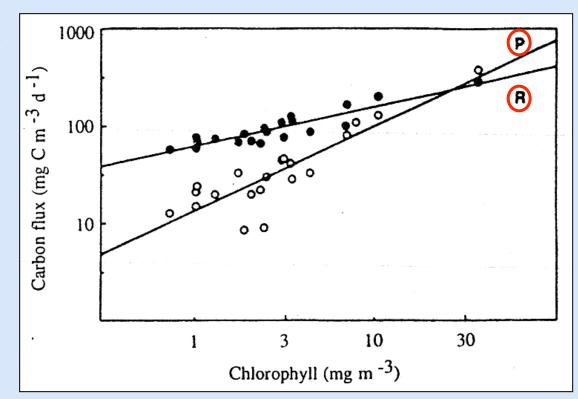


Fig. 7.12. Mean summertime plankton respiration (R) and photosynthesis (P) in surface waters of lakes as a function of chlorophyll concentration, an index of overall lake productivity (del Georgio & Peters, 1994).

Lake Carbon Budgets (cont'd).

- 74% of organic inputs are respired in the lake
- 74% of that respiration occurrs in the sediment. (Deeper lakes have more respiration in the water column.)
- 8% of OC is stored in sediments, similar to terrestrial systems, but from a much lower NPP that is typical on land; reflects *inefficiency of respiration, as compared to non-saturated soils*.

Table 8.3 Origins and Fates of	Organic (Carbon in	Lawrence	Lake, Michigan ^a

	$g~C~m^{-2}~yr^{-1}$	%	% (total	
Net primary productivity (NPP)				
POC				
Phytoplankton	43.3	25.4%		
Epiphytic algae	37.9	22.1%		
Epipelic algae	2.0	1.2%		
Macrophytes	87.9	51.3%		
Total	171.2	100.0%		
DOC				
Littoral	5.5		1	
Pelagic	14.7			
Total	20.2			
Total NPP	191.4		88.4%	
Imports				
POC	4.1	16.3%		
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Total imports	25.1	100%	11.6%	
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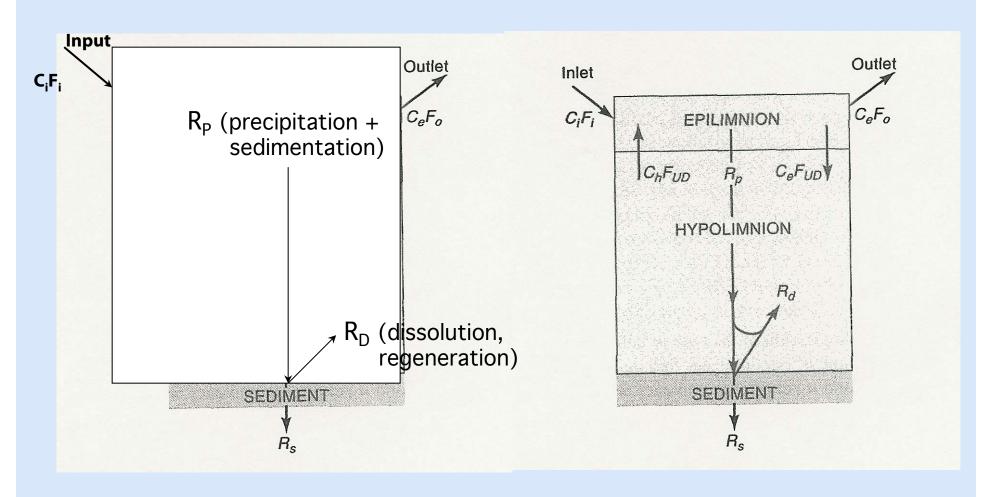
[&]quot;From Rich and Wetzel (1978).

Lake Nutrient Budgets

- Inputs: precipitation, runoff, N-fixation, groundwater
- Losses: sedimentation, outflow, release of gases, groundwater
- Nutrient budgets require an accurate water budget for the system
- Comparison of <u>nutrient residence time</u> with <u>water residence time</u> gives an indication of the importance of internal biotic cycling
 - Most lakes show a substantial net retention of N and P.
 - Lakes with high water turnover, however, may show relatively low levels of N and P storage.
- Many lakes show near-balanced budgets for Mg, Na, Cl, because these elements are highly soluble and non-limiting to phytoplankton.

One- and Two-box Models for Lakes

(after Berner and Berner, Figs. 6.5 and 6.6)



$$\Delta M/\Delta t = C_i F_i - C_e F_o + R_D - R_P$$

$$where R_S = R_P - R_D$$

$$T_r = [C] moles \div C_i F_i moles/yr$$

 F_U = rate of water transfer from hypolimnion to epilimnion F_D = rate of water transfer from epilimnion to hypolimnion

Lake Nutrient Budgets, cont.

Table 7.4 Input-Output Balance (tons/yr) for Cayuga Lake, New York, 1970–1971, and Rawson Lake, Ontario, 1970–1973^a

Element	Precipitation input	Runoff input	Total input	Discharge output	Percent retained
		Cayuga L	ake		
Phosphorus	3	167	170	61	64
Nitrogen	179	2,565	2,744	513	81 🕶
Potassium	19	3,480	3,499	3,969	-12
Sulfur	313	24,671	24,984	31,983	-22
		Rawson L	ake		
Phosphorus	0.018	0.017	0.035	0.010	71
Nitrogen	0.339	0.346	0.686	0.275	.60 ←
Carbon	2.435	19.005	21.440	10.074	53
Potassium	0.059	0.442	0.501	0.434	13
Sulfur	0.055	0.362	0.416	0.331	20

- Most lakes show a net retention of N and P
- Biogeochemical control on geochemistry of system

Lake Nutrient Budgets: N fixation

- Lakes with high rates of N fixation show large apparent accumulations of N.
 - 80% of N input to Amazon River is via N-fix' n
- However, the loss of N by denitrification >> input of N by fixation
- Denitrification removes fixed N as N_2O and (especially) N_2 .
- Anammox is another pathway for removal of fixed N: $NH_4^+ + NO_2^- = N_2 + 2H_2O$

Trophic State Lake Classification

- Oligotrophic lakes are:
 - low productivity systems
 - nutrient depleted
 - frequently geologically young
 - typically deep, with a cold hypolimnion
- Eutrophic lakes are:
 - high productivity systems
 - nutrient rich
 - dominated by nutrient inputs from the surrounding watershed
 - often shallow and warm
 - may be subject to "cultural eutrophication"

Trophic State Lake Classification (cont'd)

- Nutrient input to oligotrophic lakes is typically dominated by precipitation.
- Eutrophic lakes derive nutrients mainly from the surrounding watershed.

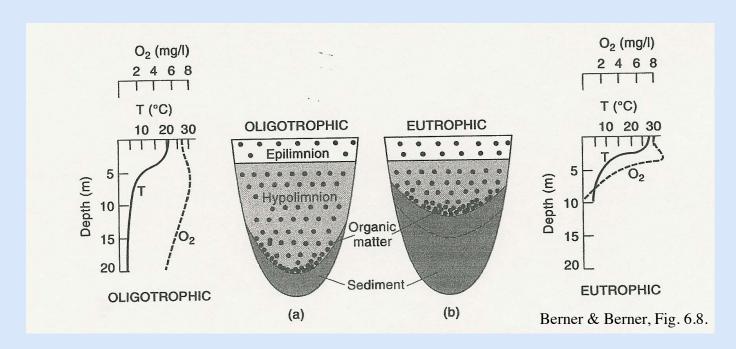
Table 7.5 Sources of Nitrogen and Phosphorus as Percentages of the Total Annual Input to Lake Ecosystems^a

	Precipitation		Runoff	
	N	P	N	P
Oligotrophic lakes	56	50	44	50
Eutrophic lakes	12	7	88	93

^a From Likens (1975a).

- Nutrient status is the most useful criterion for distinguishing oligotrophic vs. eutrophic lakes.
- Sedimentation will convert oligotrophic to eutrophic lakes: eutrophication an aging sequence of a lake.

- Eutrophication is a natural process by which accumulation of
 - sediment causes: lake shallowing
 - decreased hypolimnion volume
 - increased O₂ drawdown
- Positive feedback
 - lower O₂
 - less nutrient retention in sediments
 - higher productivity
 - higher rain of organic matter to hypolimnion



• Cultural eutrophication: human activity accelerates eutrophication.

Cultural Eutrophication

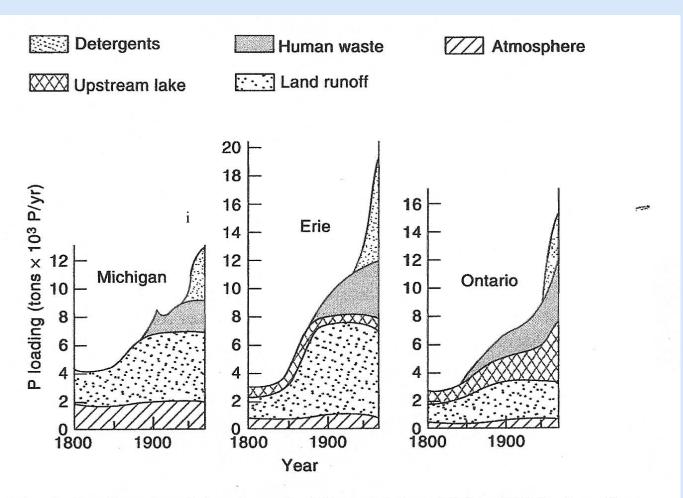


Figure 6.10. Historical loading of total phosphorus (in 10³ tons/yr) from 1800 to 1970 for three Great Lakes, Michigan, Ontario, and Erie, based on model calculation. [From Stumm and Morgan, 1981, after S. C. Chapra, "Total Phosphorus Model for the Great Lakes," *Journal of Div. of Environmental Engineering* 103(EE2): 153. Copyright © 1977. American Society Civil Engineering, reprinted by permission of the publisher.]

• Berner & Berner (2013) Fig. 6.10.

Trophic State Lake Classification (cont'd)

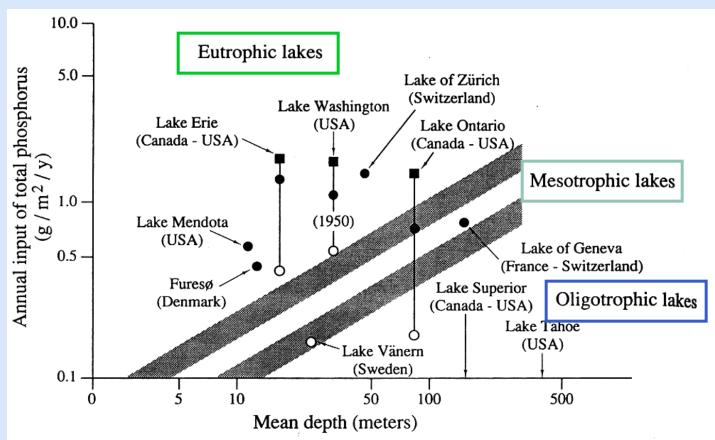


Figure 7.13 The position of important lakes relative to the annual receipt of phosphorus and their mean depth, differentiating oligotrophic and eutrophic lakes. For lakes that have undergone significant pollution, the change from previous conditions (○) to present conditions (○) is shown. From Vollenweider (1968).

Alkalinity and Acid Rain Effects

 Alkalinity is roughly equivalent to the imbalance in charge from cations and anions:

Alkalinity = Σ cations – Σ anions

- Any charge imbalance is "corrected" by changes in equilibrium in the DIC system: $HCO_3^- + H^+ = H_2CO_3$.
- Thus, Alkalinity = $[HCO_3^-] + 2[CO_3^{2-}] + [OH^-] [H^+]$
- Alkalinity <u>increases</u> by processes that consume SO_4^{2-} , NO_3^{-} or other anions, or that release DIC.
- Alkalinity decreases by processes that consume cations or DIC
- Acid rain decreases alkalinity due to addition of H⁺.

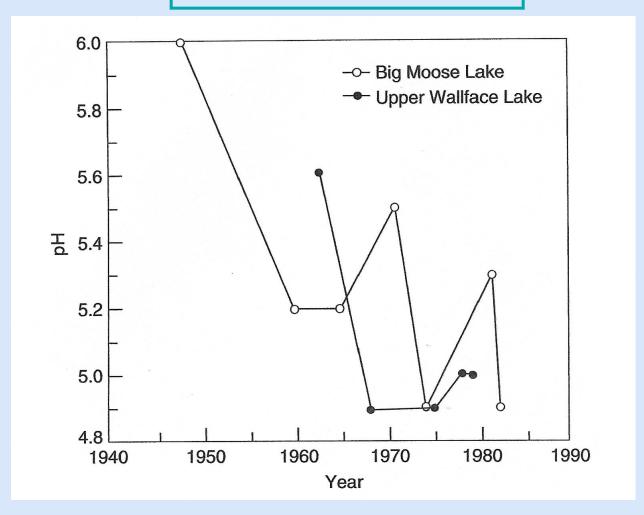
Sensitivity of Lakes to Acid Rain Effects



Figure 6.16. Lake Acidification in North America. (a) Regions in North America containing lakes that would be sensitive to potential acidification by acid precipitation (shaded areas). These areas have igneous or metamorphic bedrock geology which results in dilute lakes with low HCO₃⁻ concentrations (<0.5 mEq HCO₃⁻/l). Unshaded areas have calcareous or sedimentary bedrock geology. (From J. N. Galloway and E. B. Cowling, "The Effects of Precipitation on Aquatic and Terrestrial Ecosystems, A Proposed Precipitation Chemistry Network," *Journal of the Air Pollution Control Association* 28(3): 233. Copyright © 1978. J. of the Air Pollution Control Assoc. Reprinted by permission of the publisher.]

(after Berner and Berner, Fig. 6.16.)

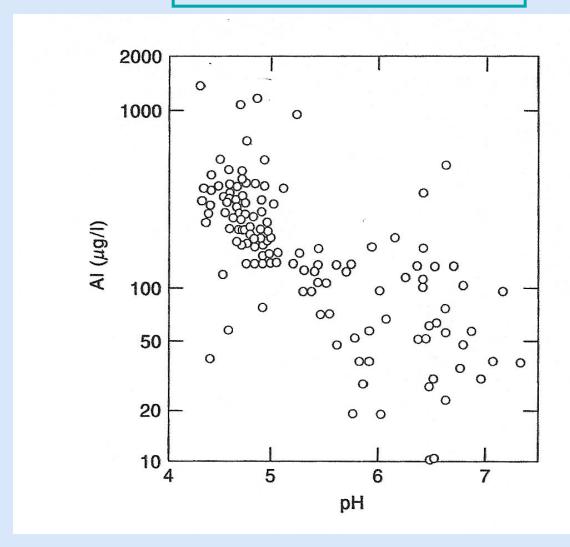
Acid Rain Effects



Berner & Berner Fig. 6.15. Changes in pH with time in lakes located in the Adirondack Mountains of New York State

Changing atmospheric conditions can alter lake ecosystem processes

Acid Rain Effects



Berner & Berner Fig. 6.18. Highly acidic weathering dissolves Al from kaolinite, plagioclase and gibbsite; these phases are not dissolved during normal weathering.

Lecture Summary / Main Points

- Physical properties of water, seasonal temperature changes, and the surrounding landscape and geology exert profound control on nutrient cycling and NPP in lakes
- Primary production is closely linked to nutrient supply
- Nutrient and carbon budgets provide a key means of assessing lake biogeochemical cycling
- Eutrophication is a natural process, which can be accelerated by anthropogenic activities
- Acid rain has had profound impacts on some lakes; underlying geology is a major factor in lake sensitivity