Lakes: Primary Production, Budgets and Cycling

Reading: Schlesinger, Chapter 8

Lecture Outline

1. Seasonal cycle of lake stratification
   • Temperature / density relationship
   • 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 denser 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

Temperature profiles over the year for a typical temperate lake. Dashed line represents maximum density at 4°C.

Freshwater Lake Classification

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

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.
Primary Production in Lakes

- 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 CO$_2$ system:
  
  \[
  \text{CO}_2 + \text{H}_2\text{O} \rightleftharpoons \text{H}_2\text{CO}_3 \rightleftharpoons \text{H}^+ + \text{HCO}_3^- \rightleftharpoons 2\text{H}^+ + \text{CO}_3^{2-}
  \]

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

Summer Stratification

- Epilimnion
- Metalimnion
- Hypolimnion
Seasonal Evolution of DIN (NO$_3^-$+NO$_2^-$+NH$_4^+$) and DIP (PO$_4^{3-}$) in a temperate lake in Massachusetts

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 (O$_2$), or
  - Measure production of $^{14}$C-labeled POC (from $^{14}$C-HCO$_3$ additions)
Looking at PP and R in terms of Reactions

- Water incubated in clear bottles:
  - Oxygen evolution (photosynthetic O₂ production)
    \[ \text{CO}_2 + \text{H}_2\text{O} \rightarrow \text{O}_2 + \text{CH}_2\text{O} \]  
    (eqn. 5.2)
  - \(^{14}\text{C}\)-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 O₂ is a measure of net respiration):
    \[ \text{O}_2 + \text{CH}_2\text{O} \rightarrow \text{CO}_2 + \text{H}_2\text{O} \]
  - Clear bottle: Net Primary Production (increase in O₂ is a measure of NPP):
    - photosynthesis in excess of respiration (NPP = P-R)
    - assumes molecular equivalence between C-fixation and O₂ production
  - GPP = NPP – R  (e.g., the sum of changes in light & dark bottles)

Primary Production and Nutrient Cycling (cont’d.)

- Dead organic matter sinks into the hypolimnion where it is decomposed by microbial respiration.
- Decay within hypolimnion consumes O₂ (low redox potential);
  - isolated from the atmosphere
  - no re-oxygenation.
- As a result of hypolimnion isolation, and of continual supply of dead organic matter and microbial respiration, O₂ is consumed and nutrients build up during the growing season.
Seasonal Evolution of DIN and DIP in a temperate lake in Massachusetts

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.

Ruttenberg and Haupert (unpubl.)
Consequence of POM Export: Nutrient build-up and $O_2$ draw-down in Hypolimnion

Lake Productivity is Linked to Nutrient Concentration

Comparison of world lakes:

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

Fig. 8.12 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 $\text{PO}_4^{3-}$.

- When N is limiting, shift to $\text{N}_2$-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 blue-green algal growth, because they are N-fixers.
- Pollutant P encourages blue-green algal growth, can account for >80% of N-input to phytoplankton.
- N-input via N-fix’n maintains P-limitation

```
0  500  1000  1500  2000  2500  3000  3500

Biomass (biomass per m$^3$)

Cyanophyceae  Diatoms  Cyanophyceae  Cyanophyceae
```

Green Algae  Blue-green Algae
Role of Sediments in P-Cycling

Oxic hypolimnion
Oxic surface sediments

\[
\text{Fe(OH)}_3 + \text{PO}_4 \rightarrow \text{Fe}^{3+} + \text{PO}_4
\]
Role of Sediments in P-Cycling

- Oxic hypolimnion
- Oxic surface sediments
- Anoxic hypolimnion
- Anoxic sedimentary Fe

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>
<thead>
<tr>
<th>Table</th>
<th>Origins and Fates of Organic Carbon in Lawrence Lake, Michigan*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g C m⁻² yr⁻¹</td>
</tr>
<tr>
<td>Net primary productivity (NPP)</td>
<td></td>
</tr>
<tr>
<td>POC</td>
<td>43.5</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>37.9</td>
</tr>
<tr>
<td>Epiphytic algae</td>
<td>2.6</td>
</tr>
<tr>
<td>Macrophytes</td>
<td>87.0</td>
</tr>
<tr>
<td>Total</td>
<td>171.2</td>
</tr>
<tr>
<td>DOC</td>
<td></td>
</tr>
<tr>
<td>Litoral</td>
<td>5.5</td>
</tr>
<tr>
<td>Pelagic</td>
<td>14.7</td>
</tr>
<tr>
<td>Total</td>
<td>20.2</td>
</tr>
<tr>
<td>Total NPP</td>
<td>191.4</td>
</tr>
<tr>
<td>Inputs</td>
<td></td>
</tr>
<tr>
<td>POC</td>
<td>4.1</td>
</tr>
<tr>
<td>DOC</td>
<td>21.0</td>
</tr>
<tr>
<td>Total imports</td>
<td>25.1</td>
</tr>
<tr>
<td>Total available organic inputs</td>
<td>216.5</td>
</tr>
<tr>
<td>Respiration</td>
<td></td>
</tr>
<tr>
<td>Benthic</td>
<td>117.5</td>
</tr>
<tr>
<td>Water column</td>
<td>42.2</td>
</tr>
<tr>
<td>Total respiration</td>
<td>159.7</td>
</tr>
<tr>
<td>Sedimentation</td>
<td></td>
</tr>
<tr>
<td>Export POB:</td>
<td>36.6</td>
</tr>
<tr>
<td>Export DOC</td>
<td>36.6</td>
</tr>
<tr>
<td>Total export</td>
<td>36.6</td>
</tr>
<tr>
<td>Total removal of carbon</td>
<td>215.1</td>
</tr>
</tbody>
</table>

* From Riff and Wierul (1978).
Autochthonous vs. Allochthonous 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.

<table>
<thead>
<tr>
<th>Table 8.2</th>
<th>Origins and Fates of Organic Carbon in Lawrence Lake, Michigan*</th>
</tr>
</thead>
<tbody>
<tr>
<td>g C m⁻³ yr⁻¹</td>
<td>%</td>
</tr>
<tr>
<td><strong>Net primary productivity (NPP)</strong></td>
<td></td>
</tr>
<tr>
<td>POC</td>
<td>171.2</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>43.5</td>
</tr>
<tr>
<td>Epiphytic algae</td>
<td>27.0</td>
</tr>
<tr>
<td>Macrophytes</td>
<td>40.7</td>
</tr>
<tr>
<td>Total NPP</td>
<td>191.4</td>
</tr>
</tbody>
</table>

- Impacts:
  - POC: 4.1 (2.2%)
  - DOC: 21.0 (8.7%)
  - Total impacts: 25.1 (100.0%)

- Total available organic input: 416.5 (100.0%)

| Respiration | | |
| Berthic | 117.5 | 23.4% |
| Water column | 42.1 | 8.6% |
| Total respiration | 159.7 | 100.0% |

| Sedimentation | | |
| Resorption | 16.6 | 7.8% |
| Export | 2.8 | 0.7% |
| DOC | 30.8 | 92.7% |
| Total export | 38.6 | 100.0% |
| Total removal of carbon | 215.1 | 100.0% |

* From Riff 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 occurs 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 4. Origin and Fate of Organic Carbon in Lawrence Lake, Michigan

<table>
<thead>
<tr>
<th>Source</th>
<th>C g m⁻² yr⁻¹</th>
<th>%</th>
<th>% (total)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary productivity (NPP)</td>
<td>171.2</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>POC</td>
<td>43.9</td>
<td>25.6%</td>
<td>25.6%</td>
</tr>
<tr>
<td>Epiphytic algae</td>
<td>37.9</td>
<td>22.1%</td>
<td>22.1%</td>
</tr>
<tr>
<td>Macroalgae</td>
<td>20.0</td>
<td>11.6%</td>
<td>11.6%</td>
</tr>
<tr>
<td>Total</td>
<td>101.8</td>
<td>59.4%</td>
<td>59.4%</td>
</tr>
<tr>
<td>DOC</td>
<td>5.6</td>
<td>3.2%</td>
<td>3.2%</td>
</tr>
<tr>
<td>Pielgon</td>
<td>14.7</td>
<td>8.6%</td>
<td>8.6%</td>
</tr>
<tr>
<td>Total</td>
<td>20.2</td>
<td>11.8%</td>
<td>11.8%</td>
</tr>
<tr>
<td>Total NPP</td>
<td>191.4</td>
<td>100%</td>
<td>100%</td>
</tr>
</tbody>
</table>

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 nutrient residence time with water residence time 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.
\[
\Delta M/\Delta t = C_{F_i} - C_{F_o} + R_D - R_P
\]

where \( R_S = R_P - R_D \)

\( T_r = [C] \text{ moles} + C_{F_i} \text{ moles/yr} \)

\( F_U = \text{rate of water transfer from hypolimnion to epilimnion} \)

\( F_D = \text{rate of water transfer from epilimnion to hypolimnion} \)

**Lake Nutrient Budgets, cont.**

<table>
<thead>
<tr>
<th>Element</th>
<th>Precipitation input</th>
<th>Runoff input</th>
<th>Total input</th>
<th>Discharge output</th>
<th>Percent retained</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(tons/yr)</td>
<td>(tons/yr)</td>
<td>(tons/yr)</td>
<td>(tons/yr)</td>
<td></td>
</tr>
<tr>
<td><strong>Cayuga Lake</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phosphorus</td>
<td>9</td>
<td>167</td>
<td>170</td>
<td>61</td>
<td>64</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>179</td>
<td>2,565</td>
<td>2,744</td>
<td>519</td>
<td>81</td>
</tr>
<tr>
<td>Potassium</td>
<td>19</td>
<td>5,480</td>
<td>5,499</td>
<td>5,069</td>
<td>-12</td>
</tr>
<tr>
<td>Sulfur</td>
<td>313</td>
<td>24,071</td>
<td>24,984</td>
<td>31,983</td>
<td>-22</td>
</tr>
<tr>
<td><strong>Rawson Lake</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phosphorus</td>
<td>0.018</td>
<td>0.017</td>
<td>0.035</td>
<td>0.010</td>
<td>71</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>0.339</td>
<td>0.346</td>
<td>0.686</td>
<td>0.275</td>
<td>-60</td>
</tr>
<tr>
<td>Carbon</td>
<td>2.435</td>
<td>19.005</td>
<td>21.440</td>
<td>10.074</td>
<td>53</td>
</tr>
<tr>
<td>Potassium</td>
<td>0.059</td>
<td>0.442</td>
<td>0.501</td>
<td>0.454</td>
<td>15</td>
</tr>
<tr>
<td>Sulfur</td>
<td>0.055</td>
<td>0.362</td>
<td>0.416</td>
<td>0.331</td>
<td>29</td>
</tr>
</tbody>
</table>

• 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:
  $$ \text{NH}_4^+ + \text{NO}_2^- = N_2 + 2\text{H}_2\text{O} $$

## 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”
• Nutrient input to oligotrophic lakes is typically dominated by precipitation.

• Eutrophic lakes derive nutrients mainly from the surrounding watershed.

• 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.

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**Trophic State Lake Classification (cont’ d)**

<table>
<thead>
<tr>
<th>Table 7.5 Sources of Nitrogen and Phosphorus as Percentages of the Total Annual Input to Lake Ecosystems*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Oligotrophic lakes</td>
</tr>
<tr>
<td>Eutrophic lakes</td>
</tr>
</tbody>
</table>

* From Likens (1975a).

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• **Eutrophication** is a natural process by which accumulation of sediment causes:
  - lake shallowing
  - decreased hypolimnion volume
  - increased O$_2$ drawdown

• Positive feedback
  - lower O$_2$
  - less nutrient retention in sediments
  - higher productivity
  - higher rain of organic matter to hypolimnion

---

• **Cultural eutrophication:** human activity accelerates eutrophication.
Cultural Eutrophication


*T 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:
  \[
  \text{Alkalinity} = \Sigma \text{cations} - \Sigma \text{anions}
  \]
- Any charge imbalance is “corrected” by changes in equilibrium in the DIC system:
  \[\textit{HCO}_3^- + H^+ = \textit{H}_2\textit{CO}_3.\]
- Thus, \(\text{Alkalinity} = [\text{HCO}_3^-] + 2[\text{CO}_3^{2-}] + [\text{OH}^-] - [H^+]\)
- Alkalinity increases by processes that consume \(\text{SO}_4^{2-}\), \(\text{NO}_3^-\) 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 \(\text{HCO}_3^-\) concentrations (<0.5 mEq/L)\(\text{HCO}_3^-\). Unshaded areas have calcareous or sedimentary bedrock geology. (From J. N. Gaither and E. B. Crootles, “The Effects of Precipitation on Aquatic and Terrestrial Ecosystems: A Proposed Precipitation Damage Network,” Journal of the Air Pollution Control Association 28(5): 233. Copyright 1978, J. of the Air Pollution Control Assoc. Reprinted by permission of the publisher.)

(after Berner and Berner, Fig. 6.16.)
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.

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