BIO 206

HYDROBIOLOGY

Course code: BIO 206

Course title: Hydrobiology

Course credit load: 2 Units

Series 1: Physical Properties and Dynamics of Water

- **Part 1.1: Unique Physical and Chemical Properties of Water**
  - Sub Part 1.1.1: Molecular structure and hydrogen bonding
  - Sub Part 1.1.2: Density, viscosity, and surface tension
  - Sub Part 1.1.3: Thermal properties and their biological significance
- **Part 1.2: Light and Sound in Aquatic Environments**
  - Sub Part 1.2.1: Penetration and attenuation of light in water
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- **Part 1.3: Water Movements: Waves and Currents**
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- **Part 1.4: Dissolved Gases and Inorganic Ions in Freshwater**
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  - Sub Part 1.4.3: Major inorganic ions and their roles

Introduction

Water is the medium of life for aquatic organisms and the substrate of the discipline of hydrobiology. Its physical and chemical properties are unique among common substances and are directly responsible for the structure, distribution, and functioning of aquatic ecosystems. Understanding why water behaves as it does provides the foundation for interpreting every aspect of lake, river, estuarine, and marine biology covered in this course.

This Series covers the molecular basis of water's anomalous properties, the behaviour of light and sound in aquatic systems, the forces generating waves and currents and their ecological consequences, and the dissolved gases and inorganic ions that determine water chemistry and biological productivity. These physical and chemical parameters recur throughout all subsequent series of this course.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- SLO 1.1 explain how the molecular structure of water gives rise to its unique physical and chemical properties (Linked to Part 1.1),
- SLO 1.2 describe the density anomaly of water and its ecological consequences for aquatic organisms (Linked to Part 1.1),
- SLO 1.3 explain the penetration and attenuation of light in water and define the photic, aphotic, and compensation zones (Linked to Part 1.2),
- SLO 1.4 describe the formation of waves and currents and explain their effects on aquatic substrata and organisms (Linked to Part 1.3),
- SLO 1.5 explain the factors controlling dissolved oxygen concentration in freshwater and state its biological significance (Linked to Part 1.4),
- SLO 1.6 describe the carbonate-bicarbonate buffering system and explain how it regulates pH in freshwater (Linked to Part 1.4), and
- SLO 1.7 name the major inorganic ions in freshwater and describe their ecological roles (Linked to Part 1.4).

1.1 Unique Physical and Chemical Properties of Water

1.1.1 Molecular structure and hydrogen bonding

Water (H2O) is a polar molecule: the two hydrogen atoms are bonded to one oxygen atom at an angle of approximately 104.5 degrees. The oxygen atom is strongly electronegative, drawing the shared electrons toward itself and creating a partial negative charge (delta-) on the oxygen and partial positive charges (delta+) on the hydrogens. This polarity enables water molecules to form hydrogen bonds with each other and with other polar or charged molecules: the delta+ hydrogen of one molecule is attracted to the delta- oxygen of a neighbouring molecule.

Hydrogen bonds (individually weak, collectively very strong) are responsible for most of water's anomalous properties: its high boiling point (100 degrees Celsius, far higher than predicted for a molecule of its size); high specific heat capacity; high latent heat of vaporisation; high surface tension; and the expansion of water upon freezing. Water is also a universal solvent: its polarity enables it to dissolve ionic compounds (which dissociate into ions surrounded by water molecules) and polar organic molecules. This solvent power underlies the chemical richness of natural waters.

Fill in the blank: Water molecules form ________ bonds with each other because the electronegative oxygen atom creates a partial negative charge that attracts the partial positive charge on the hydrogen atoms of neighbouring molecules.

1.1.2 Density, viscosity, and surface tension

The density of water reaches its maximum at 4 degrees Celsius (1,000 kg/m^3) and decreases both above and below this temperature. As water cools below 4 degrees Celsius, the hydrogen bond network becomes more ordered and open, causing ice to be less dense than liquid water; this is why ice floats. In lakes, this density anomaly drives seasonal turnover (mixing) and determines the structure of thermal stratification (covered in Series 2). Freshwater is less dense than seawater (approximately 1,025 kg/m^3) due to dissolved salts; the density difference affects stratification at river mouths and estuaries.

Viscosity is the resistance of a fluid to flow. Water's viscosity decreases with increasing temperature; warm water flows more freely than cold water. Viscosity is ecologically important because it governs the drag experienced by swimming organisms, the sinking rate of particles and plankton, and the delivery of nutrients to cell surfaces. Surface tension arises from the cohesive hydrogen bonds between surface water molecules, which have no neighbours above; the result is a film strong enough to support small organisms (e.g. water striders, Gerris) that exploit the water surface as a habitat. Surface tension also drives capillary rise in soils and plant cells.

Fill in the blank: Water reaches its maximum density at ________ degrees Celsius; below this temperature it becomes less dense, causing ice to float on liquid water, which insulates aquatic organisms from freezing in cold climates.

1.1.3 Thermal properties and their biological significance

The specific heat capacity of water (4,182 J/kg/K) is exceptionally high compared to other common liquids. It takes a large input of heat energy to raise water temperature and a large loss of energy to lower it; water bodies therefore heat and cool slowly, buffering aquatic organisms against rapid temperature fluctuations. This thermal stability is critical in tropical African lakes such as Lake Chad and the Niger Delta wetlands, where diurnal air temperature swings are large but water temperature remains relatively stable.

The high latent heat of vaporisation (2,260 kJ/kg) means that a large amount of energy is absorbed when water evaporates; this is the basis of evaporative cooling in organisms and in climate regulation. The latent heat of fusion (334 kJ/kg) means that freezing or thawing a water body requires the exchange of large amounts of heat, moderating temperature changes at the freezing point. Together, these thermal properties make aquatic habitats thermally stable relative to terrestrial environments, allowing ectothermic aquatic organisms to maintain enzyme function and metabolic activity within a narrow range.

Fill in the blank: The high specific heat capacity of water means that a large input of ________ energy is required to raise its temperature; this causes water bodies to heat and cool slowly, buffering aquatic organisms against rapid temperature fluctuations.

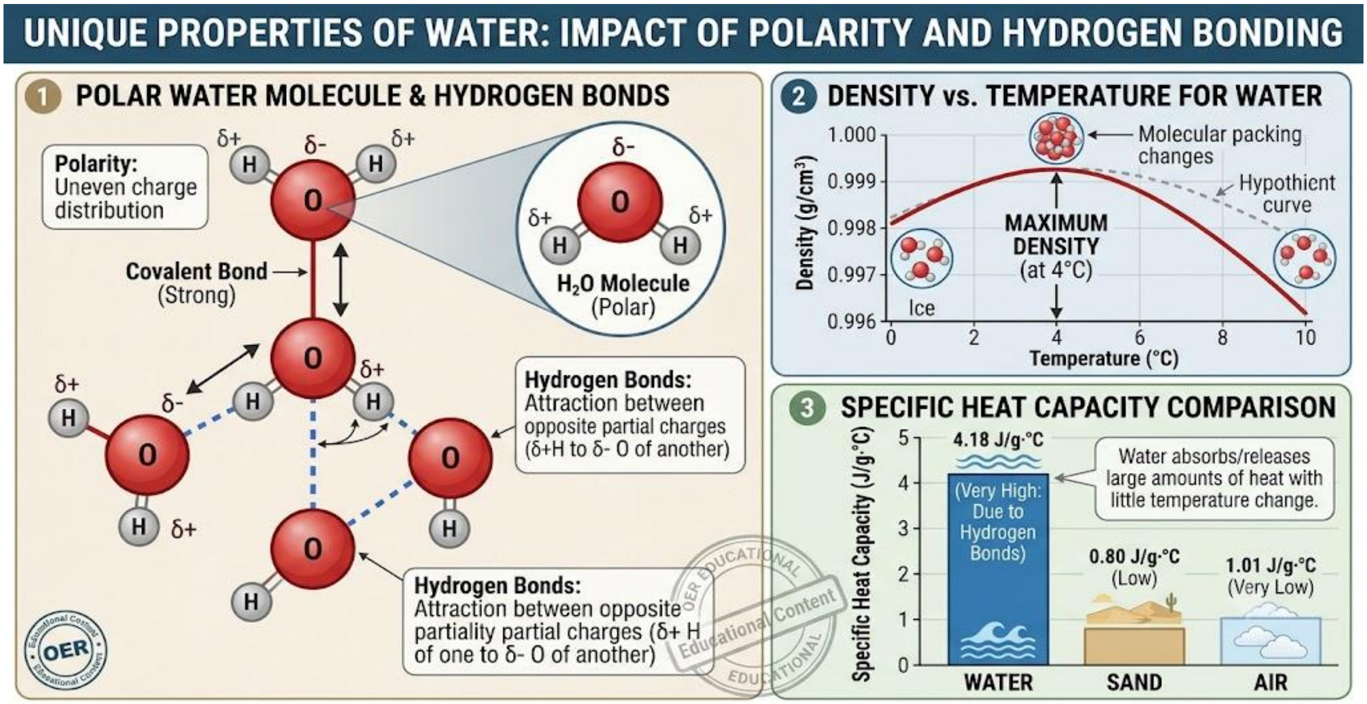

Figure 1.1: Molecular structure of water, the density-temperature relationship, and the comparative specific heat capacity of water

Pilot questions 1.1

1. Explain how the polarity of the water molecule gives rise to hydrogen bonding.
2. Explain the density anomaly of water and state two ecological consequences.
3. Explain why viscosity is ecologically important for aquatic organisms.
4. State two ways in which the high specific heat capacity of water benefits aquatic organisms.
5. Name three properties of water that arise directly from hydrogen bonding.

1.2 Light and Sound in Aquatic Environments

1.2.1 Penetration and attenuation of light in water

Light is rapidly attenuated (reduced in intensity) as it passes through water by three processes: absorption (conversion of light energy to heat by water molecules and dissolved substances); scattering (redirection of light by particles and molecules); and reflection at the water surface (approximately 2 to 5% of incident light for calm conditions; up to 100% at shallow angles). The combined effect is described by the extinction coefficient (k): intensity at depth z = surface intensity x e^(-kz). A higher k (turbid water) means more rapid light attenuation with depth.

Different wavelengths of light are attenuated at different rates. Red and infrared light are absorbed within the first few metres; blue-green light penetrates deepest in clear oceanic water. In turbid or coloured freshwater (stained by dissolved organic matter or suspended sediment), even blue-green light is attenuated quickly. Turbidity is measured using a Secchi disk: a white disk lowered until it disappears; the Secchi depth (typically 0.3 to 30 m depending on water clarity) provides a simple index of light penetration. Turbidity is high in rivers and floodplain lakes receiving sediment-laden runoff, as is common in the Niger Delta region.

Fill in the blank: A ________ disk is lowered into the water until it just disappears from view; the depth at which this occurs (the Secchi depth) provides a simple index of water transparency and light penetration.

1.2.2 Photic, aphotic, and compensation zones

The photic zone (euphotic zone) is the surface layer of a water body where sufficient light penetrates to support net photosynthesis. It extends from the surface to the compensation depth, which is conventionally defined as the depth at which gross photosynthesis equals community respiration (approximately 1% of surface irradiance). Above the compensation depth, photosynthesis exceeds respiration and net organic matter production occurs. Below it, respiration exceeds photosynthesis, so the community is net heterotrophic.

The aphotic zone lies below the compensation depth where light is insufficient for photosynthesis. In the deep ocean, this begins at 200 m or deeper; in turbid tropical lakes and rivers, it may begin at only 0.5 to 2 m depth. The depth of the photic zone determines the depth over which primary production can occur and therefore the total productivity of the water body. The ratio of photic zone depth to total lake depth is an important predictor of whether benthic algae or phytoplankton dominate primary production. In shallow, turbid Nigerian lakes and ponds, the photic zone may extend to the bottom, enabling macrophyte growth across the whole basin.

Fill in the blank: The compensation depth is the depth at which gross photosynthesis equals community ________; above it the community shows net primary production; below it the community is net heterotrophic and relies on organic matter sinking from the photic zone.

1.2.3 Transmission of sound and pressure in water

Sound travels approximately 4.4 times faster in water (approximately 1,500 m/s) than in air (approximately 340 m/s), because water is relatively incompressible and has greater density and elasticity. Sound also travels further in water with less energy loss per unit distance than in air. These properties make acoustic communication important for aquatic animals: fish use sound for courtship, territorial defence, and predator avoidance; cetaceans (whales, dolphins) use complex vocalisations and echolocation that can propagate thousands of kilometres in the ocean. Hydrophones detect underwater sound and are used in fisheries surveys and biodiversity monitoring.

Hydrostatic pressure increases by approximately one atmosphere (101 kPa) for every 10 m of depth in water. Deep-sea organisms (hadal fauna below 6,000 m) experience pressures exceeding 600 atmospheres. Pressure affects enzyme conformation, membrane fluidity, and gas solubility; deep-sea organisms have pressure-adapted enzymes and membranes enriched in unsaturated fatty acids to maintain fluidity under compression. For freshwater organisms, pressure effects are minimal (maximum depth of large African lakes rarely exceeds 1,500 m in Lake Tanganyika) but are important in deep lakes where oxygen depletion in the hypolimnion compounds the effects of pressure.

Fill in the blank: Sound travels approximately ________ metres per second in water, which is about 4.4 times faster than in air; this facilitates long-distance acoustic communication in fish and cetaceans.

Pilot questions 1.2

1. State three processes by which light is attenuated as it passes through water.
2. Explain how a Secchi disk is used and what it measures.
3. Define the photic zone and the compensation depth.

4. Explain why sound travels faster in water than in air and give two examples of its ecological importance.
5. State how hydrostatic pressure increases with depth and explain one way in which deep-sea organisms adapt to high pressure.

1.3 Water Movements: Waves and Currents

1.3.1 Waves and their effects on the substratum

Waves are oscillations of water at the surface generated primarily by wind transferring energy to the water surface; wave size (height and wavelength) increases with wind speed, fetch (the unobstructed distance over which wind blows), and duration. Water particles in a wave move in circular orbits: in deep water the orbital diameter decreases exponentially with depth and becomes negligible at a depth equal to half the wavelength (the wave base). Below the wave base, the substratum is undisturbed. In shallow water where depth is less than half the wavelength, orbital motion is distorted and water moves back and forth along the bottom, exerting shear stress on the substratum.

Wave action on the substratum determines sediment grain size and the distribution of benthic organisms. On exposed shores with strong wave action, only coarse sediment (gravel, pebbles) or bedrock remains; fine sediment is winnowed away. Organisms in the wave-exposed littoral zone must withstand strong hydrodynamic forces: macroalgae (seaweeds) and mussels attach firmly with holdfasts and byssus threads; limpets have flat shells that reduce drag; and invertebrate larvae of wave-swept streams (blackfly larvae, net-spinning caddisfly) attach by silk threads or hooks. Protected shores accumulate fine sediment and support burrowing fauna.

Fill in the blank: Wave orbital motion becomes negligible at a depth equal to half the wavelength (the wave ________); below this depth the substratum is undisturbed by wave action regardless of conditions at the surface.

1.3.2 Currents in rivers, lakes, and oceans

River currents are driven by gravity (the hydraulic gradient); velocity increases with gradient and discharge and decreases with channel width, depth, and substrate roughness. The current velocity profile in a river channel is highest near the surface in mid-channel and lowest at the bed and banks (due to friction). The relationship between current velocity and sediment transport is described by the Hjulstrom curve: higher velocities erode and transport sediment; lower velocities deposit it. Rivers alternate between erosional and depositional zones, shaping the substratum available to benthic organisms.

Lake currents are driven by wind stress on the surface (producing surface drift and return currents), density differences (thermohaline circulation), and internal waves (seiches: standing waves that oscillate along the length of a lake basin, driven by wind). Ocean currents are driven by wind, thermohaline circulation (density differences due to temperature and salinity), and the Coriolis effect (deflection due to Earth's rotation). Major oceanic current gyres redistribute heat globally. Upwelling currents bring nutrient-rich deep water to the surface, supporting high biological productivity; this is important in the Gulf of Guinea off the Nigerian coast.

Fill in the blank: ________ are standing oscillation waves in a lake basin driven by wind; they cause the thermocline to tilt, bringing nutrient-rich hypolimnetic water to the surface at the upwind end of the lake.

1.3.3 Biological responses to water movement

Flowing water (lotic systems) carries dissolved oxygen, nutrients, and food particles to sessile organisms; many benthic invertebrates in streams (mayfly nymphs, blackfly larvae, suspension-feeding caddisflies) exploit current-delivered food. However, current also exerts drag: organisms respond with streamlining (flattened or elongated body forms), attachment organs (hooks, silk, suckers), and burrowing into the substratum. The current velocity at which an organism is dislodged or swept away is its critical erosion velocity; this determines its distributional range across stream microhabitats of different flow regimes.

Plankton in lakes and oceans cannot swim against significant currents and are therefore passively transported by water movements; their distribution patterns reflect current systems. Many planktonic organisms perform diel vertical migration (descending to deeper, darker water during the day and ascending to the photic zone at night) partly to exploit different current layers. Migratory fish such as the African catfish (Clarias gariepinus) use current direction as a navigational cue during upstream spawning migrations in Nigerian rivers. Estuarine organisms must tolerate or exploit reversing tidal currents, using behaviour (burrowing at low tide; feeding at high tide) and physiology (tolerance of salinity fluctuation) to persist.

Fill in the blank: Benthic invertebrates in fast-flowing streams respond to current drag by ________ their bodies (reducing drag), developing attachment structures such as hooks and silk threads, or burrowing beneath the substratum surface.

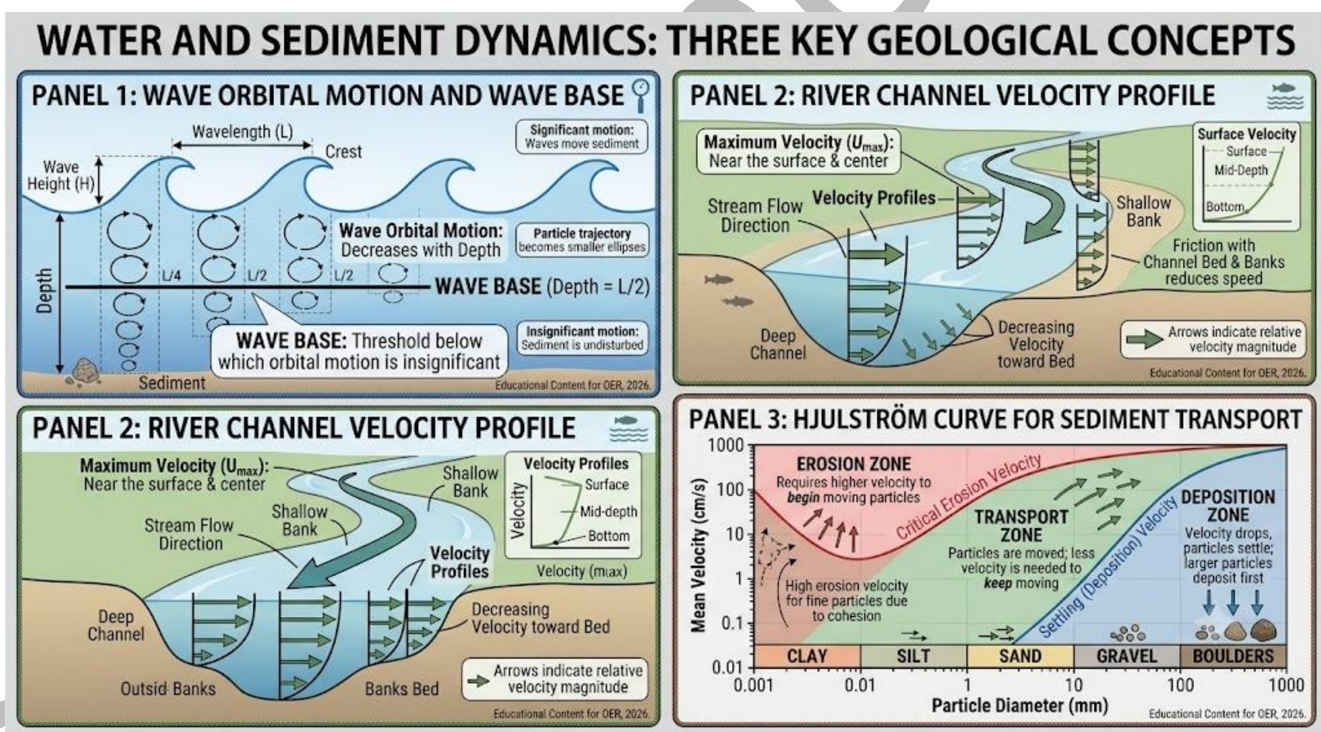

Figure 1.2: Wave orbital motion and wave base, river current velocity profile, and the Hjulstrom curve for sediment transport

Pilot questions 1.3

1. Explain how wave size is determined and describe the concept of the wave base.

2. Describe how wave action influences the grain size and fauna of exposed versus sheltered shores.
3. Distinguish between the forces driving river currents, lake currents, and ocean currents.
4. State three biological adaptations of stream invertebrates to fast currents.
5. Explain what seiches are and describe one ecological consequence of their occurrence in a lake.

1.4 Dissolved Gases and Inorganic Ions in Freshwater

1.4.1 Dissolved oxygen and its biological significance

Dissolved oxygen (DO) enters freshwater from two sources: diffusion from the atmosphere (governed by Henry's Law: solubility is proportional to partial pressure) and photosynthesis by aquatic plants and algae. DO concentration decreases with increasing temperature (cold water holds more oxygen; at 0 degrees Celsius, saturation is approximately 14.6 mg/L; at 30 degrees Celsius, approximately 7.6 mg/L), increasing salinity, and increasing altitude (lower atmospheric oxygen partial pressure). Turbulence and wind mixing increase DO by enhancing atmospheric exchange.

DO is removed by respiration of all organisms (animals, plants, bacteria) and by chemical oxidation of organic matter (biochemical oxygen demand, BOD). When organic loading is high (from sewage, agricultural runoff, or decomposing algal blooms), bacterial decomposition consumes DO rapidly, causing oxygen depletion (hypoxia: below 2 mg/L) or anoxia (zero DO). Fish require a minimum of approximately 4 to 5 mg/L for normal activity; hypoxia causes behavioural avoidance, reduced growth, and in severe cases mass mortality. Hypoxia is a major water quality problem in Nigerian urban waterways and floodplain lakes receiving domestic and agricultural effluent.

Fill in the blank: Dissolved oxygen solubility decreases with increasing ________; this means that warm tropical waters naturally hold less oxygen than cold temperate waters at the same atmospheric pressure, making tropical aquatic organisms more vulnerable to hypoxia from organic pollution.

1.4.2 Carbon dioxide, the carbonate-bicarbonate system, and pH

Carbon dioxide (CO_2) dissolves in water to form carbonic acid (H_2CO_3), which dissociates to bicarbonate (HCO_3^-) and then to carbonate (CO_3^{2-}) with increasing pH. This carbonate-bicarbonate buffer system resists changes in pH when acid or base is added: $CO_2 + H_2O = H_2CO_3 = H^+ + HCO_3^- = 2H^+ + CO_3^{2-}$. The equilibrium shifts left when pH rises (e.g. during active photosynthesis consuming CO_2) and right when pH falls (e.g. during intense respiration producing CO_2). Most freshwaters are buffered between pH 6 and 9; well-buffered hard waters (high alkalinity) resist acidification; soft waters (low alkalinity) are susceptible.

The pH of natural freshwater typically ranges from 6 to 9, with most productive waters between 7 and 8.5. Acid rain and catchment acidification (from industrial emissions, acid sulphate soils) can lower pH below 5, causing aluminium mobilisation, which is toxic to fish gills. Eutrophication can raise pH above 9 during algal blooms, which is toxic to fish through ammonia toxicity (un-ionised ammonia NH_3 increases with rising pH). CO_2 also serves as the inorganic carbon source for photosynthesis; in soft waters with low CO_2, algal growth may be limited by carbon availability rather than by nitrogen or phosphorus.

Fill in the blank: The carbonate-bicarbonate buffer system resists changes in ________ in freshwater; when photosynthesis removes CO_2, the equilibrium shifts, consuming hydrogen ions and raising pH; when respiration adds CO_2, hydrogen ions increase and pH falls.

1.4.3 Major inorganic ions and their roles

The major inorganic ions in freshwater include calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^+), potassium (K^+), bicarbonate (HCO_3^-), sulphate (SO_4^{2-}), chloride (Cl^-), nitrate (NO_3^-), and phosphate (PO_4^{3-}). Their concentrations depend on the geology of the catchment: rivers draining limestone (calcium carbonate) bedrock are hard, alkaline, and calcium-rich; rivers draining crystalline basement rocks (granite, gneiss) are soft and ion-poor. African lake water chemistry shows great diversity: Lake Chad is hard and alkaline (high Na, HCO_3); Lake Victoria has moderate hardness; while some West African rivers over laterite soils are very soft and acidic.

Biological roles: calcium is essential for shell and bone formation and for cell membrane function; magnesium is the central atom of chlorophyll; potassium is essential for osmoregulation and nerve function; nitrate and phosphate are the principal inorganic nutrients limiting algal growth in most freshwaters. Phosphorus is usually the primary limiting nutrient in freshwater (Liebig's Law of the Minimum): even small additions of phosphate from sewage or agricultural fertiliser runoff dramatically increase algal biomass (eutrophication). Nitrogen (as nitrate or ammonium) may co-limit or become the primary limiting nutrient in some systems. Silicate (Si) is essential for diatom frustule (cell wall) construction and limits diatom growth when depleted.

Fill in the blank: ________ is usually the primary limiting nutrient for algal growth in freshwater; small additions from sewage or agricultural runoff cause rapid increases in algal biomass, a process called eutrophication.

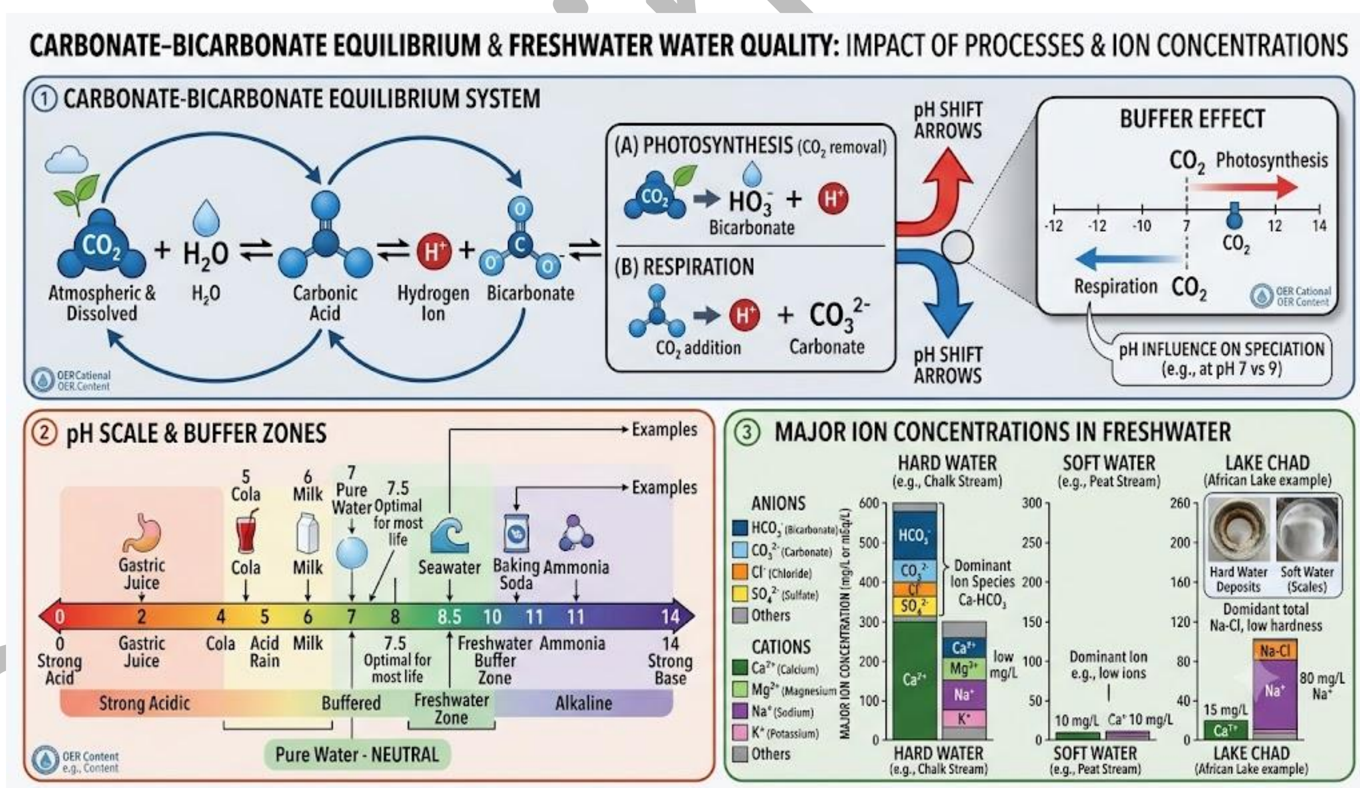

Figure 1.3: The carbonate-bicarbonate buffering system and a comparison of major ion concentrations in contrasting African freshwaters

Pilot questions 1.4

1. State four factors that reduce dissolved oxygen concentration in freshwater.
2. Explain the carbonate-bicarbonate buffer system and describe what happens to pH during an algal bloom.
3. Name the primary limiting nutrient for algal growth in most freshwaters and explain why it is limiting.
4. Distinguish between hard water and soft water with reference to their catchment geology and biological consequences.
5. Explain what biochemical oxygen demand (BOD) is and state why it is an important water quality parameter.

Series Summary

This Series examined the physical and chemical properties of water and how they create the conditions for life in aquatic environments. Water is a polar molecule whose hydrogen bonding gives it several remarkable properties: a high specific heat capacity that buffers aquatic habitats against rapid temperature change; maximum density at 4 degrees Celsius, which causes ice to float and prevents lakes from freezing solid; high surface tension, which supports surface-dwelling organisms; and exceptional solvent ability, making it the universal medium for biological chemistry. Light entering a water body is progressively lost with depth through absorption and scattering; photosynthesis is only possible in the photic zone, down to the compensation depth where light falls to about one percent of surface irradiance, below which lies the permanently dark aphotic zone. Sound travels faster and farther in water than in air, while hydrostatic pressure increases by one atmosphere for every ten metres of depth.

Water movement shapes aquatic habitats in important ways. River currents are gravity-driven; lake circulation is driven by wind and temperature-related density differences; ocean currents are governed by wind, thermohaline circulation, and the Coriolis effect. Dissolved oxygen decreases with rising temperature and is consumed by respiration and decomposition; levels below 2 mg/L indicate hypoxia and pollution stress. The carbonate-bicarbonate system buffers freshwater pH between 6 and 9. Phosphorus is the primary limiting nutrient in most freshwaters, and its addition from human activities triggers eutrophication. Together, these physical and chemical properties form the environmental template within which aquatic biological communities are built.

Glossary of Terms

- **Alkalinity:** the buffering capacity of water against acidification; primarily determined by bicarbonate and carbonate ion concentrations; expressed in mEq/L or mg $CaCO_3$/L.
- **Aphotic zone:** the layer of a water body below the compensation depth where light intensity is insufficient for net photosynthesis; the community is net heterotrophic.
- **Biochemical oxygen demand (BOD):** the amount of dissolved oxygen consumed by microbial decomposition of organic matter in a water sample over five days at 20 degrees Celsius; an index of organic pollution load.
- **Carbonate-bicarbonate system:** the chemical equilibrium between dissolved CO_2, carbonic acid, bicarbonate, and carbonate ions in water; acts as a pH buffer in most natural freshwaters.
- **Compensation depth:** the depth at which gross photosynthesis equals community respiration; approximately the depth of 1% surface irradiance; defines the base of the photic zone.
- **Coriolis effect:** the apparent deflection of moving fluids (water, air) due to Earth's rotation; deflects currents to the right in the Northern Hemisphere and to the left in the Southern Hemisphere; drives oceanic current gyres.
- **Density anomaly:** the property of water whereby its maximum density occurs at 4 degrees Celsius rather than at the freezing point; causes ice to be less dense than liquid water and to float.
- **Dissolved oxygen (DO):** oxygen gas dissolved in water; essential for aerobic respiration of aquatic organisms; decreases with increasing temperature and organic loading; measured in mg/L or % saturation.
- **Eutrophication:** the enrichment of a water body with nutrients (especially phosphorus and nitrogen), causing excessive algal growth, oxygen depletion, and loss of biodiversity; often caused by agricultural runoff and sewage discharge.
- **Extinction coefficient (k):** a measure of the rate of light attenuation with depth in water; a higher k indicates more turbid water with more rapid attenuation; used in the equation $I(z) = I(0) \times e^{(-kz)}$.

- **Fetch:** the unobstructed distance over which wind blows across a water surface; longer fetch generates larger waves; determines the wave energy reaching a shoreline.
- **Hard water:** freshwater with high concentrations of calcium and magnesium ions, derived from limestone or chalk catchments; has high alkalinity and buffers well against acidification.
- **Hjulstrom curve:** a graph showing the critical current velocity required to erode, transport, or deposit sediment particles of different sizes; used to predict substratum composition from current velocity measurements.
- **Hydrogen bond:** a weak electrostatic attraction between the partial positive charge on a hydrogen atom covalently bonded to an electronegative atom (O, N) and the partial negative charge on a neighbouring electronegative atom; responsible for most of water's anomalous properties.
- **Hypoxia:** a condition in which dissolved oxygen concentration falls below approximately 2 mg/L; causes reduced fish activity and growth, behavioural avoidance, and in severe cases mass mortality of aquatic organisms.
- **Limiting nutrient:** the nutrient present in lowest supply relative to biological demand that restricts primary production; phosphorus is the primary limiting nutrient in most freshwaters; nitrogen in many estuarine and coastal waters.
- **Photic zone:** the surface layer of a water body from the surface down to the compensation depth; sufficient light penetrates for net photosynthesis to occur; primary production exceeds respiration.
- **Secchi depth:** the depth at which a white Secchi disk just disappears from view when lowered into the water; a simple index of water transparency and light penetration; inversely related to turbidity.
- **Seiche:** a standing oscillation wave in an enclosed or semi-enclosed water body (lake, bay) driven by wind; causes the thermocline to tilt and may bring nutrient-rich deep water to the surface at the upwind end.
- **Specific heat capacity:** the amount of heat energy required to raise the temperature of 1 kg of a substance by 1 Kelvin; water's value (4,182 J/kg/K) is exceptionally high, giving water bodies thermal stability.
- **Wave base:** the depth equal to half the surface wavelength below which wave orbital motion is negligible and the substratum is undisturbed by surface wave action.

Concept Check Questions [Series 1]

Objective Questions

1. Water reaches its maximum density at ________ degrees Celsius, causing ice to float on liquid water. (Linked to SLO 1.2)
2. The depth at which gross photosynthesis equals community respiration is called the ________ depth; it defines the base of the photic zone. (Linked to SLO 1.3)
3. ________ are standing oscillation waves in lake basins driven by wind; they cause the thermocline to tilt and can bring nutrient-rich deep water to the surface. (Linked to SLO 1.4)
4. Dissolved oxygen solubility ________ with increasing temperature; warm water naturally holds less oxygen than cold water. (Linked to SLO 1.5)
5. ________ is the primary limiting nutrient for algal growth in most freshwaters; its addition from sewage or agricultural runoff causes eutrophication. (Linked to SLO 1.7)

Short-Answer Questions

6. Name three anomalous properties of water and explain how each arises from hydrogen bonding. (Linked to SLO 1.1)
7. Define the photic zone, aphotic zone, and compensation depth and explain their ecological significance. (Linked to SLO 1.3)
8. Distinguish between the forces driving currents in rivers, lakes, and oceans and state one ecological consequence of each. (Linked to SLO 1.4)
9. Explain the carbonate-bicarbonate buffer system and describe the pH changes during photosynthesis and respiration in a lake. (Linked to SLO 1.6)
10. State four major inorganic ions in freshwater and give one biological role for each. (Linked to SLO 1.7)

Long-Answer Questions

11. Describe the molecular basis of water's physical properties (polarity, hydrogen bonding, density anomaly, specific heat capacity, surface tension) and explain the biological significance of each in aquatic ecosystems. (Linked to SLOs 1.1, 1.2)

12. Describe how light is attenuated in water; define the photic, aphotic, and compensation zones; explain the formation and ecological effects of waves and currents in freshwater systems. (Linked to SLOs 1.3, 1.4)
13. Describe dissolved oxygen dynamics in freshwater; explain the carbonate-bicarbonate system and pH buffering; name the major inorganic ions and explain eutrophication with reference to the primary limiting nutrient. (Linked to SLOs 1.5, 1.6, 1.7)

Answers to Concept Check Questions [Series 1]

Objective Questions

1. 4.
2. Compensation.
3. Seiches.
4. Decreases.
5. Phosphorus.

Short-Answer Questions

6. High specific heat capacity: hydrogen bonds require large energy input to break on heating, so water resists temperature change; buffers aquatic organisms against rapid temperature shifts. Density anomaly (maximum at 4 degrees Celsius): as water freezes, hydrogen bond network expands, making ice less dense; ice floats and insulates the water below. High surface tension: cohesive hydrogen bonds between surface molecules resist disruption; supports surface-dwelling organisms (e.g. Gerris water striders).
7. Photic zone: surface layer from the surface to the compensation depth; sufficient light for net photosynthesis; primary production exceeds respiration; supports photoautotrophs. Aphotic zone: below the compensation depth; insufficient light for photosynthesis; community is net heterotrophic; dependent on organic matter sinking from the photic zone. Compensation depth: depth of approximately 1% surface irradiance where gross photosynthesis equals respiration; defines boundary between autotrophic and heterotrophic zones; determines the vertical extent of primary production.

8. Rivers: gravity-driven (hydraulic gradient); ecological consequence: current shapes substratum grain size (Hjulstrom curve), determining benthic invertebrate communities. Lakes: wind-driven surface drift, density currents, and seiches; ecological consequence: seiches bring nutrient-rich hypolimnetic water to the surface, stimulating phytoplankton growth. Oceans: wind, thermohaline circulation, Coriolis effect; ecological consequence: upwelling currents bring nutrients to the surface, supporting high fish productivity.
9. The carbonate-bicarbonate system: $CO_2 + H_2O = H_2CO_3 = H^+ + HCO_3^- = 2H^+ + CO_3^{2-}$. This buffers pH in most freshwaters (pH 6 to 9). During photosynthesis: CO_2 is consumed, the equilibrium shifts left, H^+ decreases, pH rises (may exceed 9 in algal blooms, increasing ammonia toxicity). During respiration: CO_2 is produced, equilibrium shifts right, H^+ increases, pH falls (may drop below 6 at night in productive waters, stressing pH-sensitive organisms).
10. Calcium (Ca^{2+}): shell and bone formation and membrane function. Magnesium (Mg^{2+}): central atom of chlorophyll; essential for photosynthesis. Phosphate (PO_4^{3-}): primary limiting nutrient for algal growth; component of ATP, DNA, and cell membranes. Nitrate (NO_3^-): nitrogen source for protein and nucleic acid synthesis; co-limiting nutrient in many freshwaters.

Long-Answer Questions

11. Water molecule: polar; O is electronegative (delta-); H atoms are delta+; bond angle 104.5 degrees. Hydrogen bonds form between delta+ H and delta- O of adjacent molecules. Properties: high boiling point (hydrogen bonds resist disruption on heating); high specific heat capacity (4,182 J/kg/K; large energy input needed to raise temperature; buffers aquatic organisms against rapid temperature change; tropical lakes remain thermally stable despite large air temperature diurnal swings); density anomaly (maximum at 4 degrees Celsius; ice less dense than liquid water; ice floats and insulates underlying water, allowing survival of aquatic life under ice in cold climates); high surface tension (cohesive forces at surface; supports surface-dwelling organisms and drives capillary rise); universal solvent (polarity dissolves ions and polar molecules; provides the chemical medium for nutrient transport and biochemical reactions in water).
12. Light attenuation: absorption (conversion to heat by water molecules and dissolved substances); scattering (by particles and molecules); reflection at surface. Extinction coefficient (k) describes the rate; turbid water has high k. Secchi depth measures transparency. Red light absorbed near surface; blue-green penetrates deepest. Photic zone: surface to compensation depth (approximately 1% irradiance); net primary production. Aphotic zone: below compensation depth; net heterotrophic. Compensation depth: photosynthesis = respiration. Waves: generated by

wind (fetch, speed, duration); orbital motion in circular paths decreasing with depth; wave base at half-wavelength; below wave base substratum undisturbed. Effects: exposed shores: coarse substratum; organisms with holdfasts, flat shells; sheltered shores: fine sediment, burrowing fauna. Currents in rivers: gravity-driven; velocity profile highest mid-surface; Hjulstrom curve governs sediment transport; shapes substratum and benthic communities. Lake currents: wind-driven surface drift; seiches tilt thermocline, bringing nutrients to surface. Stream organisms: streamlining, attachment (silk, hooks, suckers), burrowing.

13. Dissolved oxygen: enters by atmospheric diffusion (Henry's Law) and photosynthesis; decreases with temperature, salinity, altitude; removed by respiration (BOD). At 30 degrees Celsius, saturation approximately 7.6 mg/L; at 0 degrees Celsius approximately 14.6 mg/L. Hypoxia (below 2 mg/L) causes fish avoidance, reduced growth, mass kill. BOD measures organic pollution load. Carbonate-bicarbonate system: $CO_2 + H_2O = H_2CO_3 = H^+ + HCO_3^-$; buffers pH 6 to 9. Photosynthesis removes CO_2, raises pH; respiration adds CO_2, lowers pH. Hard water (limestone catchments): high Ca, Mg, alkalinity; well-buffered; diverse fauna. Soft water (crystalline bedrock): low ions, low alkalinity; susceptible to acid rain. Major ions: Ca (shells, membranes); Mg (chlorophyll); K (osmoregulation); Na (osmoregulation); NO_3^- (nitrogen for protein synthesis); PO_4^{3-} (primary limiting nutrient; component of ATP, DNA). Eutrophication: phosphorus addition from sewage/agricultural runoff raises algal biomass; algal blooms die; bacterial decomposition depletes DO; hypoxia kills fish and benthic invertebrates; loss of biodiversity. Primary limiting nutrient in freshwater: phosphorus (Liebig's Law of the Minimum).

Answers to Pilot Questions [Series 1]

Part 1.1

1. The water molecule is polar because oxygen is strongly electronegative, drawing the shared electrons toward itself, creating a delta- charge on oxygen and delta+ charges on the two hydrogen atoms bonded at 104.5 degrees. The delta+ hydrogen of one molecule is electrostatically attracted to the delta- oxygen of a neighbouring molecule, forming a hydrogen bond.

2. Water reaches maximum density at 4 degrees Celsius. Below 4 degrees Celsius, hydrogen bond ordering creates a more open lattice structure; ice (0 degrees) is therefore less dense than liquid water at 4 degrees and floats. Ecological consequences: (1) ice insulates the liquid water below, preventing complete freezing and allowing aquatic organisms to survive winter; (2) the density maximum at 4 degrees drives seasonal overturn (mixing) in temperate lakes, renewing nutrients in deep water.
3. Viscosity governs the drag experienced by swimming organisms (high viscosity increases drag, requiring more energy to swim); it determines the sinking rate of phytoplankton and organic particles (higher viscosity slows sinking, prolonging residence in the photic zone); and it affects the delivery of dissolved nutrients to cell surfaces by controlling the thickness of the diffusion boundary layer around cells.
4. Water bodies heat and cool slowly, buffering aquatic organisms against rapid temperature fluctuations that would disrupt enzyme function and metabolism; the thermal stability of tropical lakes such as Lake Chad provides a predictable physical environment for fish and invertebrates despite large diurnal air temperature swings.
5. High specific heat capacity; high latent heat of vaporisation; high surface tension; density anomaly (maximum at 4 degrees Celsius); high boiling point relative to molecular weight.

Part 1.2

1. Absorption (conversion of light to heat by water molecules and dissolved substances such as dissolved organic carbon); scattering (redirection of photons by suspended particles and molecules); and reflection at the water surface (2 to 5% under calm conditions; greater at low solar angles).
2. A white Secchi disk is lowered vertically into the water on a calibrated line until it just disappears from view; the depth at which this occurs is the Secchi depth. It measures water transparency (an index of light penetration and turbidity); a greater Secchi depth indicates clearer water with less attenuation.
3. Photic zone: the surface layer from the water surface to the compensation depth, where sufficient light penetrates for net photosynthesis to occur. Compensation depth: the depth at which gross photosynthesis equals community respiration (approximately 1% of surface irradiance); below this depth, the community is net heterotrophic (the aphotic zone).
4. Sound travels faster in water because water is less compressible and has higher elasticity than air, transmitting pressure waves more efficiently. Two ecological examples: (1) fish use underwater

sound production for courtship and territorial signalling; (2) dolphins and whales use echolocation (biosonar) to navigate and hunt prey, with calls that can propagate thousands of kilometres in the ocean.

5. Hydrostatic pressure increases by approximately one atmosphere (101 kPa) for every 10 m depth. Adaptation: deep-sea organisms maintain membrane fluidity under high pressure by incorporating a higher proportion of unsaturated fatty acids into their membranes; unsaturated fatty acids have kinked chains that resist the packing caused by compression, preventing membranes from becoming too rigid.

Part 1.3

1. Wave size (height and wavelength) increases with wind speed, fetch (unobstructed distance over which wind blows), and duration of wind. Wave base is the depth equal to half the wavelength; below this depth, wave orbital motion is negligible and the substratum is undisturbed regardless of surface wave conditions.
2. Exposed shores: strong wave action winnows away fine sediment, leaving coarse gravel or bedrock; organisms must withstand strong hydrodynamic forces using holdfasts (macroalgae), byssus threads (mussels), flat shells (limpets), or silk attachments (stream invertebrates). Sheltered shores: wave energy is low; fine sediment accumulates; soft-sediment burrowing fauna (worms, bivalves) dominate and macrophytes can establish.
3. Rivers: gravity (hydraulic gradient); flow rate controlled by gradient, channel geometry, and substratum roughness. Lakes: wind stress on surface (surface drift and return currents); thermohaline density differences; seiches (wind-driven standing waves). Oceans: wind; thermohaline circulation driven by temperature and salinity differences; Coriolis effect deflects currents and generates large current gyres.
4. Streamlining (flattened or elongated body forms reduce drag; e.g. flattened mayfly nymphs); attachment structures (silk threads, hooks, or suckers anchor the organism to the substratum against the current; e.g. blackfly larvae, net-spinning caddisfly); burrowing into the substratum below the surface layer where current velocity is negligible.
5. Seiches are standing oscillation waves within an enclosed lake basin driven by wind; when wind pushes surface water to the downwind end, it piles up there; when the wind stops, the water oscillates back and forth (seiche). Ecological consequence: the thermocline tilts during the seiche, bringing cold, nutrient-rich hypolimnetic water to the surface at the upwind end of the lake; this nutrient upwelling stimulates phytoplankton growth and may cause localised algal blooms.

Part 1.4

1. Increasing temperature (warmer water holds less dissolved oxygen); increasing salinity (salting-out effect); high organic loading and bacterial decomposition (BOD consumes DO); respiration by large plant or algal biomass at night; reduced mixing and turbulence (limiting atmospheric diffusion); high altitude (lower atmospheric oxygen partial pressure).
2. CO_2 dissolves in water to form carbonic acid (H_2CO_3), which dissociates to H^+ and HCO_3^-, then to $2H^+$ and CO_3^{2-}. This buffer resists pH change when acid or base is added. During an algal bloom: intense photosynthesis removes CO_2 from the water; the equilibrium shifts left, consuming H^+; pH rises, potentially exceeding 9; at high pH, un-ionised ammonia (NH_3) increases and becomes toxic to fish.
3. Phosphorus (as phosphate, PO_4^{3-}) is the primary limiting nutrient in most freshwaters. It is limiting because: natural background concentrations in freshwater are very low (often below 0.01 mg/L); phosphorus is efficiently retained in sediments and biomass; and the N:P ratio of aquatic organisms requires approximately 16 atoms of nitrogen per atom of phosphorus (Redfield ratio), so phosphorus is proportionally scarcer than nitrogen in most freshwaters.
4. Hard water: drains limestone or chalk bedrock; high Ca^{2+} and Mg^{2+} concentrations; high alkalinity; pH 7 to 8.5; well-buffered against acid rain; supports diverse mollusc fauna (shells require calcium) and well-structured food webs. Soft water: drains crystalline basement rocks (granite, gneiss); low ion concentrations; low alkalinity; pH often 5 to 7; poorly buffered; susceptible to acidification by acid rain, which mobilises aluminium toxic to fish gills.
5. BOD (biochemical oxygen demand) is the amount of dissolved oxygen consumed by microbial decomposition of organic matter in a water sample over 5 days at 20 degrees Celsius, measured in mg O_2/L. It is an important water quality parameter because it quantifies the organic pollution load: a high BOD indicates high concentrations of decomposable organic matter (from sewage, agricultural effluent, or decomposing algae) that will deplete DO as it is broken down by bacteria, potentially causing hypoxia and mass mortality of fish.

References and Attributions [Series 1]

Textual References (Books and External Sources)

- Hutchinson, G. E. (1957). A treatise on limnology: Vol. 1. Geography, physics, and chemistry. Wiley.
- Kalff, J. (2002). Limnology: Inland water ecosystems. Prentice Hall.
- Lowe-McConnell, R. H. (1987). Ecological studies in tropical fish communities. Cambridge University Press.
- Wetzel, R. G. (2001). Limnology: Lake and river ecosystems (3rd ed.). Academic Press.

Figures, Plates, Tables, and Boxes

- Figure 1.1: Water molecule structure, density-temperature relationship, and specific heat capacity comparison Attribution: AI generated. Suggested OER search string: "water molecule hydrogen bonds density temperature graph specific heat capacity comparison OER diagram".
- Figure 1.2: Wave orbital motion and wave base, river velocity profile, and Hjulstrom curve Attribution: AI generated. Suggested OER search string: "wave base orbital motion diagram river velocity profile Hjulstrom curve sediment transport OER".
- Figure 1.3: Carbonate-bicarbonate buffering system and major ion comparison for African freshwaters Attribution: AI generated. Suggested OER search string: "carbonate bicarbonate buffer system freshwater pH diagram major ions hard soft water African lakes OER".

Course code: BIO 206

Course title: Hydrobiology

Course credit load: 2 Units

Series 2: Thermal Stratification and Lake Chemistry

- **Part 2.1: Thermal Stratification of Lakes**
  - Sub Part 2.1.1: Formation of the thermocline and lake zones
  - Sub Part 2.1.2: Seasonal mixing and lake turnover
  - Sub Part 2.1.3: Stratification patterns in tropical African lakes
- **Part 2.2: Oligotrophic and Eutrophic Lakes**
  - Sub Part 2.2.1: Characteristics of oligotrophic lakes
  - Sub Part 2.2.2: Characteristics of eutrophic lakes
  - Sub Part 2.2.3: Cultural eutrophication and its consequences
- **Part 2.3: Chemical Composition of African Lake Waters**
  - Sub Part 2.3.1: Factors determining lake water chemistry
  - Sub Part 2.3.2: Chemical profiles of major African lakes
  - Sub Part 2.3.3: Soda lakes and saline lakes
- **Part 2.4: Hypolimnetic Chemistry and Sediment Interactions**
  - Sub Part 2.4.1: Oxygen depletion and redox chemistry in the hypolimnion
  - Sub Part 2.4.2: Nutrient release from sediments
  - Sub Part 2.4.3: Limnic eruptions and meromictic lakes

Introduction

The physical and chemical character of a lake is not uniform from surface to bottom. Solar heating of the surface layer creates density differences that stratify the water column into distinct thermal zones, isolating deep water from atmospheric oxygen and surface nutrients. This stratification profoundly shapes the distribution of organisms and the cycling of nutrients. At the same time, the overall nutrient status of a lake determines whether it is clear and species-rich (oligotrophic) or turbid and algae-dominated (eutrophic).

This Series covers thermal stratification and the seasonal dynamics of lake mixing, the trophic classification of lakes, the distinctive chemistry of African lake waters including soda and saline lakes, and the chemical processes occurring in the hypolimnion and at the sediment-water interface. Together these topics explain why different lakes support fundamentally different biological communities.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- SLO 2.1 explain how thermal stratification develops in lakes and define the epilimnion, thermocline, and hypolimnion (Linked to Part 2.1),
- SLO 2.2 describe the seasonal cycle of stratification and mixing (turnover) in temperate and tropical lakes (Linked to Part 2.1),
- SLO 2.3 distinguish between oligotrophic and eutrophic lakes by their physical, chemical, and biological characteristics (Linked to Part 2.2),
- SLO 2.4 explain cultural eutrophication, its causes, consequences, and management (Linked to Part 2.2),
- SLO 2.5 describe the factors controlling the chemical composition of African lake waters and compare the chemistry of selected lakes (Linked to Part 2.3),
- SLO 2.6 explain oxygen depletion and redox chemistry in the hypolimnion and describe internal phosphorus loading from sediments (Linked to Part 2.4), and

- SLO 2.7 define meromictic lakes and limnic eruptions and explain their ecological significance (Linked to Part 2.4).

2.1 Thermal Stratification of Lakes

2.1.1 Formation of the thermocline and lake zones

Solar radiation heats the surface layer of a lake; because warm water is less dense than cold water, the heated surface layer floats on the cooler water beneath. Wind mixing distributes heat through the upper layer but cannot overcome the density barrier at a certain depth. The result is a three-layer structure: the epilimnion (warm, well-mixed surface layer; uniform temperature; in contact with the atmosphere); the thermocline (metalimnion; the zone of rapid temperature decline with depth; typically 1 degree Celsius or more per metre); and the hypolimnion (cold, dense, stable bottom layer; cut off from the atmosphere once stratification is established).

The stability of stratification is measured by the Schmidt stability index: the energy (in joules per square metre) required to mix the entire lake to a uniform temperature. A high Schmidt stability indicates strong, persistent stratification. The depth of the thermocline depends on wind energy (stronger winds deepen the thermocline by mixing), lake area (larger lakes experience stronger winds), and solar input. In deep lakes, the thermocline acts as a physical barrier preventing exchange between the warm, productive epilimnion and the cold, nutrient-rich hypolimnion.

Fill in the blank: The ________ is the zone of rapid temperature decrease with depth in a stratified lake; it acts as a physical barrier between the warm, well-mixed epilimnion above and the cold, stable hypolimnion below.

2.1.2 Seasonal mixing and lake turnover

In temperate dimictic lakes (which mix twice per year), stratification develops in spring as surface water warms; it persists through summer; in autumn, surface water cools and its density increases until it matches the density of deeper water, at which point the thermocline breaks down and wind mixing drives complete turnover (holomixis). A second, weaker stratification (inverse stratification: surface ice over denser water below) may form in winter; turnover occurs again in spring as ice melts and surface water warms to 4 degrees Celsius. Turnover redistributes oxygen to the depths and nutrients to the surface.

Monomictic lakes mix once per year (cold monomictic: always cold; warm monomictic: tropical or subtropical lakes that stratify in the warm season and mix in the cooler or windier season). Polymictic lakes mix frequently (shallow lakes where wind continuously disrupts stratification). Meromictic lakes never fully mix (permanent chemical stratification prevents complete turnover, discussed in Part 2.4). The frequency and completeness of mixing determines how efficiently nutrients are recycled from the hypolimnion to the epilimnion and thus controls primary productivity.

Fill in the blank: A ________ lake mixes twice per year: once in spring when ice melts and surface water warms to 4 degrees Celsius, and once in autumn when surface cooling eliminates the thermocline and wind drives complete holomixis.

2.1.3 Stratification patterns in tropical African lakes

Tropical lakes do not experience the strong seasonal temperature contrast of temperate lakes and therefore stratify differently. Because water temperature is high year-round (25 to 32 degrees Celsius at the surface), small temperature differences create large density differences (due to the steep density-temperature relationship near 25 to 30 degrees Celsius). This makes tropical stratification highly stable even with only a 2 to 3 degree temperature difference between epilimnion and hypolimnion. Most large tropical African lakes are warm monomictic: they stratify during the warm calm season and mix during the cooler, windier dry season.

Lake Victoria (the largest tropical lake in the world by area) stratifies weakly during the hot season and mixes during the cooler southeast trade wind season; mixing brings nutrients from the hypolimnion to the epilimnion, stimulating phytoplankton blooms. Lake Tanganyika is deep (maximum 1,470 m) and permanently stratified below approximately 200 m; the lower hypolimnion is permanently anoxic. Lake Chad, being shallow (maximum 7 m), is polymictic and well-mixed year-round. Lake Malawi stratifies seasonally and has a permanently anoxic hypolimnion below 200 to 250 m.

Fill in the blank: Tropical lakes stratify more ________ than temperate lakes of similar depth because the density-temperature relationship of water is steeper at high temperatures, meaning even small temperature differences produce large density differences that resist wind mixing.

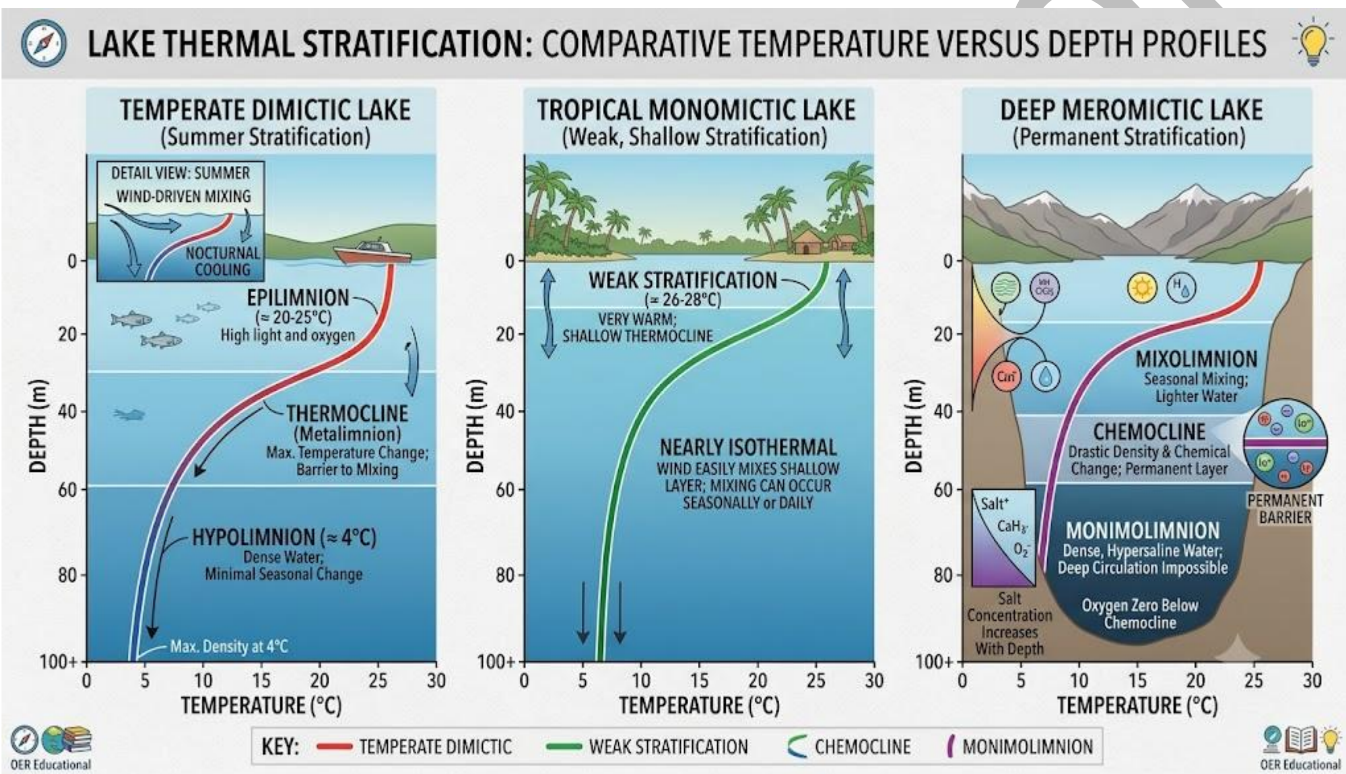

Figure 2.1: Temperature-depth profiles for a temperate dimictic lake, a tropical monomictic lake, and a deep meromictic lake

Pilot questions 2.1

1. Define the epilimnion, thermocline, and hypolimnion of a stratified lake.
2. Describe the seasonal cycle of stratification and turnover in a temperate dimictic lake.
3. Distinguish between dimictic, monomictic, polymictic, and meromictic lakes.
4. Explain why tropical lakes tend to stratify more stably than temperate lakes of similar depth.
5. State the mixing regime of Lake Victoria, Lake Tanganyika, and Lake Chad and explain one ecological consequence of each.

2.2 Oligotrophic and Eutrophic Lakes

2.2.1 Characteristics of oligotrophic lakes

Oligotrophic lakes are nutrient-poor, typically receiving water from catchments with poorly weathered, crystalline bedrock or from precipitation with low nutrient loads. Their characteristic features: very low phosphorus (below 10 micrograms/L total phosphorus) and nitrogen concentrations; low phytoplankton biomass (chlorophyll-a below 2 micrograms/L); high water transparency (Secchi depth often exceeding 10 m); clear blue or blue-green colour; high dissolved oxygen throughout the water column, including the hypolimnion; low primary productivity; high species diversity of zooplankton and fish but low abundance; and well-developed benthic communities in the photic littoral zone.

Examples of oligotrophic African lakes: Lake Tanganyika (one of the world's oldest and deepest lakes; exceptionally clear water; extraordinarily high endemism of cichlid fish, invertebrates, and algae; Secchi depth up to 20 m in some areas) and Lake Malawi (also deep and old; highly endemic cichlid fauna; clear water). These lakes are oligotrophic because their large volume relative to catchment area dilutes nutrient inputs, and because the permanently stratified hypolimnion sequesters nutrients in the deep water, preventing their return to the photic zone.

Fill in the blank: Oligotrophic lakes typically have total phosphorus concentrations below ________ micrograms per litre, high water transparency (Secchi depth often exceeding 10 m), and dissolved oxygen present throughout the water column including the hypolimnion.

2.2.2 Characteristics of eutrophic lakes

Eutrophic lakes are nutrient-rich, typically receiving high phosphorus and nitrogen inputs from agricultural catchments, sewage discharge, or weathering of nutrient-rich sedimentary rocks. Characteristics: high total phosphorus (above 35 micrograms/L) and nitrogen; high phytoplankton biomass with frequent algal blooms (chlorophyll-a above 20 micrograms/L); low water transparency (Secchi depth often less than 1 to 2 m); green, brown, or turbid colour;

hypolimnetic oxygen depletion (often complete anoxia) during summer stratification; high primary productivity; low species diversity but high abundance of algae and tolerant invertebrates; fish dominated by tolerant species (e.g. tilapia, catfish in African systems).

Mesotrophic lakes are intermediate between oligotrophic and eutrophic; they have moderate nutrient levels, moderate transparency, seasonal hypolimnetic oxygen depletion, and relatively high biodiversity. Hypereutrophic lakes are extremely nutrient-rich, with almost permanent algal bloom conditions, very low transparency, and complete hypolimnetic anoxia for most of the year. Many urban and peri-urban lakes in Nigeria have become hypereutrophic due to uncontrolled sewage and agricultural runoff; examples include parts of the Niger Delta floodplain lakes and Lake Asejire near Ibadan.

Fill in the blank: Eutrophic lakes are characterised by total phosphorus concentrations above ________ micrograms per litre, high phytoplankton biomass, low water transparency, and oxygen depletion in the hypolimnion during stratification.

2.2.3 Cultural eutrophication and its consequences

Cultural (anthropogenic) eutrophication is the accelerated enrichment of a water body with nutrients as a result of human activities. Principal sources: agricultural runoff (fertilisers containing nitrate and phosphate washed from fields); sewage effluent (domestic and industrial wastewater rich in phosphorus from detergents and organic nitrogen); urban stormwater runoff; atmospheric deposition of nitrogen from combustion; and fish farming waste. In Nigeria, rapid urbanisation without adequate sewage treatment has caused severe cultural eutrophication of many rivers, lakes, and coastal lagoons.

Consequences: algal blooms (including toxic cyanobacterial blooms; cyanotoxins such as microcystin damage fish livers and are dangerous to humans and livestock drinking the water); hypolimnetic anoxia and fish kills; replacement of sensitive species by pollution-tolerant ones; invasion by water hyacinth (Eichhornia crassipes) and other macrophytes that form dense floating mats blocking light and reducing oxygen; loss of fisheries productivity and biodiversity; and impairment of drinking water quality. Management strategies include nutrient reduction at source (reducing fertiliser application, improved sewage treatment, phosphorus removal), biomanipulation (stocking of planktivorous fish to reduce zooplankton, releasing grazing pressure on phytoplankton), and sediment dredging or alum treatment to bind phosphorus.

Fill in the blank: ________ cyanobacterial blooms in eutrophic lakes can produce toxins such as microcystin that damage fish livers and are hazardous to humans and livestock consuming untreated water from affected lakes.

Pilot questions 2.2

1. Distinguish between oligotrophic and eutrophic lakes using at least five characteristics.
2. State three African examples of oligotrophic lakes and explain why they remain oligotrophic.
3. State four principal sources of nutrients causing cultural eutrophication in Nigerian water bodies.
4. State three ecological consequences of cyanobacterial bloom development in a eutrophic lake.
5. Describe two management strategies for reversing cultural eutrophication.

2.3 Chemical Composition of African Lake Waters

2.3.1 Factors determining lake water chemistry

The chemical composition of a lake is determined by: catchment geology (the dominant control; weathering of rocks releases ions into river inflow); precipitation chemistry (rain brings dissolved ions, including sea salts in coastal areas and pollutants from combustion); groundwater inputs (may be ion-rich if passing through soluble rock strata); evaporation (concentrates dissolved ions; important in closed basins with no outflow where evaporation exceeds inflow, causing salt accumulation); biological uptake and release (organisms remove nutrients from the water and return them on death and decomposition); and in-lake chemistry (redox reactions at the sediment-water interface alter concentrations of iron, manganese, phosphorus, and sulphur).

The ionic composition of lake water is commonly represented by the ratio of major cations (Ca^{2+}, Mg^{2+}, Na^+, K^+) to major anions (HCO_3^-, Cl^-, SO_4^{2-}). Most freshwater lakes are dominated by calcium and bicarbonate (reflecting limestone or chalk weathering). Sodium and chloride dominate in lakes receiving marine aerosols or draining sodium-rich geological formations. African Rift Valley lakes show exceptional chemical diversity due to the varied geology, aridity, and geological age of the basin.

Fill in the blank: In closed lake basins where evaporation exceeds inflow, dissolved ions become progressively ________ over time, eventually producing saline or alkaline soda lakes; this process explains the high salinity of many East African Rift Valley lakes.

2.3.2 Chemical profiles of major African lakes

Lake Victoria: conductivity approximately 90 to 100 microsiemens/cm; dominated by magnesium and bicarbonate; relatively dilute; pH 7.5 to 9 depending on algal activity; has undergone progressive eutrophication since the 1980s due to nutrient input from agricultural catchments around the lake shore and the proliferation of Nile perch (Lates niloticus), which caused extinction of hundreds of endemic haplochromine cichlid species. Lake Tanganyika: very old (9 to 12 million years); low conductivity (approximately 600 microsiemens/cm); dominated by magnesium, calcium, and bicarbonate; permanently stratified below 200 m with anoxic hypolimnion; exceptional endemic biodiversity.

Lake Chad: a large, shallow, endorheic lake (drains internally into a closed basin) in the Sahel; historically the fourth largest lake in Africa; dramatically shrunken in recent decades due to reduced rainfall and increased irrigation withdrawals; conductivity low to moderate (100 to 500 microsiemens/cm depending on water level); dominated by sodium and bicarbonate; highly productive and supports important fisheries for Nigeria, Niger, Chad, and Cameroon. Lake Albert (Mobutu): medium conductivity; Na-Mg-HCO_3 type; supports productive Nile tilapia and Nile perch fisheries shared between Uganda and the Democratic Republic of Congo.

Fill in the blank: Lake Chad is an ________ basin with no outflow to the sea; its water level and chemical composition fluctuate with rainfall and evaporation; it has shrunk dramatically in recent decades due to reduced rainfall and increased irrigation withdrawals.

2.3.3 Soda lakes and saline lakes

Soda lakes are closed-basin lakes in arid or semi-arid regions where evaporative concentration has produced extremely high pH (9 to 12) and very high sodium carbonate and bicarbonate concentrations. They are among the most chemically extreme aquatic habitats on Earth. East African examples include Lake Natron (Tanzania; pH up to 10.5; extremely high Na_2CO_3; the main breeding ground of lesser flamingo, Phoeniconaias minor); Lake Magadi (Kenya; pH up to 12; sodium trona deposits); and Lake Bogoria (Kenya; moderate salinity; pH approximately 10). Despite their extreme chemistry, soda lakes can support extraordinary biological productivity dominated by cyanobacteria (Arthrospira platensis, formerly Spirulina) that are consumed by enormous flocks of flamingos.

Saline lakes have high total dissolved solids but are not necessarily alkaline. Lake Turkana (Kenya; salinity approximately 2.5 g/L; slightly alkaline; supports important tilapia and Nile perch fisheries) and the Dead Sea (Jordan-Israel; approximately 340 g/L; too saline for most life except halophilic bacteria and algae) represent different points on the salinity spectrum. In Nigeria, saline groundwater contributes to the chemistry of some inland ponds and streams in the Benue valley; coastal lagoons such as Lagos Lagoon are brackish, mixing freshwater and marine water. Organisms in saline and soda lakes are extreme halophiles or natrophiles with special ionic regulation mechanisms.

Fill in the blank: Soda lakes such as Lake Natron support extraordinary productivity of ________ (Arthrospira platensis), which form the primary food base for huge flocks of lesser flamingo; few other organisms can tolerate the extreme pH and sodium carbonate concentrations of these lakes.

Lake	**pH**	**Conductivity**	**Dominant Ions**	**Trophic State**	**Notable Biology**
Victoria	~7.5–8.5	Low–moderate (100–200 µS/cm)	Calcium, bicarbonate	Eutrophic (nutrient-rich)	High fish diversity, esp. cichlids; Nile perch introduction

					altered ecosystem
Tanganyika	~8.4–9.2	Moderate (600–700 µS/cm)	Sodium, bicarbonate	Oligotrophic–mesotrophic	Endemic cichlids, pelagic sardines; deep stratification supports unique fauna
Chad	~7.5–8.0	Variable (200–400 µS/cm)	Calcium, chloride	Mesotrophic	Tilapia, catfish; shrinking size affects biodiversity
Natron	Highly alkaline (9–10.5)	Very high (>5,000 µS/cm)	Sodium carbonate, bicarbonate	Hypersaline/alkaline system	Breeding ground for lesser flamingos; extremophile microbes
Turkana	~8.5–9.0	High (1,000–2,000 µS/cm)	Sodium, bicarbonate	Mesotrophic	Nile tilapia, endemic cichlids; crocodiles and migratory birds
Lagos Lagoon	~6.5–7.5	Variable (brackish, 500–1,500 µS/cm)	Chloride, sodium	Eutrophic (pollution-driven)	Mangroves, shrimps, tilapia; impacted by

					urban runoff and industry

Box 2.1: Comparative chemistry and biology of selected African lakes

Pilot questions 2.3

1. State four factors that determine the chemical composition of lake water.
2. Explain why closed-basin lakes become progressively more saline over time.
3. Compare the chemistry of Lake Victoria and Lake Tanganyika.
4. Explain what soda lakes are and give two East African examples with their characteristic organisms.
5. Explain why Lake Chad has fluctuated dramatically in area and chemistry over recent decades.

2.4 Hypolimnetic Chemistry and Sediment Interactions

2.4.1 Oxygen depletion and redox chemistry in the hypolimnion

Once thermal stratification isolates the hypolimnion from the atmosphere, its oxygen supply is fixed at the level present when stratification began. Bacterial decomposition of organic matter sinking from the epilimnion consumes this oxygen; in productive lakes, the hypolimnion may become completely anoxic (oxygen-free) within weeks to months of stratification onset. As oxygen is depleted, redox potential (Eh) drops and the sequence of terminal electron acceptors used by bacteria shifts progressively: nitrate reduction (denitrification: NO_3^- to N_2); manganese reduction (Mn^{4+} to Mn^{2+}); iron reduction (Fe^{3+} to Fe^{2+}); sulphate reduction (SO_4^{2-} to H_2S); and finally methanogenesis (CO_2 to CH_4).

Hydrogen sulphide (H_2S) produced by sulphate reduction is toxic to most organisms and gives stratified anoxic hypolimnia their characteristic rotten-egg odour. Reduced iron (Fe^{2+}) is soluble; reduced manganese (Mn^{2+}) is also soluble. Methane gas accumulates in the sediment and overlying water. These redox transformations create a chemical gradient (redoxcline) at the oxic-anoxic boundary, which is exploited by chemolithotrophic bacteria and supports a diverse microbial community. When turnover occurs, reduced compounds (H_2S, Fe^{2+}, Mn^{2+}) are oxidised rapidly by oxygen, consuming large amounts of DO and potentially causing fish kills at lake overturn.

Fill in the blank: As oxygen is depleted in the hypolimnion, sulphate-reducing bacteria produce ________ sulphide (H_2S), which is toxic to most organisms and gives anoxic hypolimnia their characteristic rotten-egg odour; its oxidation at lake overturn can cause large-scale fish kills.

2.4.2 Nutrient release from sediments

Lake sediments are a major reservoir of phosphorus, nitrogen, and other nutrients. Under oxic conditions, iron (Fe^{3+}) in the sediment surface binds phosphate strongly, preventing its release into the overlying water. When the hypolimnion becomes anoxic and Fe^{3+} is reduced to soluble Fe^{2+}, this iron-phosphate binding is released, and phosphate enters the water column: a process called internal phosphorus loading or sediment phosphorus release. In eutrophic lakes, internal loading can sustain algal blooms even after external nutrient inputs are controlled, making eutrophication reversal extremely slow and difficult.

Nitrogen dynamics: denitrification in anoxic sediments converts nitrate (NO_3^-) to nitrogen gas (N_2), permanently removing nitrogen from the lake system. Ammonium (NH_4^+) accumulates in anoxic hypolimnia from decomposition of organic nitrogen. At turnover, ammonium is oxidised to nitrate by nitrifying bacteria; this nitrate is available for phytoplankton in the epilimnion, contributing to post-turnover algal blooms. Silicate is released from diatom frustules as they decompose in the sediment; this silicate return supports diatom growth in subsequent seasons.

Fill in the blank: Under anoxic conditions in the hypolimnion, iron is reduced from Fe^{3+} to Fe^{2+}; this releases ________ from iron-bound sediment complexes into the water column, a process called internal phosphorus loading that can sustain algal blooms after external nutrient inputs are reduced.

2.4.3 Limnic eruptions and meromictic lakes

A meromictic lake is one in which the water column never completely mixes; permanent chemical stratification (chemocline) is maintained by a density difference due to dissolved salts rather than temperature. The upper freshwater layer (mixolimnion) mixes seasonally; the deep layer (monimolimnion) is permanently isolated, typically anoxic, rich in dissolved minerals, and may accumulate CO_2, H_2S, or methane over centuries. African examples: Lake Kivu (Rwanda-DRC border) has enormous volumes of dissolved CO_2 (approximately 250 km^3) and methane (approximately 55 km^3) in its deep monimolimnion, maintained by geothermal inputs from the volcanic Virunga Mountains.

A limnic eruption (lake overturn) is a sudden, catastrophic release of dissolved CO_2 from the deep water of a meromictic lake triggered by a disturbance (earthquake, landslide, or volcanic activity). As the CO_2-saturated deep water rises and pressure drops, CO_2 comes out of solution explosively; the resulting gas cloud descends into surrounding valleys (CO_2 is denser than air) and asphyxiates humans and animals. The 1986 Lake Nyos disaster (Cameroon) released approximately 1.6 million tonnes of CO_2 and killed approximately 1,700 people and 3,500 livestock in the Nyos valley. Lake Monoun (Cameroon, 1984) caused a smaller eruption. Degassing pipes now draw deep CO_2-rich water to the surface to prevent future disasters at Lake Nyos and Lake Kivu.

Fill in the blank: The 1986 Lake Nyos disaster in ________ was a limnic eruption in which dissolved CO_2 was released explosively from the deep meromictic water; the resulting gas cloud killed approximately 1,700 people and 3,500 livestock in the surrounding valley.

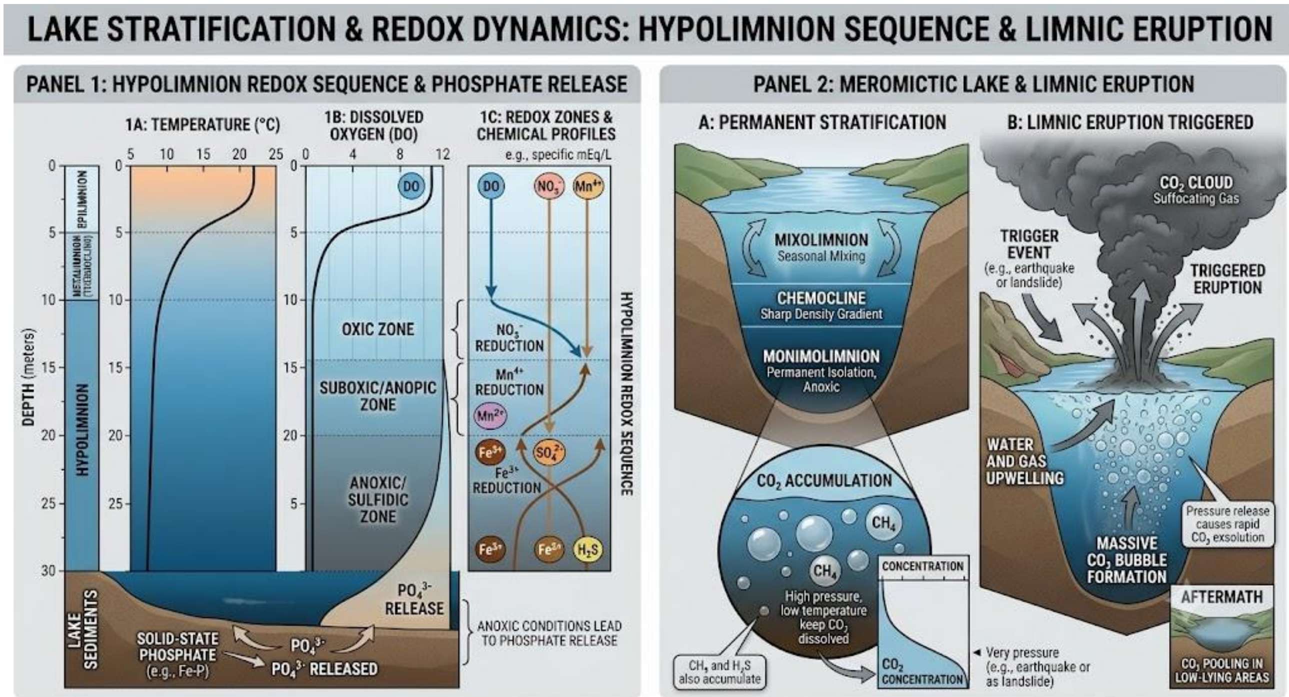

Figure 2.2: Hypolimnetic redox chemistry and nutrient profiles in a stratified eutrophic lake, and the structure of a meromictic lake with limnic eruption potential

Pilot questions 2.4

1. Explain how the hypolimnion of a stratified eutrophic lake becomes anoxic during summer stratification.
2. State the sequence of electron acceptors used by bacteria as redox potential decreases in an anoxic hypolimnion.
3. Explain the mechanism of internal phosphorus loading from lake sediments.
4. Define a meromictic lake and explain what a limnic eruption is.
5. Describe the Lake Nyos disaster of 1986 and state the management intervention now in place.

Series Summary

This Series covered thermal stratification and lake chemistry. Solar heating creates the three-layer structure: epilimnion (warm, mixed), thermocline (rapid temperature decline), and hypolimnion (cold, stable). Dimictic lakes (temperate) mix twice per year; monomictic lakes once; polymictic lakes frequently; meromictic lakes never fully mix. Tropical lakes stratify stably with small temperature differences due to the steep density-temperature relationship. Large African lakes show varied mixing regimes: Victoria (warm monomictic), Tanganyika (permanently stratified below 200 m), Chad (polymictic). Oligotrophic lakes are nutrient-poor, clear, and DO-rich throughout; eutrophic lakes are nutrient-rich, turbid, with hypolimnetic anoxia and algal blooms.

Cultural eutrophication arises from agricultural runoff, sewage, and urban stormwater; consequences include cyanobacterial blooms (microcystin toxins), hypolimnetic anoxia, fish kills, and water hyacinth invasion. African lake chemistry varies with geology, evaporation, and basin type; closed basins concentrate ions producing soda (Lake Natron: pH up to 10.5, flamingo habitat) and saline lakes. In the hypolimnion, sequential reduction of NO3-, Mn, Fe, SO4^2- produces anoxia and accumulates H2S; iron reduction releases phosphate from sediments (internal loading). Meromictic lakes (Lake Kivu, Lake Nyos) accumulate CO2 and CH4 in the monimolimnion; limnic eruptions release CO2 catastrophically, as at Lake Nyos (1986), killing 1,700 people. Degassing pipes now mitigate this hazard. These topics address SLOs 2.1 to 2.7.

Glossary of Terms

- **Chemocline:** the zone of sharp chemical gradient (especially salinity or redox potential) that maintains permanent density stratification in a meromictic lake; equivalent to the thermocline in thermally stratified lakes.
- **Cultural eutrophication:** accelerated enrichment of a water body with nutrients (especially phosphorus and nitrogen) as a direct result of human activities such as agriculture, sewage discharge, and urban runoff.

- **Cyanotoxin:** a toxin produced by cyanobacteria (blue-green algae); includes microcystin (a hepatotoxin damaging liver cells) and cylindrospermopsin; produced during harmful algal blooms in eutrophic waters.
- **Denitrification:** microbial reduction of nitrate (NO_3^-) to nitrogen gas (N_2) or nitrous oxide (N_2O) under anoxic conditions; permanently removes nitrogen from the aquatic system.
- **Dimictic lake:** a lake that undergoes complete mixing (turnover) twice per year, typically in spring and autumn; characteristic of temperate regions where seasonal temperature contrasts are strong.
- **Endorheic basin:** a closed drainage basin with no outflow to the sea; water accumulates and evaporates within the basin, progressively concentrating dissolved ions; characteristic of arid and semi-arid regions.
- **Epilimnion:** the warm, well-mixed surface layer of a thermally stratified lake; in contact with the atmosphere; the zone of active photosynthesis and wind-driven circulation.
- **Holomixis:** complete mixing of the entire water column of a lake from surface to bottom; occurs during turnover when thermal stratification breaks down; redistributes oxygen, nutrients, and heat.
- **Hypolimnion:** the cold, dense, stable bottom layer of a thermally stratified lake; isolated from the atmosphere during stratification; typically depleted in oxygen in productive lakes.
- **Internal phosphorus loading:** the release of phosphate from iron-bound sediment complexes when the overlying water becomes anoxic; iron is reduced from Fe^{3+} to Fe^{2+}, liberating bound phosphate into the water column; sustains algal blooms after external inputs are controlled.
- **Limnic eruption:** a catastrophic release of dissolved CO_2 from the deep water of a meromictic lake triggered by a disturbance; the CO_2 cloud descends into surrounding valleys and can asphyxiate humans and animals; occurred at Lake Nyos, Cameroon in 1986.
- **Meromictic lake:** a lake in which permanent chemical stratification prevents complete mixing; the deep monimolimnion is permanently isolated, anoxic, and often rich in dissolved CO_2, CH_4, or H_2S.
- **Mesotrophic lake:** a lake with intermediate nutrient levels, moderate transparency, seasonal hypolimnetic oxygen depletion, and relatively high biodiversity; intermediate between oligotrophic and eutrophic.
- **Microcystin:** a hepatotoxic cyanotoxin produced by cyanobacteria (e.g. Microcystis aeruginosa) during harmful algal blooms; damages liver cells of fish and mammals; hazardous to humans drinking contaminated water.

- **Mixolimnion:** the upper, seasonally mixing freshwater layer of a meromictic lake, above the permanent chemocline; supports aerobic organisms and seasonal phytoplankton blooms.
- **Monimolimnion:** the permanently isolated, anoxic deep layer of a meromictic lake below the chemocline; accumulates dissolved gases (CO2, CH4, H2S) and reduced ions over centuries.
- **Oligotrophic lake:** a nutrient-poor lake with low phytoplankton biomass, high water transparency, dissolved oxygen throughout the water column, and high biodiversity; characteristic of catchments with crystalline bedrock and minimal human disturbance.
- **Redoxcline:** the boundary zone between oxic and anoxic water in a lake, where redox potential drops sharply; supports chemolithotrophic bacteria and is a zone of intense biogeochemical cycling.
- **Schmidt stability:** the energy (in joules per square metre) required to mix the entire water column of a lake to a uniform temperature; a measure of the resistance of thermal stratification to wind-driven mixing.
- **Thermocline (metalimnion):** the layer of rapid temperature decrease with depth in a stratified lake; acts as a physical barrier between the epilimnion and hypolimnion; defined as the zone where temperature declines by 1 degree Celsius or more per metre.

Concept Check Questions [Series 2]

Objective Questions

1. The ________ is the zone of rapid temperature decrease with depth in a stratified lake, separating the warm epilimnion above from the cold hypolimnion below. (Linked to SLO 2.1)
2. A ________ lake mixes twice per year (spring and autumn) and is characteristic of temperate regions with strong seasonal temperature contrasts. (Linked to SLO 2.2)
3. Oligotrophic lakes typically have total phosphorus concentrations below ________ micrograms per litre and high water transparency. (Linked to SLO 2.3)
4. Under anoxic hypolimnetic conditions, Fe^3+ is reduced to Fe^2+, releasing ________ from sediment complexes into the water column; this internal loading sustains algal blooms after external inputs are reduced. (Linked to SLO 2.6)

5. The 1986 Lake Nyos disaster was a ________ eruption in which dissolved CO2 was released catastrophically, killing approximately 1,700 people in Cameroon. (Linked to SLO 2.7)

Short-Answer Questions

1. Define epilimnion, thermocline, and hypolimnion; explain the ecological significance of the thermocline. (Linked to SLO 2.1)
2. Distinguish between oligotrophic and eutrophic lakes using four characteristics. (Linked to SLO 2.3)
3. State three causes and three ecological consequences of cultural eutrophication. (Linked to SLO 2.4)
4. Explain the mechanism of internal phosphorus loading from lake sediments. (Linked to SLO 2.6)
5. Define a meromictic lake and explain what distinguishes it from a dimictic lake. (Linked to SLO 2.7)

Long-Answer Questions

1. Describe the development of thermal stratification in a lake; define the three zones; explain the seasonal cycle of stratification and mixing in both temperate dimictic and tropical monomictic lakes; give examples of African lakes for each. (Linked to SLOs 2.1, 2.2)
2. Compare oligotrophic and eutrophic lakes; explain cultural eutrophication, its consequences, and management strategies; describe the chemistry of African lake waters with reference to soda lakes. (Linked to SLOs 2.3, 2.4, 2.5)
3. Describe oxygen depletion and the redox sequence in an anoxic hypolimnion; explain internal phosphorus loading; define meromictic lakes; describe limnic eruptions with reference to the Lake Nyos disaster. (Linked to SLOs 2.6, 2.7)

Answers to Concept Check Questions [Series 2]

Objective Questions

1. Thermocline (metalimnion).
2. Dimictic.
3. 10.

4. Phosphate.
5. Limnic.

Short-Answer Questions

1. Epilimnion: warm, well-mixed surface layer; in contact with atmosphere; zone of photosynthesis. Thermocline: layer of rapid temperature decline (at least 1 degree Celsius per metre); acts as physical barrier between epilimnion and hypolimnion; prevents exchange of oxygen (downward) and nutrients (upward). Ecological significance: isolates the hypolimnion from oxygen, causing anoxia in productive lakes; traps nutrients below the photic zone, limiting algal growth in oligotrophic systems. Hypolimnion: cold, stable bottom layer; isolated from atmosphere during stratification; typically depleted of oxygen.
2. Oligotrophic: total phosphorus below 10 micrograms/L; Secchi depth exceeding 10 m; chlorophyll-a below 2 micrograms/L; DO present throughout including hypolimnion; high species diversity; low abundance. Eutrophic: total phosphorus above 35 micrograms/L; Secchi depth below 1 to 2 m; chlorophyll-a above 20 micrograms/L; hypolimnetic anoxia; low species diversity but high phytoplankton abundance.
3. Causes: agricultural runoff (fertilisers); sewage discharge (phosphorus from detergents, organic nitrogen); urban stormwater runoff. Consequences: toxic cyanobacterial blooms (microcystin hazard to humans and livestock); hypolimnetic anoxia and fish kills; invasion by water hyacinth (Eichhornia crassipes) blocking light and reducing oxygen.
4. Under aerobic conditions, Fe^3+ in sediment surface binds phosphate strongly (iron-phosphate complex). When the hypolimnion becomes anoxic, bacteria reduce Fe^3+ to soluble Fe^2+; the iron-phosphate complex breaks down and phosphate is released into the overlying water column. This internal loading can maintain elevated phosphorus concentrations and sustain algal blooms even after all external nutrient inputs are eliminated, making eutrophication reversal slow.
5. A meromictic lake has a permanent chemical stratification (chemocline) maintained by dissolved salt density differences that prevents the deep monimolimnion from ever mixing with the upper mixolimnion. A dimictic lake mixes completely twice per year when thermal stratification is eliminated by seasonal cooling; a meromictic lake never achieves complete mixing because the chemical density gradient is stronger than any thermal driving force.

Long-Answer Questions

1. Thermal stratification: solar heating warms the surface; warm water (less dense) floats on cold water; wind mixes the upper layer but cannot overcome the density barrier below. Three zones: epilimnion (warm, mixed; in contact with atmosphere); thermocline (rapid temperature decline, at least 1 degree per metre; physical barrier); hypolimnion (cold, stable; isolated from atmosphere). Dimictic (temperate): stratifies in spring; persists through summer; autumn cooling reduces epilimnion temperature until it matches hypolimnion density; thermocline breaks down; holomixis driven by wind; weak winter inverse stratification; spring turnover when ice melts. Example: temperate European and North American lakes. Tropical monomictic (e.g. Lake Victoria): stable year-round water temperature (25 to 30 degrees); stratifies during hot calm season; small temperature difference (2 to 3 degrees) creates large density difference (steep density-temperature relationship at high temperatures); mixing during cooler, windier dry season releases nutrients from hypolimnion, stimulating phytoplankton blooms. Lake Tanganyika: deep (1,470 m); permanently stratified below 200 m; lower hypolimnion permanently anoxic. Lake Chad: shallow (maximum 7 m); polymictic; well-mixed year-round; productive but fluctuating with rainfall.
2. Oligotrophic: TP below 10 micrograms/L; Secchi depth above 10 m; chlorophyll-a below 2 micrograms/L; DO throughout; high endemism; deep clear lakes (Lake Tanganyika, Lake Malawi). Eutrophic: TP above 35 micrograms/L; Secchi depth below 1 to 2 m; turbid; hypolimnetic anoxia; frequent algal blooms; low diversity; examples: many Nigerian urban lakes. Cultural eutrophication: agricultural runoff (nitrate, phosphate); sewage effluent (phosphorus, organic N); urban stormwater; atmospheric nitrogen deposition; fish farming waste. Consequences: toxic cyanobacterial blooms (microcystin damages fish livers and is dangerous to humans and livestock); hypolimnetic anoxia causing fish kills; water hyacinth invasion (blocks light, reduces oxygen); loss of fisheries; impaired drinking water. Management: nutrient reduction at source (reduce fertiliser, improve sewage treatment, phosphorus removal); biomanipulation (planktivorous fish to reduce algae grazing pressure); sediment dredging or alum treatment to bind phosphorus. African lake chemistry: controlled by catchment geology, precipitation, evaporation, biological uptake, and in-lake redox. Most freshwater lakes: Ca-HCO3 dominated. Lake Chad: Na-HCO3; closed basin (endorheic); shrinking. Soda lakes (closed basins in arid regions): high Na2CO3, pH 9 to 12; Lake Natron (pH 10.5; flamingo breeding; cyanobacteria Arthrospira dominate); Lake Magadi (pH up to 12; trona deposits); exceptionally productive despite extreme chemistry.

3. Hypolimnetic anoxia: stratification isolates hypolimnion from atmosphere; bacterial decomposition of sinking organic matter consumes fixed oxygen; in productive lakes, complete anoxia develops in weeks to months. Redox sequence (decreasing Eh): NO_3^- reduction (denitrification, N_2 produced); Mn^{4+} to Mn^{2+}; Fe^{3+} to Fe^{2+}; SO_4^{2-} to H_2S (sulphate reduction; rotten-egg odour; toxic to fish); CO_2 to CH_4 (methanogenesis). Redoxcline at oxic-anoxic boundary supports chemolithotrophs. At turnover: H_2S, Fe^{2+}, Mn^{2+} oxidised by oxygen; large DO consumption; fish kills possible. Internal phosphorus loading: Fe^{3+} in sediment binds phosphate under aerobic conditions; anoxia reduces Fe^{3+} to Fe^{2+}; iron-phosphate complex dissolves; phosphate released into water column; sustains algal blooms after external nutrient reduction; makes eutrophication reversal slow. Meromictic lake: permanent chemical stratification (chemocline); dense monimolimnion never mixes with upper mixolimnion; anoxic; accumulates CO_2, CH_4, H_2S. Lake Kivu: 250 km^3 CO_2 and 55 km^3 CH_4 in monimolimnion; geothermal input from Virunga volcanoes. Limnic eruption: disturbance (earthquake, landslide) triggers rapid ascent of CO_2-saturated deep water; pressure drop causes explosive CO_2 degassing; dense CO_2 cloud descends into valleys; asphyxiates humans and animals. Lake Nyos (Cameroon, 1986): approximately 1.6 million tonnes CO_2 released; approximately 1,700 humans and 3,500 livestock killed. Lake Monoun (Cameroon, 1984): smaller event. Management: degassing pipes installed at Lake Nyos and Lake Kivu draw CO_2-rich deep water to surface, releasing gas gradually and safely, preventing pressure build-up.

Answers to Pilot Questions [Series 2]

Part 2.1

1. Epilimnion: warm, well-mixed surface layer in contact with the atmosphere; uniform temperature; zone of active photosynthesis and wind-driven turbulence. Thermocline (metalimnion): zone of rapid temperature decrease (at least 1 degree Celsius per metre) between the epilimnion and hypolimnion; acts as a physical barrier preventing exchange of oxygen (down) and nutrients (up). Hypolimnion: cold, dense, stable bottom layer; isolated from the atmosphere once stratification forms; typically depleted of oxygen in productive lakes.
2. Spring: ice melts; surface water warms to 4 degrees Celsius (maximum density); holomixis driven by wind; nutrients from hypolimnion return to surface (spring turnover). Late spring to

summer: surface continues to warm; epilimnion develops; thermocline establishes; hypolimnion isolated. Summer: stable stratification; hypolimnion may become anoxic in productive lakes. Autumn: surface cools; epilimnion density increases; thermocline weakens; autumn turnover when surface and deep water reach equal density; wind drives holomixis; oxygen returns to depth. Winter: possible weak inverse stratification under ice (surface water below 4 degrees Celsius is less dense).

3. Dimictic: mixes twice per year (spring and autumn; temperate lakes). Monomictic: mixes once per year (warm monomictic: tropical and subtropical lakes mix during the cooler or windier season; cold monomictic: always cold, mixes in summer). Polymictic: mixes very frequently; shallow lakes where wind continuously disrupts any developing stratification; well-mixed and productive. Meromictic: never fully mixes; permanent chemical stratification (chemocline) maintains a permanently isolated, anoxic monimolimnion below the seasonally mixing mixolimnion.
4. The density-temperature relationship of water is steeper at high temperatures (25 to 30 degrees Celsius) than at low temperatures; even a 2 to 3 degree temperature difference between surface and deep water in a tropical lake creates a large density difference that strongly resists wind mixing. In contrast, a temperate lake at 10 to 20 degrees Celsius requires a much larger temperature difference to create the same density stratification; therefore tropical lakes stratify stably with relatively small temperature gradients.
5. Lake Victoria (warm monomictic): stratifies during the hot calm season; mixes during the cooler southeast trade wind season; mixing brings hypolimnetic nutrients to the surface, stimulating phytoplankton blooms that support the lake's fisheries. Lake Tanganyika (meromictic below 200 m): permanently stratified; lower hypolimnion permanently anoxic; deep water sequesters nutrients from the photic zone, keeping the upper lake nutrient-poor and the water exceptionally clear with high endemic biodiversity. Lake Chad (polymictic): shallow (maximum 7 m); well-mixed year-round by wind; high productivity; water level and chemistry fluctuate dramatically with rainfall and irrigation withdrawals, creating an unstable habitat for fish and supporting fluctuating fisheries for riparian nations.

Part 2.2

1. Oligotrophic: TP below 10 micrograms/L; Secchi depth above 10 m; chlorophyll-a below 2 micrograms/L; DO throughout including hypolimnion; high species diversity; low abundance; clear blue water. Eutrophic: TP above 35 micrograms/L; Secchi depth below 1 to

2 m; chlorophyll-a above 20 micrograms/L; hypolimnetic anoxia; low species diversity; high algal abundance; turbid green or brown water.

2. Lake Tanganyika and Lake Malawi remain oligotrophic because: their large volume relative to catchment area greatly dilutes all nutrient inputs; permanent deep stratification sequesters nutrients in the permanently anoxic hypolimnion below the photic zone, preventing their return to the surface; and their catchments are in relatively low-nutrient geological settings with limited agricultural development in historical times.
3. Agricultural runoff from fertilised fields (nitrate, phosphate leaching into rivers and lakes); sewage effluent from domestic and industrial sources (phosphorus from detergents, organic nitrogen from human waste); urban stormwater runoff carrying nutrients and organic matter from impervious surfaces; atmospheric nitrogen deposition from combustion (vehicle exhaust, power generation).
4. Production of microcystin and other cyanotoxins that are toxic to fish, livestock, and humans consuming untreated water; dense bloom biomass dies and decomposes, consuming dissolved oxygen and causing hypolimnetic (and sometimes epilimnetic) anoxia and large-scale fish kills; blooms reduce light penetration and shading kills submerged macrophytes, simplifying habitat structure and further reducing biodiversity.
5. Nutrient reduction at source: improve sewage treatment with phosphorus removal (chemical precipitation using alum or lime); reduce agricultural fertiliser application and create riparian buffer strips to intercept runoff before it reaches the lake. Biomanipulation: stock predatory fish to reduce planktivorous fish populations, allowing zooplankton (Daphnia) to recover and graze down phytoplankton biomass (top-down control of algal blooms).

Part 2.3

1. Catchment geology (dominant factor; weathering releases ions); precipitation chemistry (dissolved ions and sea salts from rain); groundwater inputs (ion-rich if passing through soluble rock); evaporation (concentrates ions in closed basins); biological uptake and release (organisms remove and return nutrients); in-lake redox chemistry (alters iron, manganese, phosphorus, and sulphur concentrations).
2. In closed (endorheic) basins, water cannot leave by a surface outflow; evaporation removes water but leaves dissolved ions behind; over time, ion concentrations increase progressively. The dominant ions become those derived from catchment geology and precipitation; in East

African Rift Valley basins with volcanic sodium carbonate rocks, sodium, carbonate, and bicarbonate accumulate, eventually producing high-pH soda lakes.

3. Lake Victoria: conductivity 90 to 100 microsiemens/cm; Mg-HCO3 dominated; relatively dilute freshwater; pH 7.5 to 9; undergoing eutrophication. Lake Tanganyika: conductivity approximately 600 microsiemens/cm; Mg-Ca-HCO3 dominated; higher dissolved solids due to geological age and evaporative concentration; oligotrophic; permanently stratified; exceptional endemic biodiversity; one of the world's oldest and deepest lakes.
4. Soda lakes are closed-basin lakes in arid regions where evaporation has concentrated sodium carbonate and bicarbonate, producing extreme pH (9 to 12) and high Na-CO3-HCO3 chemistry. Lake Natron (Tanzania): pH up to 10.5; breeding ground for over 75% of the world's lesser flamingo (Phoeniconaias minor), which feed on the cyanobacterium Arthrospira platensis (formerly Spirulina) that dominates the highly productive alkaline water. Lake Magadi (Kenya): pH up to 12; sodium trona deposits mined commercially; even more extreme than Natron; supports specialised algae and brine flies.
5. Lake Chad is an endorheic (closed) basin; historically one of Africa's largest lakes; has shrunk by approximately 90% since the 1960s due to: reduced Sahel rainfall during prolonged drought periods; greatly increased irrigation abstraction from the rivers (Chari, Yobe-Komadougou) that feed it; increased evapotranspiration from expanding irrigated agriculture around the lake shore. Chemical fluctuations follow water level: when the lake shrinks, dissolved ion concentrations rise; when water levels recover, concentrations fall.

Part 2.4

1. When stratification isolates the hypolimnion from the atmosphere, the dissolved oxygen present at stratification onset is the only supply; no replenishment occurs from above. Bacteria decomposing organic matter (phytoplankton and particles) sinking from the productive epilimnion consume this oxygen. In productive (eutrophic) lakes the organic flux is large; oxygen is depleted rapidly (weeks to months), producing complete anoxia in the hypolimnion.
2. As oxygen is depleted and Eh falls, bacteria sequentially use the following electron acceptors: nitrate (NO3- reduced to N2 or N2O; denitrification); manganic manganese (Mn^4+ reduced to Mn^2+); ferric iron (Fe^3+ reduced to Fe^2+); sulphate (SO4^2- reduced to H2S; sulphate reduction); carbon dioxide (CO2 reduced to CH4; methanogenesis).

3. Under oxic conditions, Fe^{3+} hydroxides in the sediment surface adsorb and bind phosphate strongly; phosphorus is trapped in the sediment. When the overlying water becomes anoxic, sediment bacteria reduce Fe^{3+} to soluble Fe^{2+}, dissolving the iron-phosphate complex; phosphate is released into the water column (internal phosphorus loading). This phosphate is available to phytoplankton when it reaches the photic zone; in eutrophic lakes, internal loading can sustain algal blooms for decades after external phosphorus inputs are eliminated.
4. Meromictic lake: a lake in which permanent chemical stratification (chemocline) maintained by dissolved salt density differences prevents complete mixing; the deep monimolimnion is permanently isolated, anoxic, and accumulates dissolved gases (CO_2, CH_4, H_2S) and reduced ions over centuries. Limnic eruption: a sudden, catastrophic release of dissolved CO_2 from the deep water triggered by a disturbance (earthquake, landslide, or volcanic activity); as CO_2-saturated deep water rises and pressure drops, CO_2 comes out of solution explosively; the dense CO_2 gas cloud flows into surrounding valleys and asphyxiates humans and animals.
5. Lake Nyos (Cameroon, 21 August 1986): a volcanic crater lake with meromictic stratification; CO_2 from underlying volcanic rock had saturated the deep monimolimnion over many years. A disturbance (possibly a small landslide or rockfall on the crater wall) triggered the ascent of deep water; explosive CO_2 degassing released approximately 1.6 million tonnes of CO_2; the dense gas cloud rolled down the Nyos valley, asphyxiating approximately 1,700 humans and 3,500 livestock within 25 km. A smaller event at Lake Monoun (Cameroon, 1984) killed 37 people. Management: degassing pipes have been installed at Lake Nyos (since 2001) and plans exist at Lake Kivu; the pipes draw CO_2-rich deep water to the surface continuously, releasing gas gradually and safely, preventing the dangerous build-up of supersaturation in the monimolimnion.

References and Attributions [Series 2]

Textual References (Books and External Sources)

- Hecky, R. E., & Kling, H. J. (1987). Phytoplankton ecology of the great lakes in the rift valleys of Central Africa. Archiv fur Hydrobiologie, 25, 197 to 228.
- Kalff, J. (2002). Limnology: Inland water ecosystems. Prentice Hall.

- Kling, G. W., Clark, M. A., Compton, H. R., Devine, J. D., Evans, W. C., Humphrey, A. M., Koenigsberg, E. J., Lockwood, J. P., Tuttle, M. L., & Wagner, G. N. (1987). The 1986 Lake Nyos gas disaster in Cameroon, West Africa. Science, 236, 169 to 175.
- Wetzel, R. G. (2001). Limnology: Lake and river ecosystems (3rd ed.). Academic Press.

Figures, Plates, Tables, and Boxes

- Figure 2.1: Temperature-depth profiles for temperate dimictic, tropical monomictic, and deep meromictic lakes Attribution: AI generated. Suggested OER search string: "lake thermal stratification temperature depth profile epilimnion thermocline hypolimnion tropical temperate OER diagram".
- Figure 2.2: Hypolimnetic redox chemistry and nutrient profiles, and meromictic lake structure with limnic eruption Attribution: AI generated. Suggested OER search string: "hypolimnion redox sequence anoxic lake dissolved oxygen phosphorus sediment meromictic limnic eruption diagram OER".
- Box 2.1: Comparative chemistry and biology of selected African lakes Attribution: AI generated. Suggested OER search string: "African lakes chemistry comparison pH conductivity ions trophic state table OER".

Course code: BIO 206

Course title: Hydrobiology

Course credit load: 2 Units

Series 3: Freshwater Communities and Their Productivity

- **Part 3.1: Aquatic Macrophytes**
  - Sub Part 3.1.1: Types and distribution of aquatic macrophytes
  - Sub Part 3.1.2: Factors influencing macrophyte productivity
  - Sub Part 3.1.3: Ecological roles of macrophytes
- **Part 3.2: Phytoplankton and Benthic Algae**
  - Sub Part 3.2.1: Phytoplankton: composition and distribution
  - Sub Part 3.2.2: Factors influencing phytoplankton productivity
  - Sub Part 3.2.3: Benthic algae and periphyton
- **Part 3.3: Zooplankton in Freshwater**
  - Sub Part 3.3.1: Major zooplankton groups and their characteristics
  - Sub Part 3.3.2: Factors controlling zooplankton distribution
  - Sub Part 3.3.3: Role of zooplankton in freshwater food webs
- **Part 3.4: Primary Productivity and Trophic Dynamics**
  - Sub Part 3.4.1: Measuring primary productivity in freshwater
  - Sub Part 3.4.2: Oligotrophic and eutrophic lake productivity
  - Sub Part 3.4.3: Freshwater food webs and energy flow

Introduction

Freshwater ecosystems support a diverse array of biological communities whose structure and productivity are shaped by physical, chemical, and biological interactions. The principal producers in these systems are aquatic macrophytes, phytoplankton, and benthic algae, which together fix solar energy and provide the organic matter that sustains all higher trophic levels. Zooplankton serve as the critical link between primary producers and fish, influencing both nutrient cycling and energy transfer through the water column.

This Series examines the major freshwater communities, the factors governing their distribution and productivity, and the trophic dynamics that connect them. Understanding these communities is fundamental to interpreting the biological functioning of lakes, rivers, and wetlands, and to assessing the ecological impact of nutrient enrichment and human disturbance.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 3.1** describe the types and distribution of aquatic macrophytes and explain factors influencing their productivity (Linked to Part 3.1),
- **SLO 3.2** state the ecological roles of macrophytes in freshwater systems (Linked to Part 3.1),
- **SLO 3.3** describe the composition of phytoplankton and benthic algae communities and list factors controlling their productivity (Linked to Part 3.2),
- **SLO 3.4** identify the major zooplankton groups, explain factors controlling their distribution, and describe their role in freshwater food webs (Linked to Part 3.3),
- **SLO 3.5** explain methods of measuring primary productivity and distinguish between oligotrophic and eutrophic lake productivity (Linked to Part 3.4), and
- **SLO 3.6** describe freshwater food webs and explain how energy flows through trophic levels (Linked to Part 3.4).

3.1 Aquatic Macrophytes

3.1.1 Types and distribution of aquatic macrophytes

Aquatic macrophytes are large, visible water plants rooted in or floating on freshwater bodies. They are classified by growth form into four groups: emergent macrophytes (e.g. Typha, Phragmites) grow with roots submerged and shoots above water at lake margins; floating-leaved plants (e.g. Nymphaea, Nuphar) are rooted but have leaves resting on the surface; submerged macrophytes (e.g. Ceratophyllum, Myriophyllum) grow entirely below the water surface; and free-floating plants (e.g. Eichhornia, Pistia) drift unanchored on the surface.

Distribution is governed by water depth, substrate type, light penetration, and nutrient availability. Emergent species dominate shallow margins (0 to 1 m); submerged species extend to the limit of the photic zone, rarely beyond 6 m in turbid African lakes. Macrophytes are most diverse and abundant in nutrient-rich, shallow, sheltered water bodies with stable shorelines.

Fill in the blank: Aquatic macrophytes that grow with roots submerged and shoots above water at lake margins are called ________ macrophytes; examples include Typha and Phragmites.

3.1.2 Factors influencing macrophyte productivity

Light is the primary factor limiting macrophyte productivity; turbidity caused by suspended sediment or phytoplankton blooms restricts the depth to which submerged species can grow. Nutrient availability, particularly nitrogen and phosphorus, promotes vigorous growth. Water level fluctuations affect macrophyte establishment: prolonged drawdown exposes emergent species while extended flooding suppresses emergent growth. Substrate stability and organic matter content also influence rooting success.

Temperature influences growth rates, with most tropical macrophytes showing peak productivity in warm months. Wave action and current velocity limit macrophyte establishment in exposed shores. Water pH affects nutrient speciation and availability. In African lakes such as Lake Chad and the Niger Delta floodplains, seasonal flooding and recession cycles are the dominant controls on macrophyte biomass and community composition.

Fill in the blank: The primary factor limiting submerged macrophyte productivity is ________, because turbidity caused by suspended sediment or algal blooms prevents sufficient light from reaching plants below the surface.

3.1.3 Ecological roles of macrophytes

Aquatic macrophytes perform several critical ecological functions. They are primary producers that fix atmospheric carbon dioxide and supply organic matter to the detrital food chain upon decomposition. Their structural complexity provides habitat and refugia for invertebrates, juvenile fish, amphibians, and waterfowl. Submerged macrophytes oxygenate the water during photosynthesis and stabilise sediments by reducing wave erosion and current turbulence.

Macrophytes also play a role in nutrient cycling: they absorb dissolved inorganic nitrogen and phosphorus from sediment and water, temporarily immobilising nutrients in plant tissue before releasing them on decomposition. Dense macrophyte beds can competitively suppress phytoplankton by shading the water column and depleting nutrients. Free-floating species such as Eichhornia crassipes (water hyacinth) can become invasive, reducing dissolved oxygen and impeding water use when they proliferate unchecked.

Fill in the blank: Aquatic macrophytes stabilise lake sediments, provide structural habitat for invertebrates and fish, and absorb dissolved ________ and phosphorus from the water, temporarily removing these nutrients from the water column.

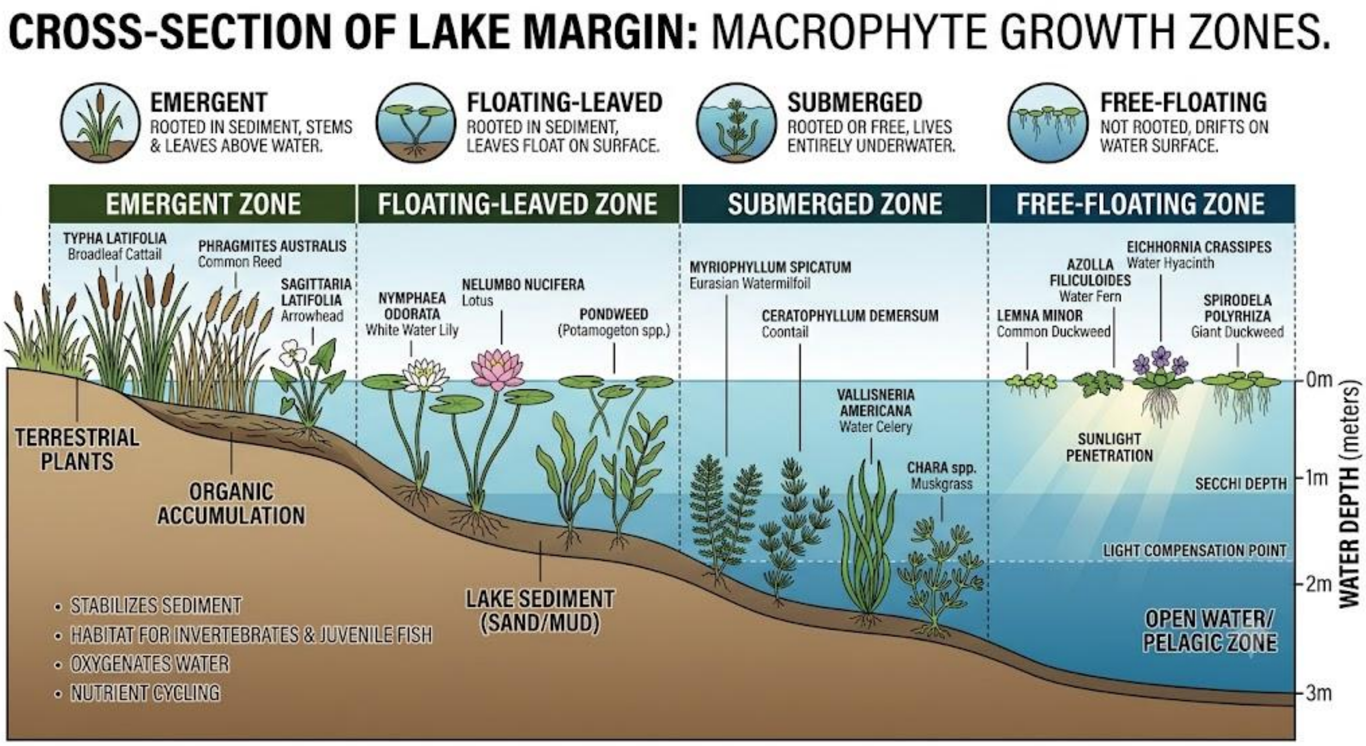

Figure 3.1: Zonation of aquatic macrophytes from shallow margin to open water

Pilot questions 3.1

1. Name the four growth-form groups of aquatic macrophytes and give one example of each.
2. State four factors that influence the distribution and productivity of aquatic macrophytes.
3. Describe three ecological roles of aquatic macrophytes in freshwater systems.
4. Explain why Eichhornia crassipes is considered a problematic species in African freshwater bodies.
5. How do macrophytes suppress phytoplankton growth in a lake?

3.2 Phytoplankton and Benthic Algae

3.2.1 Phytoplankton: composition and distribution

Phytoplankton are microscopic, photosynthetic organisms suspended in the water column. The major taxonomic groups found in freshwater include Chlorophyta (green algae, e.g. Chlorella, Scenedesmus), Cyanobacteria (blue-green algae, e.g. Microcystis, Anabaena), Bacillariophyta (diatoms, e.g. Cyclotella, Melosira), Euglenophyta (e.g. Euglena), Dinophyta (dinoflagellates), and Chrysophyta (golden algae). Diatoms and green algae dominate oligotrophic lakes; cyanobacteria dominate eutrophic and hypertrophic systems.

Phytoplankton distribution is stratified vertically: maximum abundance occurs in the epilimnion where light and nutrients are available. In stratified lakes, a deep chlorophyll maximum may form at the thermocline where light diminishes but nutrients from the hypolimnion become accessible. Seasonal succession drives community shifts: diatoms flourish in cooler, well-mixed conditions; green algae peak in spring and autumn; cyanobacteria bloom in warm, stable, nutrient-rich waters in tropical lakes.

Fill in the blank: In eutrophic lakes, ________ (blue-green algae) dominate the phytoplankton community, forming surface blooms in warm, nutrient-rich, thermally stratified water; they are largely absent from cold, oligotrophic systems.

3.2.2 Factors influencing phytoplankton productivity

Phytoplankton productivity is controlled primarily by light and nutrients. Light availability decreases exponentially with depth according to the Beer-Lambert law; turbidity from suspended sediment or dense phytoplankton self-shading limits the depth of the photic zone. Phosphorus is typically the limiting nutrient in freshwater lakes, controlling algal biomass; nitrogen limitation occurs in certain tropical and shallow systems. Silica limits diatom growth specifically.

Temperature affects enzyme kinetics and metabolic rates; most algal groups have optimal growth temperatures between 15 and 30 degrees C. Mixing depth determines whether phytoplankton cells remain in the photic zone long enough to achieve positive net production. Grazing pressure from zooplankton, particularly large-bodied Cladocera such as Daphnia, strongly controls phytoplankton standing stock. Viral lysis and fungal parasitism also contribute to phytoplankton mortality.

Fill in the blank: In most freshwater lakes, ________ is the nutrient that most commonly limits phytoplankton productivity; its concentration in the epilimnion determines the maximum algal biomass a lake can support.

3.2.3 Benthic algae and periphyton

Benthic algae grow attached to or within submerged substrates such as sediment, rocks, macrophytes, wood, and debris. Periphyton refers to the complex community of algae, bacteria, fungi, and associated organic matter that forms a biofilm on submerged surfaces. Major benthic algal groups include diatoms (Bacillariophyta), which dominate hard substrates in streams; green algae (Chlorophyta) on macrophyte surfaces; and filamentous forms such as Spirogyra and Cladophora in shallow, nutrient-enriched littoral zones.

Periphyton is particularly important in shallow, clear lakes and streams where benthic light availability is high and phytoplankton biomass is low. Nutrient concentration in the overlying water and substrate type govern periphyton productivity. In shallow African lakes, benthic algal mats can constitute a significant proportion of total lake primary production. Periphyton also serves as a high-quality food source for invertebrate grazers, including chironomid larvae, snails, and caddisfly nymphs.

Fill in the blank: ________ is the term for the complex community of algae, bacteria, fungi, and organic matter forming a biofilm on submerged surfaces in freshwater; it is an important food source for benthic invertebrate grazers.

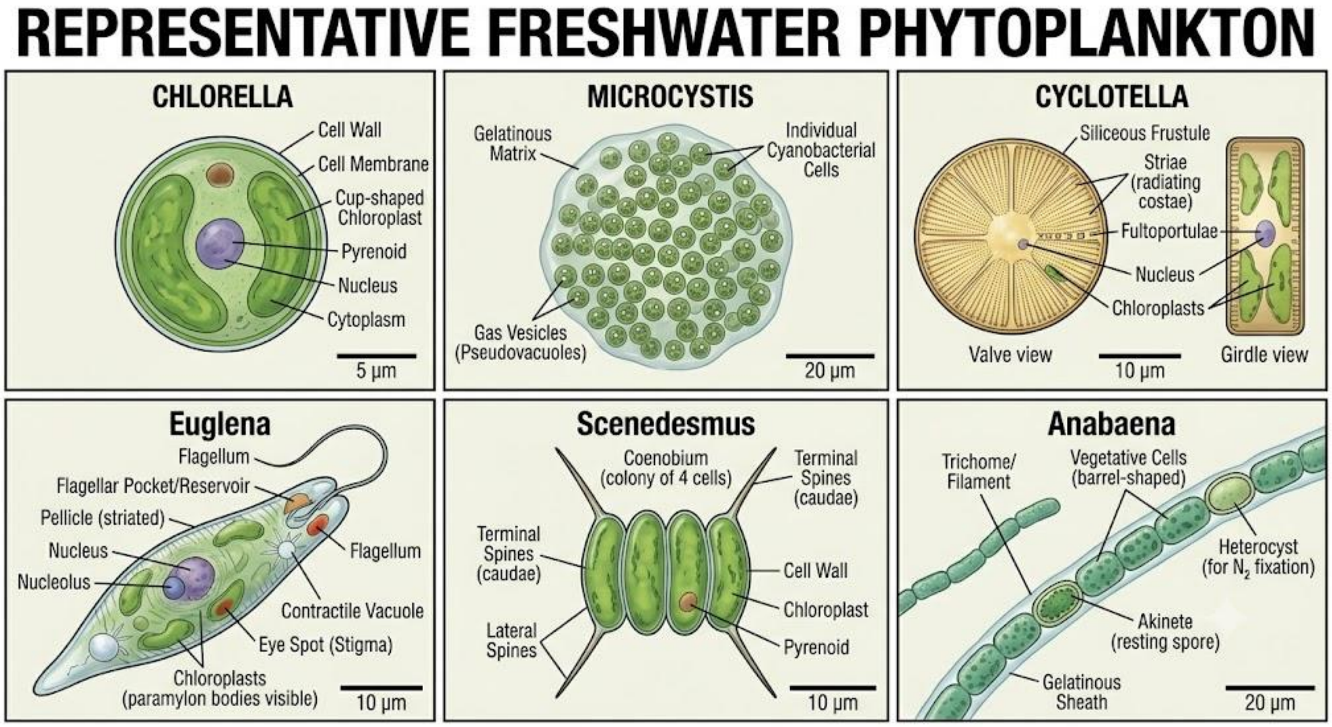

Figure 3.2: Representative freshwater phytoplankton from major taxonomic groups

Pilot questions 3.2

1. Name four major taxonomic groups of freshwater phytoplankton and give one example of each.
2. Explain why phosphorus is often the limiting nutrient for phytoplankton productivity in freshwater lakes.
3. Describe the vertical distribution of phytoplankton in a thermally stratified lake.
4. Define periphyton and explain its ecological importance in shallow freshwater ecosystems.
5. Why do cyanobacteria dominate phytoplankton communities in eutrophic tropical lakes?

3.3 Zooplankton in Freshwater

3.3.1 Major zooplankton groups and their characteristics

Freshwater zooplankton are small, heterotrophic animals that drift or weakly swim in the water column. Three major groups dominate: Cladocera (water fleas, e.g. Daphnia, Bosmina, Ceriodaphnia) are crustaceans with a transparent carapace; they filter-feed on phytoplankton, bacteria, and detritus, and reproduce rapidly by parthenogenesis. Copepoda (e.g. Cyclops, Diaptomus) are crustaceans with a segmented body and paired antennae; they include herbivores, omnivores, and predators; reproduction is sexual and slower than Cladocera.

Rotifera (wheel animals, e.g. Brachionus, Keratella, Asplanchna) are microscopic, soft-bodied animals with a ciliated corona used for feeding and locomotion; they are among the most abundant zooplankton in tropical lakes. Protozoa (e.g. ciliates, flagellates) occupy the microbial loop, feeding on bacteria and picoplankton. In African lakes, Cladocera diversity is generally lower than in temperate lakes, while copepods and rotifers are prominent components of the zooplankton assemblage.

Fill in the blank: Cladocera such as Daphnia reproduce rapidly by ________, which allows population numbers to increase very quickly when food is abundant and conditions are favourable.

3.3.2 Factors controlling zooplankton distribution

Food availability is the primary control on zooplankton abundance; phytoplankton biomass and bacterial production determine carrying capacity for herbivorous and microbivorous species. Predation by planktivorous fish (e.g. juvenile tilapia, Clupeid species) exerts intense top-down control: fish selectively remove large-bodied Cladocera, shifting zooplankton communities toward small-bodied, less-visible species such as rotifers and small copepods. This predation effect is a major driver of zooplankton body-size distribution.

Temperature affects metabolic rates, reproduction, and development times. Diel vertical migration (DVM) is a behavioural response to fish predation: zooplankton descend to deeper, darker water during the day and ascend to productive surface waters at night to feed. Dissolved oxygen levels restrict the depth range of most zooplankton, excluding them from anoxic hypolimnia. Turbidity and cyanobacterial blooms reduce food quality and can inhibit filter-feeding Cladocera by clogging filtering apparatus.

Fill in the blank: Diel vertical migration is a behaviour in which zooplankton descend to deeper water during the day and rise to the surface at night; it is primarily a response to predation pressure from ________ fish.

3.3.3 Role of zooplankton in freshwater food webs

Zooplankton are the central link between primary producers and higher trophic levels in pelagic freshwater food webs. Herbivorous zooplankton (primarily Cladocera and copepod nauplii) graze on phytoplankton, converting algal biomass into animal tissue that is accessible to planktivorous fish. Large Daphnia populations can suppress algal blooms through intensive grazing, a process called biomanipulation when applied in lake management. Predatory zooplankton (e.g. Chaoborus larvae, Bythotrephes) feed on smaller zooplankton, adding complexity to pelagic food webs.

Zooplankton are also key in nutrient cycling: excretion of nitrogen and phosphorus in dissolved inorganic forms stimulates phytoplankton growth. Their faecal pellets and dead bodies sink as particulate organic matter, transporting carbon and nutrients from the surface to the sediment. In African lakes such as Lake Victoria, changes in zooplankton community structure following the introduction of Nile perch (Lates niloticus) led to cascading trophic effects throughout the food web.

Fill in the blank: The deliberate manipulation of fish predation pressure to allow large Daphnia populations to recover and suppress algal blooms through grazing is known as ________; it is used as a management strategy to improve water quality in eutrophic lakes.

Pilot questions 3.3

1. Name the three major zooplankton groups in freshwater and state one distinguishing feature of each.
2. Explain diel vertical migration and state the main reason for this behaviour.
3. Describe how fish predation alters the body-size structure of a zooplankton community.
4. Explain what biomanipulation is and how it can be used to control algal blooms in eutrophic lakes.
5. State two ways in which zooplankton contribute to nutrient cycling in freshwater lakes.

3.4 Primary Productivity and Trophic Dynamics

3.4.1 Measuring primary productivity in freshwater

Primary productivity is the rate at which photosynthetic organisms fix carbon dioxide into organic matter. Gross primary production (GPP) is the total carbon fixed; net primary production (NPP) is GPP minus autotrophic respiration. The light and dark bottle method measures GPP and NPP: water samples in paired clear (light) and opaque (dark) bottles are incubated at known depths for a set period; changes in dissolved oxygen indicate photosynthesis and respiration rates. NPP = change in DO in light bottle; GPP = NPP + respiration (from dark bottle).

The carbon-14 (14C) radiotracer method offers greater sensitivity: bottles spiked with 14C-labelled bicarbonate are incubated in situ; carbon fixed by phytoplankton is measured by radioactivity of filtered material. Chlorophyll a concentration, measured by spectrophotometry or fluorometry, is widely used as a proxy for phytoplankton biomass and an indirect productivity estimate. Remote sensing of surface chlorophyll is now used for large lake monitoring.

Fill in the blank: In the light and dark bottle method, gross primary production is calculated as the sum of net primary production and the respiration rate measured in the ________ bottle, which prevents photosynthesis but allows respiration to continue.

3.4.2 Oligotrophic and eutrophic lake productivity

Oligotrophic lakes are nutrient-poor: they have low phosphorus and nitrogen concentrations, high water clarity, low phytoplankton biomass (low chlorophyll a), deep photic zones, high dissolved oxygen throughout the water column, and low overall productivity. Their food webs are long and energy-inefficient. Examples include Lake Tanganyika and Lake Malawi, which are deep, ancient African lakes with slow nutrient turnover. Species diversity of fish is often high, but biomass production per unit area is low.

Eutrophic lakes are nutrient-rich: they have high phosphorus and nitrogen, frequent algal blooms (especially cyanobacteria), high turbidity, shallow photic zones, hypolimnetic anoxia during stratification, and high gross production but low fish diversity. Mesotrophic lakes are intermediate. Cultural eutrophication, driven by agricultural runoff, sewage discharge, and urban drainage, has accelerated nutrient loading in many Nigerian and West African lakes and reservoirs, causing shifts from oligotrophic to eutrophic conditions.

Fill in the blank: Eutrophic lakes are characterised by high nutrient concentrations, frequent algal blooms, shallow photic zones, and ________ in the hypolimnion during thermal stratification, which causes the death of benthic organisms and reduces fish diversity.

Attribute	**Oligotrophic Lakes**	**Eutrophic Lakes**
Nutrients	Low nutrient concentrations (nitrogen, phosphorus)	High nutrient concentrations, especially phosphorus
Water Clarity	Very clear, low turbidity	Murky, reduced clarity due to suspended algae
Photic Zone	Deep photic zone, light penetrates far	Shallow photic zone, light blocked by algal blooms
Chlorophyll a	Low concentrations	High concentrations
Algal Blooms	Rare or absent	Frequent, sometimes harmful
Dissolved Oxygen	High throughout water column	Often depleted in deeper layers (hypoxia)
Fish Diversity	High diversity, cold-water species (e.g., trout)	Lower diversity, warm-water tolerant species (e.g., carp)
Productivity	Low primary productivity	High primary productivity

Box 3.1: Comparison of oligotrophic and eutrophic lake characteristics

3.4.3 Freshwater food webs and energy flow

Freshwater food webs consist of two main pathways: the grazing food chain and the detrital food chain. In the grazing chain, energy flows from primary producers (phytoplankton, macrophytes, periphyton) to herbivorous zooplankton, then to planktivorous fish, and finally to piscivorous fish or birds. Only approximately 10 percent of energy is transferred between trophic levels (Lindeman's trophic efficiency), with the remainder lost as heat through respiration.

In the detrital chain, dead organic matter from all trophic levels is colonised by bacteria and fungi, which are consumed by detritivores and deposit feeders such as chironomid larvae, oligochaetes, and snails. The microbial loop processes dissolved organic carbon through bacteria and flagellates, returning nutrients to phytoplankton. In many African lakes, the detrital pathway sustains more production than the grazing chain, reflecting high allochthonous organic inputs from surrounding watersheds.

Fill in the blank: Lindeman's trophic efficiency states that approximately ________ percent of energy is transferred from one trophic level to the next; the remainder is lost as metabolic heat during respiration at each level.

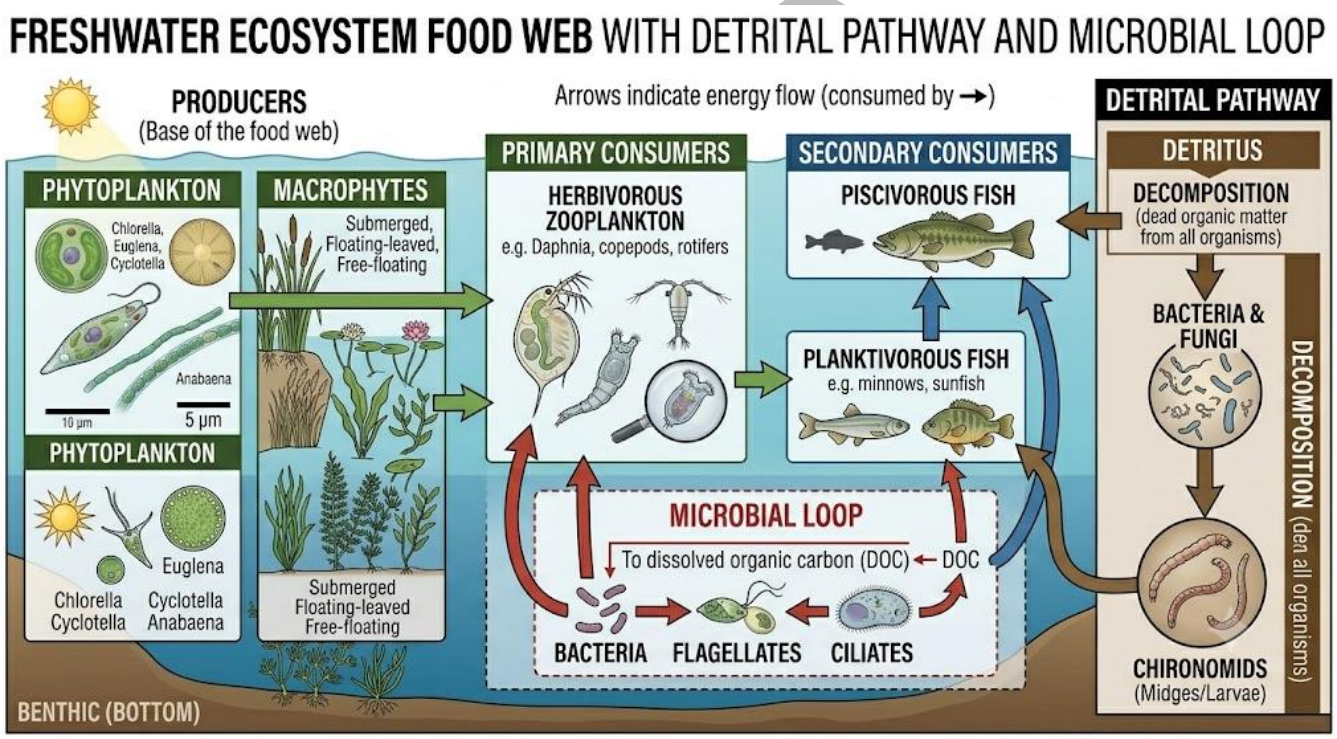

Figure 3.3: A simplified freshwater food web showing grazing and detrital pathways and the microbial loop

Pilot questions 3.4

1. Describe the light and dark bottle method for measuring primary productivity in a lake.
2. State five differences between oligotrophic and eutrophic lakes.
3. Distinguish between the grazing food chain and the detrital food chain in freshwater ecosystems.

4. Explain Lindeman's trophic efficiency and state its implications for the number of trophic levels a food web can support.
5. What is cultural eutrophication and what are its main causes in Nigerian freshwater bodies?

Series Summary

This Series examined the major freshwater biological communities and their productivity. Aquatic macrophytes are classified as emergent, floating-leaved, submerged, and free-floating; their distribution is governed by light, nutrients, water-level fluctuation, and substrate. They serve as primary producers, habitat providers, sediment stabilisers, and nutrient sinks. Phytoplankton include Chlorophyta, Cyanobacteria, Bacillariophyta, and Euglenophyta; productivity is controlled by phosphorus, light, temperature, and grazing. Cyanobacteria dominate eutrophic systems. Benthic algae and periphyton form biofilms on submerged surfaces and are important in shallow, clear lakes.

Freshwater zooplankton comprise Cladocera (filter-feeders; parthenogenetic), Copepoda (diverse feeders; sexual reproduction), and Rotifera (ciliated; abundant in tropical lakes). Distribution is controlled by food availability, fish predation, temperature, and dissolved oxygen. Zooplankton link primary producers to fish and mediate nutrient cycling. Primary productivity is measured by the light-dark bottle method and the 14C technique. Oligotrophic lakes are nutrient-poor and clear; eutrophic lakes are nutrient-rich with algal blooms and hypolimnetic anoxia. Energy flows through grazing and detrital pathways with approximately 10 percent efficiency between trophic levels.

Glossary of Terms

- **Benthic algae:** photosynthetic algae growing on or within submerged substrates such as sediment, rocks, and macrophyte surfaces in freshwater bodies.
- **Biomanipulation:** the deliberate management of fish stocks or food web structure to control algal blooms through enhanced zooplankton grazing, particularly by Daphnia.

- **Chlorophyll a:** the primary photosynthetic pigment in most algae and plants; its concentration in water is used as a proxy for phytoplankton biomass and lake trophic status.
- **Cladocera:** small crustacean zooplankton (water fleas) such as Daphnia; they are filter-feeders that reproduce by parthenogenesis and are key grazers of phytoplankton in freshwater lakes.
- **Cultural eutrophication:** accelerated nutrient enrichment of a water body caused by human activities such as agricultural runoff, sewage discharge, and urban drainage.
- **Diel vertical migration (DVM):** the daily movement of zooplankton from surface waters at night (to feed) to deeper water during the day (to avoid visual predators such as fish).
- **Emergent macrophyte:** an aquatic plant with roots anchored in the sediment and shoots extending above the water surface; examples include Typha (bulrush) and Phragmites (common reed).
- **Eutrophic:** describing a water body with high nutrient concentrations, abundant algal biomass, low water clarity, and hypolimnetic anoxia during thermal stratification.
- **Gross primary production (GPP):** the total rate of carbon fixation by photosynthetic organisms per unit area and time, before subtracting autotrophic respiration losses.
- **Macrophyte:** any large, visible aquatic plant rooted in or floating on a water body; classified as emergent, floating-leaved, submerged, or free-floating according to growth form.
- **Microbial loop:** a pathway in aquatic food webs in which dissolved organic carbon is taken up by bacteria, which are then grazed by flagellates and ciliates, returning energy to higher trophic levels.
- **Net primary production (NPP):** gross primary production minus the carbon consumed by autotrophic respiration; the organic matter actually available to heterotrophs.
- **Oligotrophic:** describing a water body with low nutrient concentrations, high water clarity, low phytoplankton biomass, deep photic zone, and high dissolved oxygen throughout; low overall productivity.
- **Parthenogenesis:** asexual reproduction in which unfertilised eggs develop into offspring; used by Cladocera (e.g. Daphnia) under favourable conditions, allowing rapid population growth.
- **Periphyton:** the complex community of algae, bacteria, fungi, and organic matter forming a biofilm on submerged surfaces in freshwater; an important food source for benthic invertebrate grazers.
- **Phytoplankton:** microscopic, photosynthetic organisms suspended in the water column; major groups in freshwater include Chlorophyta, Cyanobacteria, Bacillariophyta, and Euglenophyta.

- **Rotifera:** microscopic, soft-bodied aquatic animals with a ciliated corona used for feeding and locomotion; among the most abundant zooplankton in tropical freshwater lakes.
- **Trophic efficiency:** the proportion of energy (approximately 10 percent) transferred from one trophic level to the next in a food chain; first quantified by Lindeman (1942).
- **Zooplankton:** small, heterotrophic animals that drift or weakly swim in the water column; major freshwater groups are Cladocera, Copepoda, and Rotifera; they link primary producers to fish in pelagic food webs.

Concept Check Questions [Series 3]

Objective Questions

1. Aquatic macrophytes that grow with roots in the sediment and shoots above the water surface are called ________ macrophytes. (Linked to SLO 3.1)
2. The primary nutrient limiting phytoplankton productivity in most freshwater lakes is ________. (Linked to SLO 3.3)
3. Cladocera reproduce asexually by ________ under favourable conditions, allowing rapid population increase. (Linked to SLO 3.4)
4. Approximately ________ percent of energy is transferred between trophic levels in a freshwater food web, according to Lindeman's trophic efficiency. (Linked to SLO 3.6)
5. The complex biofilm of algae, bacteria, fungi, and organic matter on submerged surfaces is called ________. (Linked to SLO 3.3)

Short-Answer Questions

1. Name the four growth-form groups of aquatic macrophytes and give one example of each. (Linked to SLO 3.1)
2. State four factors that control phytoplankton productivity in freshwater lakes. (Linked to SLO 3.3)
3. Name the three major zooplankton groups and state one distinguishing feature of each. (Linked to SLO 3.4)
4. State five differences between oligotrophic and eutrophic lakes. (Linked to SLO 3.5)
5. Describe the light and dark bottle method for measuring primary productivity. (Linked to SLO 3.5)

Long-Answer Questions

1. Describe the types and ecological roles of aquatic macrophytes, and explain the factors that influence their distribution and productivity in freshwater bodies. (Linked to SLOs 3.1, 3.2)
2. Describe the major groups of freshwater phytoplankton, explain factors controlling their productivity, and compare the characteristics of benthic algae with phytoplankton. (Linked to SLO 3.3)
3. Describe the major freshwater zooplankton groups, explain how fish predation and food availability influence their distribution, and discuss their role in nutrient cycling and food web dynamics. Compare oligotrophic and eutrophic lake productivity and explain how energy flows through trophic levels. (Linked to SLOs 3.4, 3.5, 3.6)

Answers to Concept Check Questions [Series 3]

Objective Questions

1. Emergent.
2. Phosphorus.
3. Parthenogenesis.
4. 10.
5. Periphyton.

Short-Answer Questions

1. Emergent (Typha); floating-leaved (Nymphaea); submerged (Ceratophyllum); free-floating (Eichhornia).
2. Light availability; phosphorus concentration; temperature; grazing by zooplankton; turbidity; mixing depth.
3. Cladocera (crustaceans; filter-feeders; parthenogenetic; e.g. Daphnia); Copepoda (crustaceans; diverse feeders; sexual reproduction; e.g. Cyclops); Rotifera (soft-bodied; ciliated corona; very abundant in tropical lakes; e.g. Brachionus).
4. Oligotrophic vs eutrophic: nutrients (low vs high); water clarity (high vs low); photic zone (deep vs shallow); chlorophyll a (low vs high); algal blooms (rare vs frequent); dissolved oxygen in hypolimnion (high vs anoxic); fish diversity (high vs low).
5. Water samples are placed in paired light (clear) and dark (opaque) bottles and incubated at depth. Change in dissolved oxygen in the light bottle gives NPP; the dark bottle measures respiration. GPP = NPP + respiration. Multiple depths are sampled to profile productivity through the water column.

Long-Answer Questions

1. Macrophyte types: emergent (Typha; rooted; shoots above water); floating-leaved (Nymphaea; rooted; leaves on surface); submerged (Ceratophyllum; fully underwater); free-floating (Eichhornia; unanchored). Distribution controlled by light (turbidity limits submerged species), nutrients (N and P promote growth), water-level fluctuation, substrate stability, wave action, and temperature. Productivity factors: light is primary; phosphorus and nitrogen availability; seasonal flooding (African lakes); temperature; pH; grazing. Ecological roles: primary producers supplying detrital food chain; habitat and refugia for invertebrates, fish, and waterfowl; sediment stabilisation; nutrient absorption from water and sediment; competitive suppression of phytoplankton by shading. Eichhornia crassipes is invasive when unchecked, reducing dissolved oxygen and impeding water use.
2. Phytoplankton groups: Chlorophyta (Chlorella, Scenedesmus); Cyanobacteria (Microcystis, Anabaena); Bacillariophyta (diatoms: Cyclotella); Euglenophyta (Euglena). Productivity factors: phosphorus (most common limiting nutrient); light (Beer-Lambert; photic zone depth); temperature (15 to 30 degrees C optimal); mixing depth; zooplankton grazing; viral lysis. Cyanobacteria dominate eutrophic systems due to buoyancy regulation, nitrogen fixation (Anabaena), and toxin production. Vertical distribution: maximum in epilimnion; deep chlorophyll maximum at thermocline. Benthic algae vs phytoplankton: benthic algae are attached to substrate (rocks, sediment, macrophytes); periphyton is a mixed biofilm; important in shallow, clear systems; governed by substrate type and overlying water nutrients. Phytoplankton are suspended; controlled by mixing, light, and nutrients in the water column.
3. Zooplankton groups: Cladocera (Daphnia; filter-feeders; parthenogenetic; key phytoplankton grazers); Copepoda (Cyclops; diverse; sexual; slower reproduction); Rotifera (Brachionus; ciliated corona; abundant in tropical lakes). Distribution controls: food availability (phytoplankton biomass); fish predation (removes large-bodied Cladocera; shifts to small rotifers and copepods); diel vertical migration (down by day to avoid visual predators; up at night to feed); dissolved oxygen (excludes zooplankton from anoxic hypolimnia); temperature. Nutrient cycling: excretion of dissolved N and P stimulates phytoplankton; faecal pellets and bodies sink, exporting carbon to sediment. Biomanipulation: reducing planktivorous fish allows Daphnia to recover and suppress algal blooms. Oligotrophic lakes: low nutrients; clear; deep photic zone; low chlorophyll a; high DO; high fish diversity; low production. Eutrophic lakes: high nutrients; turbid; frequent cyanobacterial blooms; hypolimnetic anoxia; low fish diversity; high gross production. Energy flow: approximately

10 percent transferred per trophic level (Lindeman); grazing chain (phytoplankton to zooplankton to planktivorous fish to piscivorous fish); detrital chain (dead organic matter to bacteria to detritivores); microbial loop (DOC to bacteria to flagellates). Cultural eutrophication in Nigerian lakes driven by agricultural runoff, sewage, and urban drainage.

Answers to Pilot Questions [Series 3]

Part 3.1

1. Emergent (Typha, Phragmites); floating-leaved (Nymphaea, Nuphar); submerged (Ceratophyllum, Myriophyllum); free-floating (Eichhornia, Pistia).
2. Light availability; nutrient concentrations (N and P); water-level fluctuation; substrate type and stability; wave action and current; temperature; water pH.
3. Primary production supplying the detrital food chain; provision of structural habitat and refugia for invertebrates, fish larvae, and waterfowl; sediment stabilisation by reducing wave erosion; nutrient absorption from water and sediment, temporarily immobilising N and P.
4. Eichhornia crassipes (water hyacinth) grows very rapidly in nutrient-enriched water, forming dense mats that shade the water column, deplete dissolved oxygen through decomposition of dead material, and obstruct navigation, fishing, and water intake. Its free-floating habit allows it to spread rapidly across water bodies with no current or wave control.
5. Dense submerged macrophyte beds shade the water column, reducing light available to phytoplankton; they also absorb dissolved N and P from the water, depriving phytoplankton of nutrients needed for growth.

Part 3.2

1. Chlorophyta (Chlorella); Cyanobacteria (Microcystis); Bacillariophyta (Cyclotella); Euglenophyta (Euglena).
2. Phosphorus is quickly taken up by algae; unlike nitrogen, freshwater lacks a large atmospheric reservoir of inorganic phosphorus to replace what is removed. Phosphorus inputs from watershed runoff and internal loading from sediments therefore set the upper limit on algal biomass.
3. Maximum abundance in the epilimnion where light and nutrients are available; decline with depth as light attenuates; a deep chlorophyll maximum may form at the thermocline where

light diminishes but hypolimnetic nutrients are accessible; virtually absent below the photic zone.

4. Periphyton is the mixed biofilm of algae, bacteria, fungi, and organic matter on submerged surfaces. It is ecologically important as a food source for invertebrate grazers (snails, chironomids, caddisfly nymphs) and as a significant primary producer in shallow, clear lakes and streams where benthic light levels are high.
5. Cyanobacteria regulate their buoyancy using gas vesicles, allowing them to position themselves at the optimal depth for light. Many fix atmospheric nitrogen (e.g. Anabaena), bypassing nitrogen limitation. They are unpalatable to most zooplankton, reducing grazing mortality. Warm, stable, nutrient-rich water in stratified tropical lakes therefore strongly favours cyanobacterial dominance.

Part 3.3

1. Cladocera (crustaceans; filter-feeders; parthenogenetic reproduction; e.g. Daphnia); Copepoda (crustaceans; diverse feeders; sexual reproduction; segmented body; e.g. Cyclops); Rotifera (soft-bodied; ciliated corona; microscopic; very abundant in tropical lakes; e.g. Brachionus).
2. Diel vertical migration: zooplankton descend to deeper, darker water during the day and rise to the surface at night. The main reason is to avoid visual predation by planktivorous fish, which hunt by sight in well-lit surface waters during daytime.
3. Planktivorous fish selectively prey on large, visible zooplankton, especially large-bodied Cladocera. This selective removal shifts the community toward small-bodied, less-visible species such as rotifers and small copepods, reducing mean body size of the zooplankton assemblage and decreasing the efficiency of phytoplankton grazing.
4. Biomanipulation reduces planktivorous fish numbers (by removal or stocking piscivores), allowing large-bodied Daphnia populations to recover. Dense Daphnia populations intensively graze phytoplankton, reducing algal biomass and improving water clarity in eutrophic lakes.
5. Zooplankton excrete dissolved inorganic N and P, which are immediately available to phytoplankton, stimulating algal growth. Faecal pellets and dead zooplankton bodies sink as particulate organic matter, transporting carbon and nutrients from the surface epilimnion to the sediment, contributing to nutrient burial and sediment enrichment.

Part 3.4

1. Water samples are placed in paired light (clear) and dark (opaque) bottles and suspended at known depths for a fixed period. In the light bottle, photosynthesis and respiration both occur; dissolved oxygen increases if GPP exceeds respiration. The dark bottle measures respiration only (dissolved oxygen decreases). NPP = change in DO in light bottle. GPP = NPP + respiration (absolute decrease in DO in dark bottle). The method is repeated across multiple depths to integrate production through the photic zone.
2. Nutrients: low in oligotrophic; high in eutrophic. Water clarity: high (deep Secchi depth) vs low. Photic zone: deep vs shallow. Chlorophyll a: low vs high. Algal blooms: rare vs frequent (cyanobacteria). Dissolved oxygen in hypolimnion: high vs anoxic during stratification. Fish diversity: high vs low.
3. Grazing food chain: energy passes from living primary producers (phytoplankton, macrophytes) to herbivorous zooplankton, then to planktivorous fish, then to piscivorous fish. Detrital food chain: dead organic matter from all trophic levels is broken down by bacteria and fungi, then consumed by detritivores (chironomids, oligochaetes, snails). The detrital pathway often dominates in African lakes with high allochthonous inputs.
4. Lindeman's trophic efficiency states that approximately 10 percent of energy available at one trophic level is converted to biomass at the next; the remaining 90 percent is lost as heat during respiration. Implication: food chains are limited to four or five trophic levels, beyond which insufficient energy remains to sustain a viable population at higher levels.
5. Cultural eutrophication is the accelerated nutrient enrichment of water bodies caused by human activities. Main causes in Nigeria: agricultural runoff delivering fertiliser-derived N and P from farms around lakes and reservoirs; domestic and municipal sewage discharge (especially in urban areas near Lagos Lagoon, Kainji Reservoir); urban stormwater runoff; and industrial effluent containing high organic loads.

References and Attributions [Series 3]

Textual References (Books and External Sources)

- Wetzel, R. G. (2001). Limnology: Lake and river ecosystems (3rd ed.). Academic Press.
- Kalff, J. (2002). Limnology: Inland water ecosystems. Prentice Hall.
- Moss, B. (2010). Ecology of fresh waters: A view for the twenty-first century (4th ed.). Wiley-Blackwell.
- Lind, O. T. (1979). Handbook of common methods in limnology (2nd ed.). C.V. Mosby.

Figures, Plates, Tables, and Boxes

- Figure 3.1: Zonation of aquatic macrophytes from shallow margin to open water. Attribution: AI generated. Suggested OER search string: “aquatic macrophyte zonation lake margin emergent submerged floating labelled diagram OER”.
- Figure 3.2: Representative freshwater phytoplankton from major taxonomic groups. Attribution: AI generated. Suggested OER search string: “freshwater phytoplankton major groups labelled diagrams cyanobacteria diatoms green algae OER”.
- Box 3.1: Comparison of oligotrophic and eutrophic lake characteristics. Attribution: AI generated. Suggested OER search string: “oligotrophic eutrophic lake comparison table nutrients clarity oxygen fish OER”.
- Figure 3.3: A simplified freshwater food web showing grazing and detrital pathways and the microbial loop. Attribution: AI generated. Suggested OER search string: “freshwater food web diagram phytoplankton zooplankton fish detrital microbial loop energy flow OER”.

Course code: BIO 206

Course title: Hydrobiology

Course credit load: 2 Units

Series 4: Estuarine Ecosystems and Adaptive Features

- **Part 4.1: The Estuarine Environment**
  - Sub Part 4.1.1: Definition, types, and formation of estuaries
  - Sub Part 4.1.2: Salinity gradients and chemical factors
  - Sub Part 4.1.3: Physical dynamics of estuaries
- **Part 4.2: Estuarine Communities**
  - Sub Part 4.2.1: Producer communities in estuaries
  - Sub Part 4.2.2: Consumer communities: invertebrates and fish
  - Sub Part 4.2.3: Mangrove ecosystems
- **Part 4.3: Adaptive Features of Estuarine Organisms**
  - Sub Part 4.3.1: Osmoregulation and ionic regulation
  - Sub Part 4.3.2: Behavioural and morphological adaptations
  - Sub Part 4.3.3: Adaptations of mangrove plants
- **Part 4.4: Importance and Threats to Estuarine Ecosystems**
  - Sub Part 4.4.1: Ecological and economic importance of estuaries
  - Sub Part 4.4.2: Pollution and human impacts on estuaries
  - Sub Part 4.4.3: Conservation of estuarine ecosystems

Introduction

Estuaries are among the most productive and biologically important ecosystems on Earth. They form where freshwater rivers meet the sea, creating transitional zones of fluctuating salinity, temperature, and turbidity that impose severe physiological stress on resident organisms. Yet these same conditions generate extraordinary biological productivity, making estuaries critical nursery grounds for marine fish, refugia for migratory birds, and major centres of nutrient cycling. Along the Nigerian coastline, estuaries and the Niger Delta complex support enormous biodiversity and sustain the livelihoods of millions of people through fisheries and ecosystem services.

This Series examines the physical and chemical characteristics of estuaries, the biological communities they support, the adaptive strategies organisms use to survive fluctuating conditions, and the ecological and economic importance of these ecosystems. It also addresses the major threats facing estuaries and the principles of their conservation.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 4.1** define an estuary, classify estuarine types, and explain the chemical and physical factors that characterise them (Linked to Part 4.1),
- **SLO 4.2** describe the producer and consumer communities of estuaries including mangrove ecosystems (Linked to Part 4.2),
- **SLO 4.3** explain osmoregulation, ionic regulation, and behavioural and morphological adaptations of estuarine animals (Linked to Part 4.3),
- **SLO 4.4** describe the structural and physiological adaptations of mangrove plants to waterlogged, saline conditions (Linked to Part 4.3),
- **SLO 4.5** state the ecological and economic importance of estuarine ecosystems (Linked to Part 4.4), and

- **SLO 4.6** identify major threats to estuaries and explain key principles of their conservation (Linked to Part 4.4).

4.1 The Estuarine Environment

4.1.1 Definition, types, and formation of estuaries

An estuary is a semi-enclosed coastal water body with a free connection to the open sea and within which seawater is measurably diluted by freshwater derived from land drainage (Pritchard, 1967). Four major types are recognised based on geomorphology: coastal plain (drowned river valley) estuaries, formed by sea-level rise flooding a river valley (e.g. the Niger Delta creek system); bar-built estuaries, where sandbars or barrier islands partially enclose a lagoon (e.g. Lagos Lagoon); tectonic estuaries, formed by faulting or subsidence; and fjord estuaries, created by glacial scouring (rare in tropical Africa).

Estuaries are also classified by mixing pattern. In stratified estuaries, a distinct freshwater wedge overlies saltwater with a sharp halocline separating the two; this occurs where river discharge is strong relative to tidal mixing. Partially mixed estuaries show intermediate stratification with some tidal mixing. Well-mixed (homogeneous) estuaries have salinity uniform from surface to bottom due to strong tidal stirring. The Bight of Benin and Niger Delta estuaries are primarily partially mixed to well-mixed systems, depending on season and tidal phase.

Fill in the blank: An estuary is a semi-enclosed coastal body of water where seawater is diluted by freshwater from land drainage; the type formed when sea-level rise floods a river valley is called a ________ estuary.

4.1.2 Salinity gradients and chemical factors

Salinity is the defining chemical gradient of estuaries, measured in practical salinity units (psu) or parts per thousand (ppt). It ranges from near 0 psu at the freshwater end to approximately 35 psu at the marine end. The Venice system classifies estuarine zones by salinity: limnetic (0 to 0.5 psu), oligohaline (0.5 to 5 psu), mesohaline (5 to 18 psu), polyhaline (18 to 30 psu), and euhaline

(30 to 40 psu). Salinity fluctuates with tidal cycles, seasonal river discharge, and evaporation; tropical estuaries can become hypersaline (greater than 35 psu) during dry seasons.

Dissolved oxygen in estuaries is highly variable: turbid, organic-rich waters have high biological oxygen demand (BOD), and stratification can promote bottom-water anoxia. Nutrients are generally abundant due to river inputs and sediment remineralisation, making estuaries highly productive. Turbidity is characteristically high; a turbidity maximum forms near the freshwater-saltwater mixing zone where suspended particles flocculate. pH in estuaries is moderately buffered by the marine carbonate system but can fall in stratified, organic-rich bottom waters.

Fill in the blank: The Venice system classifies the mesohaline zone of an estuary as having a salinity of ________ to 18 psu; this zone experiences the greatest salinity fluctuation and is physiologically the most stressful for estuarine organisms.

4.1.3 Physical dynamics of estuaries

Tides are the dominant physical forcing in most estuaries. Tidal action drives mixing of fresh and saline water, transports sediment and nutrients, and creates periodic inundation of intertidal zones. Two tidal cycles per day (semi-diurnal tides) characterise much of the West African coast. River discharge controls the extent of the freshwater-saltwater mixing zone: during high river flow (wet season), the halocline is pushed seaward; during low flow (dry season), it moves landward. Seasonal discharge variation is particularly pronounced in rivers draining the Guinea savanna zone.

Estuarine circulation involves a net upstream flow of denser saline bottom water and a net seaward flow of less-dense surface freshwater, a pattern called gravitational circulation. This two-layer flow transports nutrients landward from the sea and exports organic matter seaward. Wave action, wind mixing, and the Coriolis effect further influence estuarine hydrodynamics. Intertidal mudflats and sandflats undergo repeated exposure and immersion, creating gradients of temperature, desiccation, and salinity stress that structure benthic community zonation.

Fill in the blank: The two-layer estuarine circulation pattern in which denser saline water flows upstream along the bottom and lighter freshwater flows seaward at the surface is called ________ circulation.

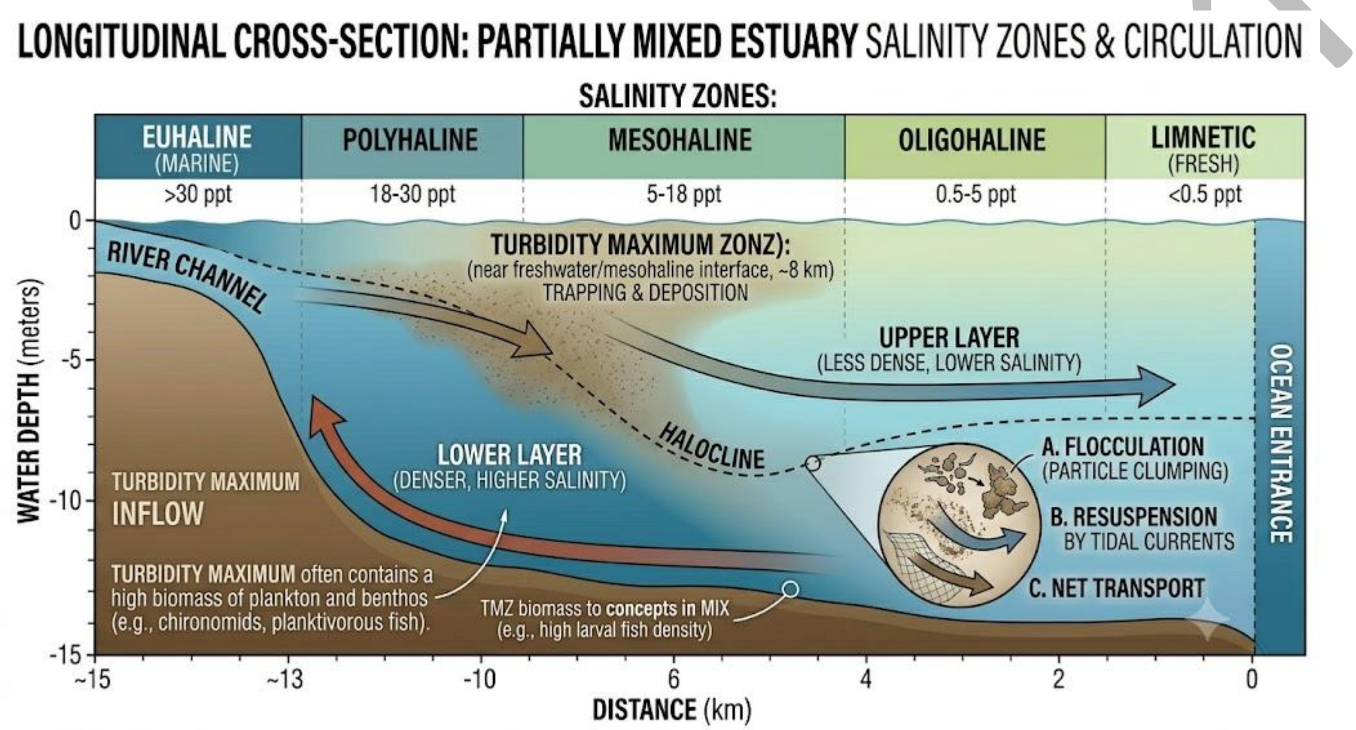

Figure 4.1: Longitudinal section of a partially mixed estuary showing salinity zones, gravitational circulation, and the turbidity maximum

Pilot questions 4.1

1. Define an estuary and name four types classified by geomorphology.
2. Name the five salinity zones of the Venice system and state the salinity range of each.
3. Distinguish between stratified, partially mixed, and well-mixed estuaries.
4. Explain gravitational circulation in an estuary and state its ecological significance.
5. Why does a turbidity maximum form in estuaries and where does it occur?

4.2 Estuarine Communities

4.2.1 Producer communities in estuaries

Estuarine primary producers include phytoplankton, benthic microalgae (diatoms and euglenoids on mudflats), submerged aquatic vegetation, saltmarsh grasses (e.g. Spartina in temperate systems; Paspalum vaginatum and Sporobolus virginicus in tropical West Africa), mangroves (the dominant macrophyte community in tropical estuaries), and epiphytic algae on mangrove roots. Phytoplankton productivity in estuaries is often light-limited due to high turbidity but is nutrient-rich; diatoms dominate in the water column.

Benthic microalgae on intertidal mudflats can achieve high productivity during emersion when light reaches the sediment surface. Mangroves are the most important structural producers in tropical estuaries; their leaf litter fuels the detrital food chain that supports the majority of estuarine secondary production. In Nigerian estuaries and the Niger Delta, mangrove forests of Rhizophora racemosa, Rhizophora harrisonii, and Avicennia germinans form the dominant vegetation along tidal creeks and river margins.

Fill in the blank: In tropical estuaries such as those of the Niger Delta, the dominant structural producers are ________, whose leaf litter forms the base of the detrital food chain that supports most estuarine secondary production.

4.2.2 Consumer communities: invertebrates and fish

Estuarine invertebrate communities are species-poor relative to fully marine or freshwater systems, reflecting the physiological stress of fluctuating salinity. Dominant benthic invertebrates include polychaete worms (e.g. Nereis, Capitella), bivalve molluscs (e.g. Crassostrea (oysters), Tellina, Corbula), gastropod molluscs (e.g. Tympanotonus fuscatus, the dominant mudskipper snail of West African mangroves), crustaceans (e.g. Uca (fiddler crabs), Sesarma (mangrove crabs), Penaeus (shrimp)), and insect larvae in upper estuarine zones.

Fish communities are characterised by euryhaline species tolerant of wide salinity ranges, and by the use of estuaries as nursery grounds. Common estuarine fish families in West Africa include Mugilidae (mullets), Cichlidae (e.g. Tilapia), Sparidae (sea breams), Sciaenidae (croakers), Ariidae (catfish), and Gobiidae (gobies). Many economically important marine species such as Ethmalosa fimbriata (bonga shad) and Chrysichthys species spend juvenile stages in estuaries before migrating offshore as adults. Mudskippers (Periophthalmus) are characteristic amphibious fish of mangrove mudflats.

Fill in the blank: Estuaries serve as ________ grounds for many commercially important marine fish, which spend their juvenile stages feeding and growing in estuaries before migrating offshore as adults.

4.2.3 Mangrove ecosystems

Mangroves are salt-tolerant trees and shrubs that form intertidal forests along sheltered tropical and subtropical coastlines. They are restricted to regions where mean winter temperature exceeds 20 degrees C, making them absent from temperate estuaries. In West Africa, the principal mangrove species are Rhizophora racemosa and R. harrisonii (red mangroves; dominate the seaward fringe; characterised by arching prop roots), Avicennia germinans (black mangrove; landward zones; characterised by pneumatophores), and Laguncularia racemosa (white mangrove; higher intertidal).

Mangrove ecosystems provide habitat and nursery areas for juvenile fish, shrimp, and crabs; roosting and nesting sites for waterbirds; and feeding grounds for mudskippers, molluscs, and crustaceans. They export large quantities of leaf litter and dissolved organic carbon to adjacent estuarine and coastal waters, fuelling detrital food webs. Root systems trap sediment, stabilise shorelines, and protect inland areas from wave energy and storm surge. Nigeria holds one of the largest mangrove areas in Africa, concentrated in the Niger Delta.

Fill in the blank: Rhizophora species (red mangroves) are characterised by arching ________ roots that anchor the tree in unstable intertidal sediment and provide attachment surfaces for oysters and other sessile organisms.

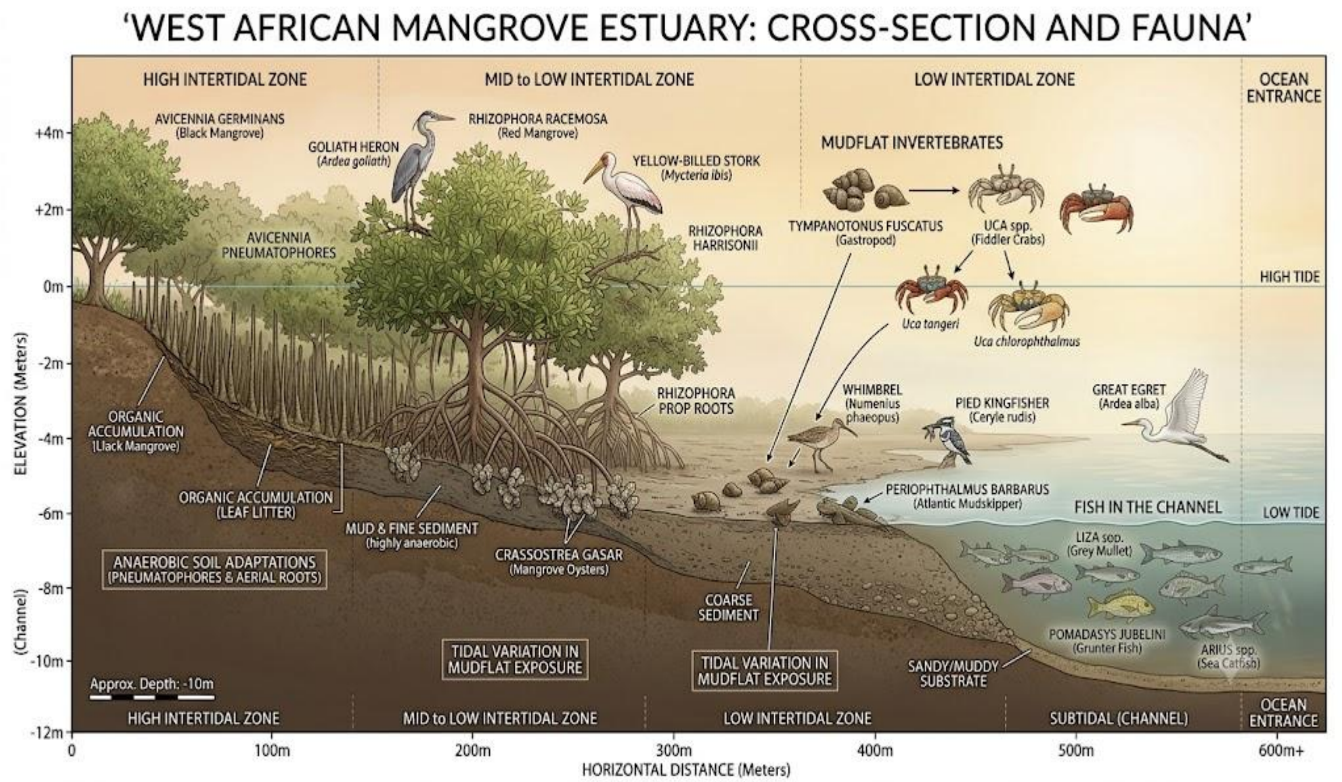

Figure 4.2: Cross-section of a West African mangrove-estuarine ecosystem showing key community components

Pilot questions 4.2

1. Name four types of primary producers found in estuaries.
2. Name three dominant mangrove species in West African estuaries and state one distinguishing feature of each.
3. State five ecological roles of mangrove ecosystems.
4. Name four benthic invertebrate groups found in estuaries and give one example of each.
5. Explain why estuarine fish communities are typically species-poor compared with fully marine communities.

4.3 Adaptive Features of Estuarine Organisms

4.3.1 Osmoregulation and ionic regulation

Osmoregulation is the ability to maintain internal body fluid osmolality (ion concentration) despite changes in external salinity. Estuarine animals are classified as osmoconformers or osmoregulators. Osmoconformers (e.g. many bivalves, some polychaetes) allow their internal osmolality to equilibrate with the surrounding medium; they tolerate wide salinity ranges by adjusting cell volume and organic solute content. Osmoregulators (e.g. fish, crustaceans such as Uca and Penaeus) maintain a relatively constant internal osmolality regardless of external salinity by actively pumping ions across gill epithelia.

Euryhaline fish such as mullet (Mugil) and tilapia regulate plasma osmolality through a dual strategy: in dilute water (low salinity) they produce copious dilute urine to expel excess water and actively absorb ions through gills; in concentrated seawater they drink water, absorb ions, and excrete salts through chloride cells in the gills. Compatible organic solutes (free amino acids, betaine, taurine) accumulate in the cells of many estuarine invertebrates, balancing osmotic pressure without disrupting enzyme function.

Fill in the blank: Animals that maintain a relatively constant internal osmolality by actively transporting ions across gill surfaces regardless of external salinity are called ________; examples include euryhaline fish such as mullet and crustaceans such as Penaeus.

4.3.2 Behavioural and morphological adaptations

Many estuarine invertebrates use behavioural strategies to avoid salinity extremes. Bivalves such as oysters (Crassostrea) close their valves at low tide to maintain a stable internal environment, a strategy called valve closure or isolation. Fiddler crabs (Uca) burrow into sediment during extreme low salinity or desiccation. Some polychaetes and nematodes migrate vertically within sediment to remain in preferred salinity layers. Fish migrate laterally to track their preferred salinity zone as tides and seasons shift the halocline position.

Morphological adaptations include thickened shells in intertidal bivalves to resist desiccation; the modified pectoral fins of mudskippers (Periophthalmus) used as crutches for locomotion on mudflats; the air-breathing ability of mudskippers using a highly vascularised buccal cavity and skin; strongly developed claws in Uca males used for display and burrow defence; and the flexible, root-gripping tubes of Polydora (polychaete) and attachment pads of barnacles for life on intertidal hard surfaces. These morphological features directly reflect the physical stresses of the intertidal estuarine habitat.

Fill in the blank: Mudskippers (Periophthalmus) breathe air using a highly vascularised ________ cavity and moist skin while out of water on mangrove mudflats; their modified pectoral fins function as crutches for terrestrial locomotion.

4.3.3 Adaptations of mangrove plants

Mangrove plants face three principal stresses: waterlogged, anoxic sediments; high salinity; and unstable, shifting substrate. Structural root adaptations address these stresses directly. Rhizophora develops arching prop roots (stilt roots) that anchor the tree across a wide base in unstable sediment and bear lenticels (pores) on their surface for gas exchange; the internal aerenchyma tissue channels oxygen to roots in anoxic mud. Avicennia germinans produces pneumatophores: vertical, pencil-like root projections that emerge above the sediment surface and carry lenticels for atmospheric oxygen uptake.

Salt management adaptations include: salt exclusion at the root (Rhizophora uses ultrafiltration to prevent salt entry); salt secretion through specialised leaf salt glands (Avicennia excretes salt crystals on leaf surfaces); and salt accumulation in older leaves before abscission. Leaves are thick, waxy, and succulent (xeromorphic) to reduce water loss despite the marine environment. Viviparous propagule production is a reproductive adaptation: seeds germinate on the parent tree, producing a propagule (seedling) that falls and rapidly roots on landing in the sediment, reducing the risk of propagule mortality in waterlogged or saline conditions.

Fill in the blank: Avicennia germinans manages salinity primarily by ________ salt through specialised glands on leaf surfaces, which can be seen as salt crystals on the leaves; it also produces pneumatophores for gas exchange in anoxic sediment.

Feature	**Rhizophora**	**Avicennia**
Root Type	Stilt (prop) roots for anchorage and stability in soft mud	Pneumatophores (vertical aerial roots) for gas exchange
Salt Management	Salt excluder: filters salt at root level, preventing entry	Salt secretor: excretes excess salt via specialized leaf glands
Leaf Characteristics	Thick, leathery leaves with waxy cuticle to reduce water loss	Grey-green leaves with salt crystals on surface; high salt tolerance

Reproductive Strategy	Vivipary: seeds germinate while attached to parent tree, producing propagules	Vivipary also occurs, but propagules are smaller and adapted for dispersal
Intertidal Zone Position	Seaward edge, tolerates frequent inundation	Landward edge, tolerates higher salinity and drier conditions

Box 4.1: Comparison of adaptive features of Rhizophora and Avicennia mangroves

Pilot questions 4.3

1. Distinguish between osmoconformers and osmoregulators and give one example of each.
2. Describe how a euryhaline fish such as mullet regulates its internal osmolality in both freshwater and seawater.
3. Describe three behavioural adaptations of estuarine invertebrates to fluctuating salinity.
4. Compare the root adaptations of Rhizophora and Avicennia mangroves.
5. Explain viviparous propagule production in mangroves and state its adaptive significance.

4.4 Importance and Threats to Estuarine Ecosystems

4.4.1 Ecological and economic importance of estuaries

Estuaries provide a suite of ecological services. They function as nursery grounds for a large proportion of commercially harvested marine fish and shrimp, which depend on estuarine productivity during juvenile stages. Estuaries support high bird diversity as feeding and roosting grounds for migratory and resident waterbirds. They process and filter large quantities of nutrients, suspended sediment, and organic matter flowing from river catchments before discharge to the sea, acting as biogeochemical buffers. Mangrove and saltmarsh vegetation in estuaries sequester significant quantities of carbon in their biomass and sediments (blue carbon).

Economic importance in Nigeria and West Africa: estuarine fisheries (artisanal and semi-commercial) provide protein and livelihoods for millions of coastal communities; mangrove timber is used for firewood and construction; tannins extracted from mangrove bark are used in leather processing; estuaries support aquaculture of shrimp, oysters, and catfish; and coastal tourism and traditional fishing culture have significant cultural and economic value. The Niger Delta estuarine system alone supports over 20 million people through fisheries and ecosystem services.

Fill in the blank: Estuaries act as biogeochemical ________ by trapping, processing, and transforming nutrients and suspended sediments that would otherwise flow unaltered from rivers into coastal seas, reducing their potential to cause coastal eutrophication.

4.4.2 Pollution and human impacts on estuaries

Estuaries are among the most heavily impacted aquatic ecosystems worldwide due to their proximity to human settlements and industrial activity. In the Niger Delta, crude oil spills from pipelines, well blowouts, and bunkering operations have caused severe mangrove mortality, sediment contamination with polycyclic aromatic hydrocarbons (PAHs), and collapse of estuarine fisheries in affected creeks. Oil coats pneumatophores and prop roots, blocking gas exchange and causing root suffocation. Bioaccumulation of petroleum hydrocarbons in shellfish and fish renders them unsafe for human consumption.

Other major threats include: mangrove deforestation for charcoal, timber, and urban expansion; sedimentation from deforestation in upstream catchments, which smothers intertidal habitats; coastal eutrophication from agricultural runoff causing hypoxic dead zones; heavy metal contamination from industrial discharge and artisanal gold mining upstream; plastic and solid waste pollution accumulating in mangrove root tangles; and over-exploitation of estuarine fisheries through fine-mesh netting and dynamite fishing. Upstream dam construction reduces freshwater inflow, shifts salinity gradients seaward, and traps sediment needed for delta maintenance.

Fill in the blank: Crude oil spills in the Niger Delta damage mangroves by coating ________ and prop roots, blocking atmospheric oxygen uptake and causing root suffocation and tree death, which leads to erosion of intertidal shorelines.

4.4.3 Conservation of estuarine ecosystems

Conservation of estuarine ecosystems requires integrated management at the catchment scale. Key strategies include: establishing marine protected areas (MPAs) and estuarine reserves that prohibit destructive fishing and habitat clearance; enforcing environmental regulations on oil companies and industrial discharges with meaningful penalties; mangrove reforestation programmes using locally sourced propagules; community-based fisheries management that limits effort and protects spawning and nursery areas; and regulation of upstream land use to reduce sediment and nutrient loading into estuaries. RAMSAR Convention designation of wetlands of international importance provides legal protection for critical estuarine habitats.

In Nigeria, the National Oil Spill Detection and Response Agency (NOSDRA) and the National Environmental Standards and Regulations Enforcement Agency (NESREA) have mandates covering estuarine protection, though enforcement has historically been weak. The Niger Delta Development Commission (NDDC) has funded some mangrove rehabilitation projects. Internationally, the Abidjan Convention provides a framework for cooperative management of the West and Central African marine environment, including estuaries. Monitoring programmes tracking water quality, fisheries landings, and mangrove cover are essential for adaptive management.

Fill in the blank: The international convention that designates wetlands of international importance and provides them with legal protection from destruction and degradation is the ________ Convention; it is a key instrument for estuarine conservation globally.

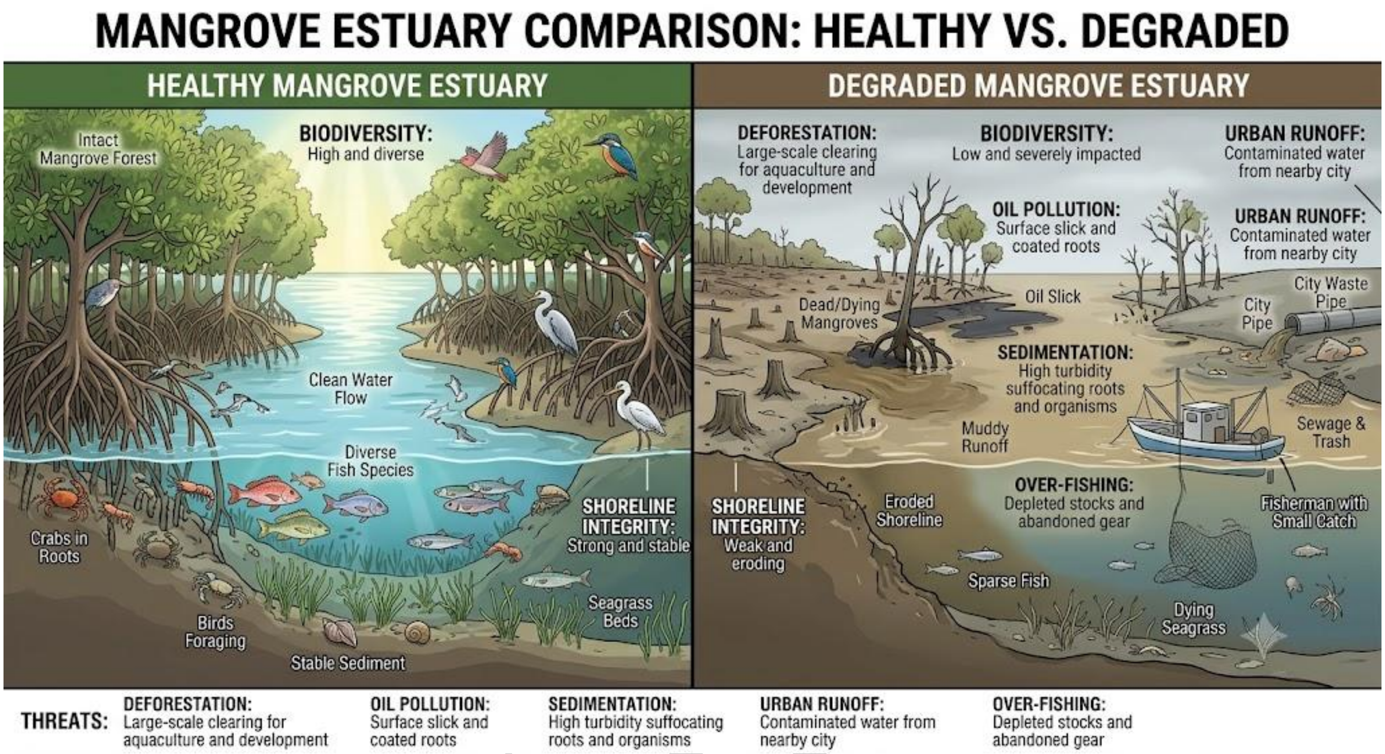

Figure 4.3: Comparison of a healthy and a degraded mangrove estuary showing major anthropogenic threats

Pilot questions 4.4

1. State five ecological services provided by estuarine ecosystems.
2. Describe four ways in which crude oil pollution damages estuarine ecosystems in the Niger Delta.
3. Explain how upstream dam construction affects estuaries downstream.
4. State four strategies for conserving estuarine and mangrove ecosystems.
5. State the economic importance of estuaries to coastal communities in Nigeria.

Series Summary

Estuaries are semi-enclosed coastal bodies where freshwater meets seawater, producing salinity gradients classified by the Venice system (limnetic to euhaline). They are formed as coastal plain, bar-built, tectonic, or fjord types, and may be stratified, partially mixed, or well-mixed. Physical dynamics are dominated by tidal action and seasonal river discharge, driving gravitational circulation and generating a turbidity maximum at the mixing zone. Chemical conditions are characterised by variable salinity, turbidity, nutrient richness, and episodic dissolved oxygen depletion.

Estuarine communities include phytoplankton, benthic microalgae, mangroves (Rhizophora, Avicennia), invertebrates (polychaetes, bivalves, crustaceans, gastropods), and euryhaline fish. Mangroves are the key structural producers in tropical systems, providing habitat, nursery areas, and carbon export. Adaptive features of estuarine organisms include osmoregulation (ion pumping in fish and crustaceans), osmoconformity with compatible solutes (invertebrates), valve closure, burrowing, and migration (behavioural); and morphological specialisations such as mudskipper fins and buccal breathing. Mangroves adapt via prop roots, pneumatophores, salt exclusion or secretion, xeromorphic leaves, and viviparous propagules. Estuaries are ecologically and economically vital but are severely threatened by oil pollution, deforestation, eutrophication, over-fishing, and sedimentation, requiring integrated catchment-scale conservation.

Glossary of Terms

- **Aerenchyma:** spongy plant tissue containing large air spaces that conduct oxygen from aerial parts to roots in waterlogged sediments; present in mangrove roots.
- **Blue carbon:** carbon sequestered by coastal and marine ecosystems, particularly mangroves, saltmarshes, and seagrasses, in their biomass and sediments; important for climate mitigation.
- **Euryhaline:** describing an organism capable of tolerating a wide range of salinities; a key characteristic of most estuarine animals.
- **Estuary:** a semi-enclosed coastal water body with a free connection to the open sea in which seawater is measurably diluted by freshwater derived from land drainage (Pritchard, 1967).
- **Gravitational circulation:** the two-layer estuarine flow pattern in which denser saline water intrudes upstream along the bottom and lighter freshwater flows seaward at the surface; drives nutrient import and organic export.
- **Halocline:** a layer in a water body where salinity changes rapidly with depth; separates freshwater and saline layers in stratified estuaries.

- **Hypersaline:** describing water with salinity greater than 35 psu (greater than standard seawater); occurs in tropical estuaries during dry seasons when evaporation exceeds freshwater input.
- **Lenticel:** a pore on the bark or root surface of a plant that allows gas exchange; present on mangrove prop roots and pneumatophores to facilitate oxygen uptake in waterlogged sediment.
- **Mangrove:** a salt-tolerant tree or shrub forming intertidal forests in tropical and subtropical estuaries and sheltered coastlines; characterised by specialised root systems, salt tolerance mechanisms, and viviparous reproduction.
- **Osmoconformer:** an organism that allows its internal osmolality to change with external salinity rather than regulating it; tolerates a range of salinities by adjusting cell volume and compatible solutes.
- **Osmoregulator:** an organism that maintains a relatively constant internal osmolality regardless of external salinity by actively transporting ions across gill epithelia or body surfaces.
- **Pneumatophore:** an aerial root projection that grows vertically out of waterlogged sediment in Avicennia mangroves; carries lenticels for atmospheric oxygen uptake to support root respiration in anoxic mud.
- **Prop root:** an arching aerial root of Rhizophora mangroves that descends from the trunk and branches into the sediment, providing structural support in unstable intertidal mud and bearing lenticels for gas exchange.
- **Turbidity maximum:** a zone of elevated suspended sediment concentration that forms near the freshwater-saltwater mixing front in estuaries due to flocculation of clay particles as salinity increases.
- **Venice system:** the international classification of estuarine salinity zones into five categories: limnetic (0 to 0.5 psu), oligohaline (0.5 to 5), mesohaline (5 to 18), polyhaline (18 to 30), and euhaline (30 to 40 psu).
- **Viviparous propagule:** a seedling that germinates on the parent mangrove tree before dispersal; it drops from the parent and rapidly roots in the intertidal sediment, improving survival in waterlogged or saline conditions.
- **Xeromorphic:** describing plant structures adapted to reduce water loss, including thick, waxy cuticles, sunken stomata, and succulent leaf tissue; present in mangrove leaves despite their marine-adjacent habitat.

Concept Check Questions [Series 4]

Objective Questions

6. An estuary formed when sea-level rise floods a river valley is called a ________ estuary. (Linked to SLO 4.1)
7. The Venice system classifies the salinity zone of 5 to 18 psu as ________. (Linked to SLO 4.1)
8. Animals that maintain a constant internal osmolality by actively pumping ions across gill surfaces are called ________. (Linked to SLO 4.3)
9. Avicennia germinans produces vertical root projections called ________ for gas exchange in anoxic sediment. (Linked to SLO 4.4)
10. Carbon sequestered in mangrove biomass and sediments is termed ________ carbon. (Linked to SLO 4.5)

Short-Answer Questions

11. Define an estuary and name four types classified by geomorphology. (Linked to SLO 4.1)
12. Explain gravitational circulation and state its importance in estuarine ecology. (Linked to SLO 4.1)
13. Distinguish between the root systems of Rhizophora and Avicennia and explain the function of each. (Linked to SLO 4.4)
14. State five ecological and economic roles of estuaries in Nigeria. (Linked to SLO 4.5)
15. Name four major threats to estuarine ecosystems in the Niger Delta and suggest one conservation response to each. (Linked to SLO 4.6)

Long-Answer Questions

14. Describe the physical and chemical characteristics of estuaries, including salinity classification, mixing types, and physical dynamics. (Linked to SLO 4.1)
15. Describe the biological communities of tropical estuaries and explain the structural and physiological adaptations of mangroves and estuarine animals to the estuarine environment. (Linked to SLOs 4.2, 4.3, 4.4)
16. Discuss the ecological and economic importance of estuarine ecosystems, identify the major threats they face in Nigeria, and outline a conservation strategy for their sustainable management. (Linked to SLOs 4.5, 4.6)

Answers to Concept Check Questions [Series 4]

Objective Questions

1. Coastal plain (drowned river valley).
2. Mesohaline.
3. Osmoregulators.
4. Pneumatophores.
5. Blue.

Short-Answer Questions

1. Estuary: a semi-enclosed coastal water body with a free connection to the sea where seawater is diluted by freshwater from land drainage. Four types by geomorphology: coastal plain (drowned river valley; e.g. Niger Delta); bar-built (lagoon behind sandbar; e.g. Lagos Lagoon); tectonic (formed by faulting or subsidence); fjord (glacially scoured; rare in tropics).
2. Gravitational circulation: denser saline bottom water flows upstream; lighter freshwater flows seaward at the surface. Importance: transports marine nutrients landward, fuelling estuarine productivity; exports organic matter seaward to coastal seas; drives sediment trapping and turbidity maximum formation near the mixing front.
3. Rhizophora: arching prop (stilt) roots that arise from trunk and branches and descend into sediment; provide structural support in unstable mud; bear lenticels for gas exchange; house internal aerenchyma to deliver oxygen to roots. Avicennia: pencil-like pneumatophores that project vertically out of sediment; bear lenticels on exposed surfaces; allow atmospheric oxygen to diffuse to roots in anoxic mud.
4. Nursery grounds for commercially important marine fish and shrimp; artisanal fisheries providing protein and income; mangrove timber for firewood and construction; shoreline stabilisation and coastal protection; carbon sequestration (blue carbon); tannins from mangrove bark for leather processing; aquaculture of shrimp and oysters; waterbird habitat and biodiversity conservation.
5. Oil pollution (response: enforce regulations; mandatory clean-up; independent monitoring); mangrove deforestation (response: reforestation programmes; community-based management); over-fishing (response: MPAs; mesh size regulations; seasonal closures); sedimentation from upstream deforestation (response: catchment reforestation; sediment control measures).

Long-Answer Questions

1. Definition: semi-enclosed coastal body where freshwater dilutes seawater. Types: coastal plain (drowned valley), bar-built (lagoon), tectonic, fjord. Salinity zones (Venice system): limnetic (0 to 0.5), oligohaline (0.5 to 5), mesohaline (5 to 18), polyhaline (18 to 30), euhaline (30 to 40 psu). Mixing types: stratified (strong river flow; sharp halocline; freshwater wedge over saltwater); partially mixed (intermediate; common in Niger Delta); well-mixed (strong tides; salinity uniform vertically). Physical dynamics: semi-diurnal tides drive mixing; seasonal river discharge shifts halocline position; gravitational circulation (saline bottom inflow; freshwater surface outflow); turbidity maximum at mixing front due to flocculation; wind and wave mixing; intertidal mudflat zonation from tidal exposure. Chemical factors: variable dissolved oxygen (high BOD; bottom anoxia in stratified systems); nutrient-rich from river inputs; high turbidity; pH buffered by marine carbonate system; possible hypersalinity in dry season.
2. Communities: producers (phytoplankton; benthic microalgae; mangroves; saltmarsh grasses); invertebrates (polychaetes, Crassostrea oysters, Tympanotonus snails, Uca crabs, Penaeus shrimp, Sesarma crabs); fish (mullet, tilapia, bonga shad, catfish, gobies, mudskippers). Mangrove adaptations: Rhizophora (prop roots for support; lenticels and aerenchyma for gas exchange; salt exclusion at roots; xeromorphic leaves; viviparous propagules); Avicennia (pneumatophores for gas exchange; salt secretion glands on leaves; viviparous propagules). Animal adaptations: osmoregulators (fish, crustaceans; ion pumping at gills; in freshwater produce dilute urine, absorb ions; in seawater drink water, excrete salts via chloride cells); osmoconformers (bivalves, some polychaetes; adjust cell volume and compatible solutes); behavioural (valve closure in oysters; burrowing in Uca; vertical migration in polychaetes; lateral migration in fish); morphological (mudskipper modified fins and buccal breathing; thickened shells; barnacle attachment pads).
3. Ecological importance: nursery for marine fish and shrimp; biogeochemical buffer (nutrient and sediment processing); blue carbon sequestration; waterbird habitat; biodiversity hotspot; shoreline protection. Economic importance: artisanal fisheries (protein and income); aquaculture; timber and tannins; coastal protection reducing storm damage costs; tourism. Major threats: oil spills (coat roots; cause mangrove death; contaminate shellfish); deforestation (charcoal, urban expansion; removes nursery habitat); eutrophication from agricultural runoff (hypoxia; bloom formation); over-fishing (destructive gear; juvenile capture); dam construction upstream (reduced freshwater flow; halocline shifts; sediment trapping). Conservation strategy: establish MPAs and estuarine reserves; enforce oil company regulations with meaningful penalties; RAMSAR designation; mangrove reforestation with

local propagules; community-based fisheries management with seasonal closures; catchment-scale sediment and nutrient control; regular monitoring of water quality, biodiversity, and mangrove cover.

Answers to Pilot Questions [Series 4]

Part 4.1

1. Estuary: a semi-enclosed coastal water body with a free connection to the sea in which seawater is measurably diluted by freshwater derived from land drainage. Four types: coastal plain (drowned river valley); bar-built (lagoon behind sandbar); tectonic (faulting or subsidence); fjord (glacially scoured).
2. Venice system salinity zones: limnetic (0 to 0.5 psu); oligohaline (0.5 to 5 psu); mesohaline (5 to 18 psu); polyhaline (18 to 30 psu); euhaline (30 to 40 psu).
3. Stratified: strong river flow creates a sharp halocline; freshwater overlies saltwater with minimal mixing. Partially mixed: intermediate river and tidal forces produce some vertical mixing but stratification persists. Well-mixed: strong tidal stirring homogenises salinity from surface to bottom; no halocline.
4. Gravitational circulation: denser saline bottom water moves upstream while lighter freshwater flows seaward at the surface. Ecological significance: imports marine nutrients landward, sustaining estuarine productivity; exports organic matter seaward; drives turbidity maximum formation; transports larvae and propagules.
5. The turbidity maximum forms at the freshwater-saltwater mixing front where rising salinity causes clay particles to flocculate (aggregate) and settle. It occurs near the halocline, where the density difference between the two water masses reduces turbulence and promotes particle deposition. This zone is mobile, shifting seaward during high river flow and landward during the dry season.

Part 4.2

1. Phytoplankton; benthic microalgae (diatoms and euglenoids on mudflats); mangroves (structural producers); saltmarsh grasses (Paspalum vaginatum).
2. Rhizophora racemosa: arching prop roots; dominates seaward fringe. Avicennia germinans: pencil-like pneumatophores; occupies landward zones; secretes salt on leaves. Laguncularia racemosa (white mangrove): higher intertidal position; less conspicuous root adaptations.

3. Nursery habitat for juvenile fish, shrimp, and crabs; roosting and nesting sites for waterbirds; leaf litter export fuelling detrital food webs; shoreline stabilisation and sediment trapping by root systems; storm and wave protection of inland areas; carbon sequestration in biomass and sediment; attachment substrate for oysters and other sessile invertebrates.
4. Polychaetes (Nereis); bivalves (Crassostrea, oysters); gastropods (Tympanotonus fuscatus); crustaceans (Uca, fiddler crabs).
5. Fluctuating salinity imposes severe physiological stress, excluding most marine stenohaline species; only euryhaline species capable of osmoregulation or osmoconformity across a wide salinity range can survive. This physiological filter reduces species richness relative to fully marine or fully freshwater environments.

Part 4.3

1. Osmoconformers allow their internal osmolality to match the surrounding medium and tolerate salinity change by adjusting cell volume and compatible solutes; example: oysters (Crassostrea). Osmoregulators maintain a constant internal osmolality by active ion transport across gill epithelia regardless of external salinity; example: mullet (Mugil), Penaeus shrimp.
2. In freshwater (low salinity): produces copious dilute urine to expel excess water entering by osmosis; actively absorbs ions through gill chloride cells to maintain plasma ion levels. In seawater (high salinity): drinks water to compensate osmotic water loss; absorbs ions from ingested water across the intestine; excretes excess salt ions through chloride cells in the gills; produces small volumes of concentrated urine.
3. Valve closure (oysters close shells at low tide to maintain stable internal environment); burrowing into sediment during salinity extremes or desiccation (Uca); vertical migration within sediment to remain in preferred salinity layer (polychaetes and nematodes).
4. Rhizophora: arching prop roots descend from trunk and branches into unstable sediment, providing structural support; root surface bears lenticels for atmospheric oxygen diffusion; internal aerenchyma channels oxygen to roots in anoxic mud. Avicennia: pencil-like pneumatophores project vertically from sediment surface; bear lenticels that open during emersion for oxygen uptake; allow root respiration in permanently waterlogged, anoxic mud.
5. Viviparous propagule: the seed germinates on the parent tree before dispersal, producing an elongated seedling (propagule) with a developed root tip. When it falls, it rapidly pierces the sediment and roots immediately. Adaptive significance: bypasses the vulnerable seed and early germination stage in waterlogged or saline conditions; the seedling arrives pre-germinated and ready to establish, greatly improving survival rate in the difficult intertidal environment.

Part 4.4

1. Nursery grounds for marine fish and shrimp; waterbird feeding and roosting habitat; biogeochemical buffering (nutrient and sediment processing); blue carbon sequestration; shoreline protection from wave energy and storm surge; biodiversity reservoir for estuarine and coastal species.
2. Oil coats pneumatophores and prop roots, blocking gas exchange causing root suffocation and mangrove death; sediment contamination with PAHs persists for decades, preventing recolonisation; bioaccumulation of petroleum hydrocarbons in shellfish and fish makes them unfit for human consumption; collapse of estuarine fisheries in oil-affected creeks deprives communities of food and income.
3. Dams trap sediment, reducing the supply of sand and silt that maintains deltas and intertidal flats; reduced freshwater discharge shifts salinity gradients seaward, stressing organisms adapted to a particular salinity zone; altered seasonal flood pulses disrupt breeding cycles of fish and invertebrates that depend on seasonal salinity change; reduced river nutrient inputs lower estuarine primary productivity.
4. Establish marine protected areas and estuarine reserves prohibiting destructive fishing and habitat clearance; enforce oil pollution regulations with mandatory clean-up and meaningful penalties; implement mangrove reforestation using locally sourced propagules; introduce community-based fisheries management with mesh size limits and seasonal closures; RAMSAR Convention designation for critical estuarine wetlands; catchment-scale land use regulation to reduce sediment and nutrient loading.
5. Artisanal fisheries providing protein and daily income for coastal families; mangrove timber for firewood and building materials; tannins from Rhizophora bark used in leather processing; aquaculture of shrimp, oysters, and catfish in estuarine pens; coastal protection reducing infrastructure damage from storms and erosion; cultural and subsistence value of estuarine resources to over 20 million Niger Delta inhabitants.

References and Attributions [Series 4]

Textual References (Books and External Sources)

- Day, J. W., Hall, C. A. S., Kemp, W. M., & Yañez-Arancibia, A. (1989). Estuarine ecology. Wiley.
- Alongi, D. M. (1998). Coastal ecosystem processes. CRC Press.
- Nybakken, J. W., & Bertness, M. D. (2005). Marine biology: An ecological approach (6th ed.). Pearson Benjamin Cummings.
- Ekwueme, B. N., & Nwankwo, D. I. (2017). Phytoplankton composition in estuaries of the Niger Delta. Journal of Aquatic Sciences, 32(1), 45–60.

Figures, Plates, Tables, and Boxes

- Figure 4.1: Longitudinal section of a partially mixed estuary. Attribution: AI generated. Suggested OER search string: “estuary cross section salinity zones gravitational circulation turbidity maximum diagram OER”.
- Figure 4.2: Cross-section of a West African mangrove-estuarine ecosystem. Attribution: AI generated. Suggested OER search string: “mangrove estuarine ecosystem West Africa cross section communities Rhizophora Avicennia fish invertebrates OER”.
- Box 4.1: Comparison of adaptive features of Rhizophora and Avicennia mangroves. Attribution: AI generated. Suggested OER search string: “Rhizophora Avicennia mangrove adaptations comparison prop roots pneumatophores salt exclusion secretion OER”.
- Figure 4.3: Comparison of a healthy and a degraded mangrove estuary. Attribution: AI generated. Suggested OER search string: “mangrove estuary threats degradation oil spill deforestation sedimentation conservation diagram OER”.

Course code: BIO 206

Course title: Hydrobiology

Course credit load: 2 Units

Series 5: Colonisation, Succession, and Interrelationships in Aquatic Systems

- **Part 5.1: Colonisation in Aquatic Ecosystems**
  - Sub Part 5.1.1: Concepts and mechanisms of aquatic colonisation
  - Sub Part 5.1.2: Pioneer species and early colonisers
  - Sub Part 5.1.3: Factors influencing colonisation success
- **Part 5.2: Ecological Succession in Aquatic Systems**
  - Sub Part 5.2.1: Primary and secondary succession in freshwater
  - Sub Part 5.2.2: Hydrosere: succession from open water to terrestrial vegetation
  - Sub Part 5.2.3: Succession in marine and estuarine habitats
- **Part 5.3: Biological Interrelationships in Aquatic Systems**
  - Sub Part 5.3.1: Predation, competition, and herbivory
  - Sub Part 5.3.2: Symbiosis, parasitism, and mutualism
  - Sub Part 5.3.3: Keystone species and trophic cascades
- **Part 5.4: Disturbance, Resilience, and Applied Ecology**
  - Sub Part 5.4.1: Disturbance ecology and the intermediate disturbance hypothesis
  - Sub Part 5.4.2: Resilience, resistance, and ecological recovery
  - Sub Part 5.4.3: Applications: biomonitoring and ecological restoration

Introduction

Aquatic ecosystems are not static; they are continuously shaped by the arrival of new species, the progressive replacement of communities over time, and the complex interactions among organisms that co-exist within them. Colonisation is the process by which organisms first establish themselves in a habitat, setting the conditions for subsequent ecological succession. Succession describes the orderly, directional change in community structure over time, driven by the physical environment and by the organisms themselves. Together, colonisation and succession explain how new water bodies develop biological communities and how disturbed systems recover.

This Series integrates these processes with the biological interrelationships, including predation, competition, symbiosis, and parasitism, that structure aquatic communities. It also examines the role of disturbance in maintaining diversity, the capacity of aquatic systems to recover from perturbation, and the practical applications of ecological knowledge in biomonitoring and restoration. The concepts covered here synthesise the whole course and provide a framework for understanding and managing aquatic ecosystems in Nigeria and globally.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 5.1** explain the mechanisms of aquatic colonisation, describe pioneer species, and identify factors that influence colonisation success (Linked to Part 5.1),
- **SLO 5.2** distinguish between primary and secondary succession, describe the hydrosere, and explain succession in marine and estuarine habitats (Linked to Part 5.2),
- **SLO 5.3** describe and give examples of predation, competition, herbivory, symbiosis, parasitism, and mutualism in aquatic ecosystems (Linked to Part 5.3),
- **SLO 5.4** explain the concept of keystone species and describe trophic cascades with aquatic examples (Linked to Part 5.3),

- **SLO 5.5** explain the intermediate disturbance hypothesis and distinguish between resilience and resistance in aquatic systems (Linked to Part 5.4), and
- **SLO 5.6** describe the use of biological indicators in biomonitoring and explain the principles of ecological restoration of aquatic systems (Linked to Part 5.4).

5.1 Colonisation in Aquatic Ecosystems

5.1.1 Concepts and mechanisms of aquatic colonisation

Colonisation is the process by which organisms disperse to and establish viable populations in a previously unoccupied or cleared habitat. In aquatic ecosystems, new habitats are created by volcanic eruption (e.g. crater lakes), dam impoundment, quarry flooding, newly formed river oxbow lakes, and coastal accretion. Dispersal mechanisms include: wind transport of algal spores and resting stages; waterfowl and other birds carrying propagules on feathers, feet, and in gut contents; passive drift of planktonic organisms via currents; active swimming of fish and mobile invertebrates; and human-mediated transfer through ballast water or fish stocking.

The rate and sequence of colonisation depend on the dispersal ability of organisms, the distance from source populations, the size and connectivity of the new habitat, and the suitability of abiotic conditions. In newly impounded Nigerian reservoirs such as Kainji (1968) and Jebba (1984), fish communities were established within a few years by immigration from the parent river system and deliberate stocking, while phytoplankton and zooplankton communities assembled even faster from waterborne inocula.

Fill in the blank: Colonisation of new aquatic habitats by phytoplankton and zooplankton occurs rapidly through passive dispersal via ________, wind, and transport by waterbirds, while fish colonise primarily by active migration and deliberate stocking.

5.1.2 Pioneer species and early colonisers

Pioneer species are the first organisms to colonise a new or disturbed habitat. In open water, phytoplankton (particularly small chlorophytes and cyanobacteria) are the earliest primary producers, establishing the photosynthetic base within days of water body formation. On bare rock or sediment surfaces, pioneer biofilms of bacteria, diatoms, and cyanobacteria form within weeks, creating a nutrient-rich substrate that facilitates attachment by invertebrates and later macrophytes. In streams recovering from disturbance, periphyton and algal crusts pioneer bare substrate before invertebrate colonisation.

Pioneer invertebrates in freshwater include chironomid (midge) larvae and oligochaete worms, which tolerate low dissolved oxygen and high organic matter and colonise soft sediments early. Rotifers and small cladocerans are early pelagic colonisers in the water column. Pioneer fish in newly formed lakes are typically small, opportunistic species such as cyprinids and cichlids that can tolerate fluctuating conditions and breed rapidly. Pioneer species share characteristics of rapid reproduction (r-selected strategy), broad environmental tolerance, and effective dispersal.

Fill in the blank: Pioneer species share three key characteristics: broad environmental tolerance, effective dispersal ability, and rapid ________ (r-selected reproductive strategy), which allows them to establish populations quickly in newly available habitats.

5.1.3 Factors influencing colonisation success

Colonisation success depends on a combination of abiotic and biotic factors. Abiotic factors include water temperature, dissolved oxygen, pH, salinity, substrate type, light availability, and nutrient concentration. A habitat must fall within the physiological tolerance range of a colonising species before establishment is possible. Habitat connectivity to source populations is critical: isolated water bodies such as crater lakes or remote floodplain pools receive fewer propagules and colonise more slowly than well-connected rivers or reservoir systems.

Biotic factors include competition from already-established species, predation pressure on arriving colonisers, availability of food resources, and the presence of mutualists (e.g. mycorrhiza-like associations in some aquatic plants). The priority effect refers to the advantage held by species that arrive first; early colonisers can modify the habitat and suppress later arrivals through competitive exclusion or by physically occupying space and resources. Invasive species such as the water hyacinth (Eichhornia crassipes) demonstrate powerful priority effects by rapidly excluding native colonisers once established.

Fill in the blank: The advantage that early-arriving species hold over later colonisers by pre-empting resources or modifying the habitat to their own benefit is called the ________ effect; it helps explain why invasive species are so difficult to displace once they have established.

Pilot questions 5.1

1. Define colonisation and name four mechanisms by which organisms disperse to new aquatic habitats.
2. State three characteristics of pioneer species and give one example of a pioneer species in freshwater.
3. Explain the priority effect and describe how it influences the colonisation of a newly formed lake.
4. State four abiotic factors that determine whether a colonising species can successfully establish in a new habitat.
5. Describe how fish communities were established in Nigerian reservoirs such as Kainji after impoundment.

5.2 Ecological Succession in Aquatic Systems

5.2.1 Primary and secondary succession in freshwater

Ecological succession is the directional, non-seasonal change in the species composition of a community over time. Primary succession occurs in habitats with no prior biological legacy: bare rock, newly formed volcanic lakes, or freshly exposed glacial basins. It begins with pioneer biofilms and progresses through a series of seral stages, each community modifying the habitat in ways that facilitate the next, until a relatively stable climax community is reached. Primary succession is slow, often taking decades to centuries in aquatic habitats.

Secondary succession occurs after a disturbance removes part or all of an existing community but leaves the soil, sediment, or substrate and seed/spore bank intact. Examples include recovery of a pond after dredging, recovery of a river reach after a flood or pollution event, or recolonisation of a floodplain pool after seasonal drying. Secondary succession is faster than primary succession because the substrate already contains organic matter, nutrients, and viable propagules. In both types, community species richness and structural complexity generally increase over time until the climax state.

Fill in the blank: ________ succession occurs after a disturbance removes an existing community but leaves the substrate, organic matter, and propagule bank intact; it proceeds more rapidly than primary succession because conditions for growth are already present.

5.2.2 Hydrosere: succession from open water to terrestrial vegetation

The hydrosere is the successional sequence that begins in open water and progresses through a series of aquatic and semi-aquatic seral stages toward a terrestrial climax community. It proceeds as follows in a typical freshwater lake. Stage 1: open deep water, colonised by phytoplankton and submerged macrophytes (e.g. Ceratophyllum, Potamogeton) in shallow margins. Stage 2: sediment accumulation from organic deposition and inorganic silt raises the lake bed; floating-leaved plants (e.g. Nymphaea) colonise shallower zones. Stage 3: emergent macrophytes (e.g. Typha, Phragmites) establish as the margin fills further, forming a reed swamp.

Stage 4: decomposition of reed litter raises the substrate above the water table; sedge and rush communities replace reeds, forming a fen or swamp meadow. Stage 5: woody shrubs (e.g. Alchornea, Raphia palm in tropical Africa) colonise as the soil dries further. Stage 6: a climax woodland or forest establishes, completing the succession from open water to terrestrial vegetation. In tropical West Africa, the entire hydrosere may be compressed or modified by seasonal flooding, fire, and human land use, resulting in persistent semi-aquatic communities rather than a forested climax.

Fill in the blank: In the hydrosere, emergent macrophytes such as Typha and Phragmites colonise at Stage 3 to form a ________ swamp; their litter accumulates and raises the substrate, allowing sedge and rush communities to establish in Stage 4.

5.2.3 Succession in marine and estuarine habitats

On intertidal rocky shores, primary succession is well documented. Bare rock is first colonised by bacterial and diatom biofilms, followed by epilithic microalgae, then barnacles (Chthamalus, Semibalanus) and limpets that graze the biofilm. Mussels (Mytilus, Perna) colonise next and can dominate space, creating a biogenic habitat used by whelks, starfish, polychaetes, and small crustaceans. On moderately exposed shores, fucoid algae (Fucus, Ascophyllum) eventually establish and form a canopy community. The final successional stage on rocky shores is typically a mixed algal-invertebrate community regulated by grazing and wave action rather than a single climax.

In estuarine mudflats, succession begins with bacterial mats and benthic diatom biofilms on bare sediment, followed by colonisation by polychaetes and bivalves that stabilise the sediment. Saltmarsh grasses or mangroves (in the tropics) then establish as sediment accretion raises the surface above low-tide level. In tropical West African estuaries, mangrove succession follows a seaward-to-landward sequence: Rhizophora colonises pioneer mudflats at the seaward fringe; as sediment builds up, Avicennia and Laguncularia occupy higher intertidal positions; ultimately terrestrial forest replaces mangrove on the highest ground.

Fill in the blank: In tropical estuarine succession, ________ (red mangrove) colonises the seaward pioneer mudflat first; as sediment accumulates and the surface rises, Avicennia and Laguncularia succeed it in higher intertidal zones.

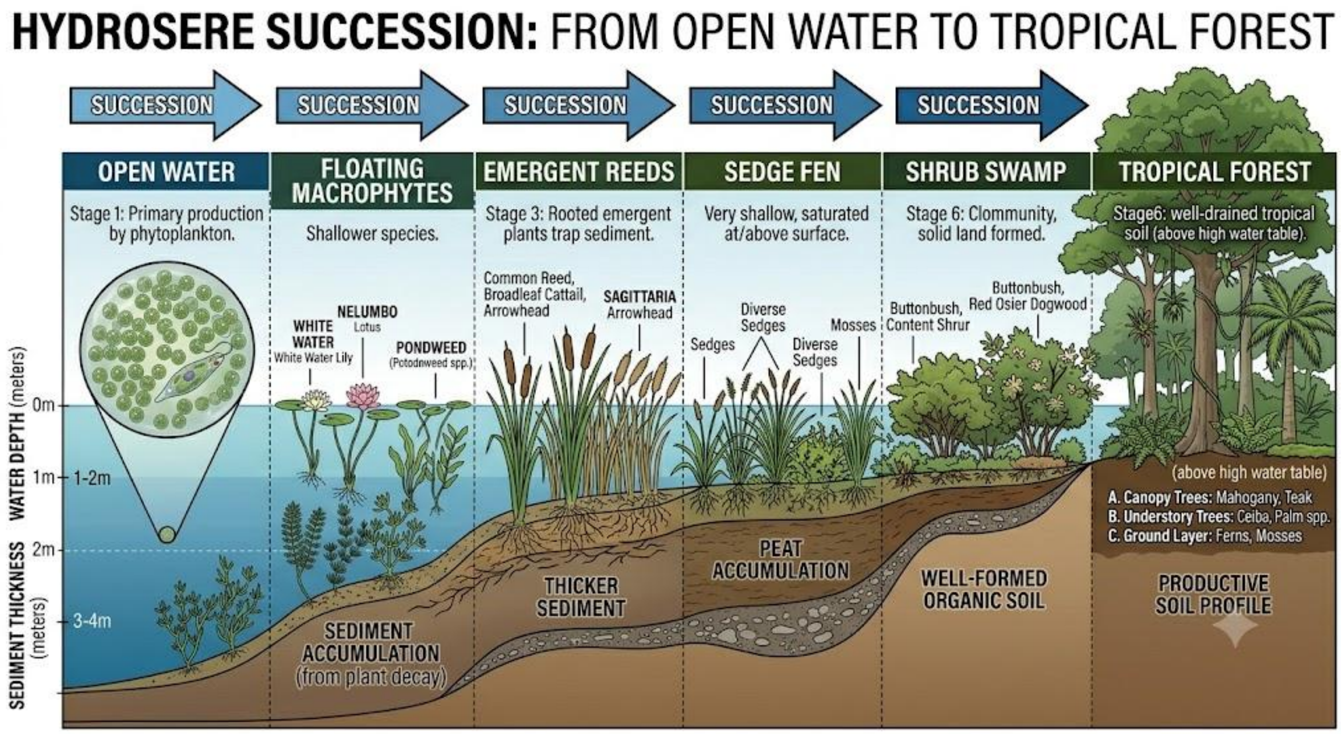

Figure 5.1: The hydrosere showing six seral stages from open water to tropical riverine forest

Pilot questions 5.2

1. Distinguish between primary and secondary succession and give one aquatic example of each.
2. Describe the six seral stages of the hydrosere in order.
3. Explain why secondary succession proceeds more rapidly than primary succession.
4. Describe the sequence of mangrove succession on a West African estuarine mudflat from pioneer to climax stage.
5. What is a climax community and why may it never be reached in tropical African freshwater systems?

5.3 Biological Interrelationships in Aquatic Systems

5.3.1 Predation, competition, and herbivory

Predation is a interaction in which one organism (the predator) kills and consumes another (the prey). In freshwater, predation structures community composition at all trophic levels:

piscivorous fish (e.g. Lates niloticus, Hydrocynus) control planktivore abundance; planktivorous fish (e.g. tilapia, sardines) regulate zooplankton body size; invertebrate predators such as dragonfly larvae (Anisoptera), Chaoborus larvae, and predatory copepods (Cyclops) control smaller invertebrates and larvae. Predation promotes prey adaptations including schooling behaviour, diel vertical migration, transparency, spines (Daphnia), and chemical defences.

Competition occurs when two or more species use the same limiting resource. Interspecific competition in aquatic systems includes: phytoplankton species competing for phosphorus, nitrogen, and light in stratified lakes; macrophytes competing with phytoplankton for nutrients and light; benthic invertebrates competing for space on hard substrates; and fish competing for food and territory. Herbivory is a form of predation on plants or algae: zooplankton grazing on phytoplankton, aquatic insects grazing periphyton in streams, and hippopotami grazing aquatic macrophytes along African river margins are all examples. Heavy herbivory can suppress primary production and alter community structure.

Fill in the blank: Planktivorous fish exert top-down control on zooplankton by selectively removing large-bodied ________ such as Daphnia, shifting zooplankton communities toward smaller, less-visible species such as rotifers and small copepods.

5.3.2 Symbiosis, parasitism, and mutualism

Symbiosis is any close, long-term association between two species. Parasitism is a symbiotic relationship in which the parasite benefits at the expense of the host. Aquatic parasites include: monogenean trematodes (gill flukes) on fish gills; digenean trematodes using snails and fish as intermediate hosts (e.g. Schistosoma mansoni with Biomphalaria snails as intermediate hosts in West African freshwaters); fish lice (Argulus); anchor worms (Lernaea); fungal infections (Saprolegnia on fish and eggs); and microsporidian parasites of copepods and cladocerans. Parasitism affects host fitness, growth, reproduction, and survival, and can regulate host population size.

Mutualism is a symbiosis in which both partners benefit. Aquatic examples include: nitrogen-fixing cyanobacteria (Anabaena) living within cells of the water fern Azolla, providing fixed nitrogen to the plant in return for photosynthate; mycorrhiza-like associations of fungi with the roots of aquatic plants aiding phosphorus uptake; cleaner fish (e.g. wrasse species) that remove ectoparasites from larger fish, benefiting both; and gut bacteria of fish and invertebrates that aid digestion of cellulose and other complex molecules. Commensalism, where one species benefits and the other is neither helped nor harmed, is seen in epibionts growing on turtle shells or crab carapaces.

Fill in the blank: The water fern Azolla benefits from a mutualistic relationship with the nitrogen-fixing cyanobacterium ________, which lives within its leaf cavities and supplies fixed nitrogen; in return, the cyanobacterium receives photosynthate from the plant.

5.3.3 Keystone species and trophic cascades

A keystone species is one whose effect on the ecosystem is disproportionately large relative to its abundance; its removal causes dramatic changes in community structure. In freshwater, large piscivorous fish such as Lates niloticus (Nile perch) function as keystones: their predation on planktivorous haplochromine cichlids in Lake Victoria, following introduction in the 1950s to 1960s, caused the extinction of over 200 endemic cichlid species and fundamentally restructured the lake's food web. Daphnia acts as a keystone grazer in small lakes: when abundant, it suppresses phytoplankton and maintains clear water.

A trophic cascade is a top-down effect in which a change at one trophic level propagates through multiple levels below it. Classic freshwater example: reduction of piscivorous fish (by fishing) releases planktivorous fish from predation; planktivorous fish increase and graze down large zooplankton (Daphnia); without Daphnia grazing, phytoplankton biomass increases, causing algal blooms and turbid water. Reversing this cascade (biomanipulation) restores clear water. In estuaries, removal of top predators such as sharks or large predatory fish releases mesopredators from control, altering benthic invertebrate and seagrass communities in a multi-level cascade.

Fill in the blank: A ________ cascade occurs when a change at one trophic level propagates downward through the food web; the classic freshwater example involves the release of planktivorous fish from piscivore predation, leading to collapse of zooplankton and algal bloom formation.

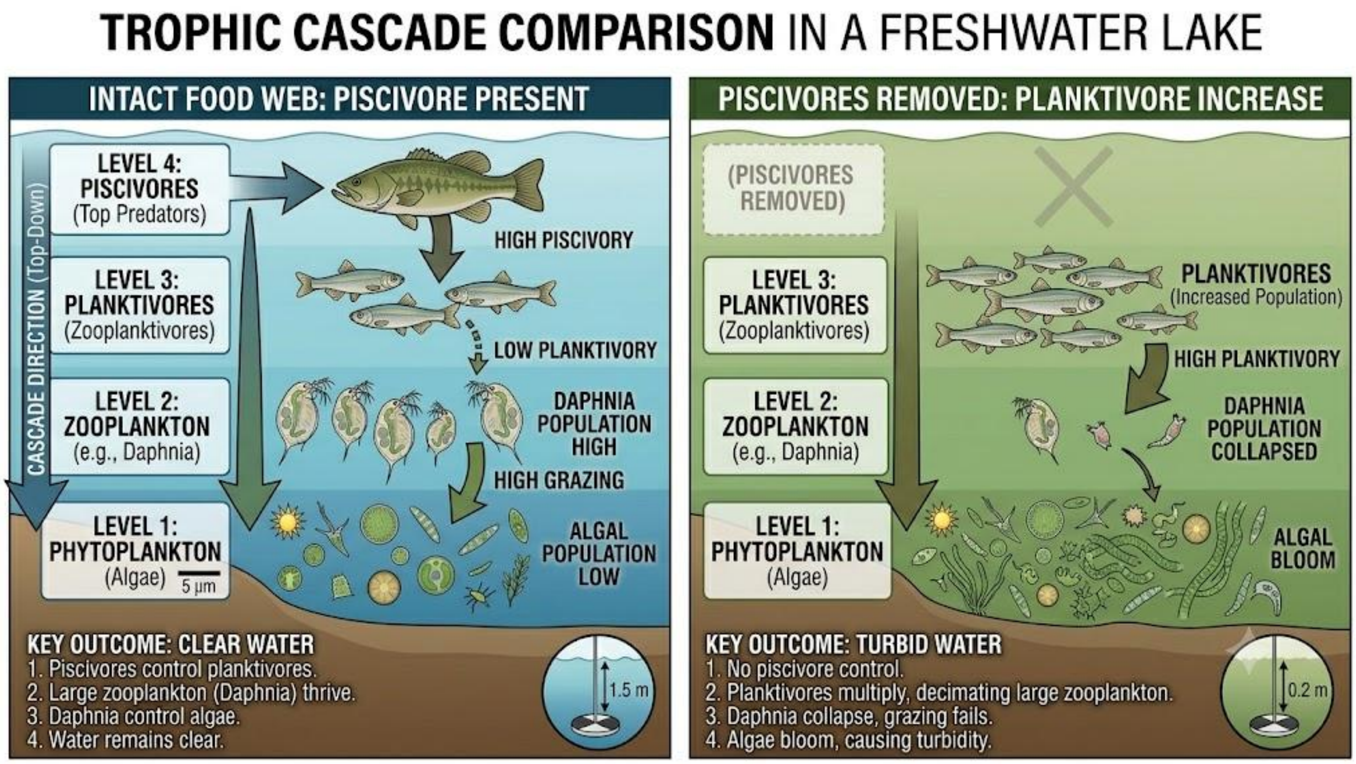

Figure 5.2: A trophic cascade in a freshwater lake showing the effect of piscivore removal on lower trophic levels and water clarity

Pilot questions 5.3

1. Name three invertebrate predators found in freshwater and state the prey of each.
2. Distinguish between parasitism and mutualism and give one aquatic example of each.
3. Explain the role of Lates niloticus as a keystone species in Lake Victoria.
4. Describe the freshwater trophic cascade that results from the removal of piscivorous fish.
5. State three prey adaptations to predation found in freshwater organisms.

5.4 Disturbance, Resilience, and Applied Ecology

5.4.1 Disturbance ecology and the intermediate disturbance hypothesis

Disturbance is any discrete event that disrupts ecosystem structure, community composition, or resource availability. In aquatic systems, natural disturbances include floods, droughts, storm-generated turbulence, fire (in riparian zones), volcanic eruptions, and seasonal hypoxia.

Anthropogenic disturbances include pollution events, eutrophication, dam construction, dewatering, dredging, and introduced species. Disturbance frequency, intensity, and spatial extent determine its ecological impact; frequent, severe disturbances prevent late-successional species from establishing, while rare, mild disturbances allow competitive dominants to exclude subordinate species.

The intermediate disturbance hypothesis (IDH), proposed by Connell (1978), states that species diversity is maximised at intermediate levels of disturbance frequency and intensity. At low disturbance, competitive exclusion allows a few dominant species to monopolise resources, reducing diversity. At high disturbance, only stress-tolerant pioneer species persist, again reducing diversity. At intermediate disturbance, no single species can competitively exclude others because the habitat is regularly reset, allowing coexistence of many species. Coral reefs, stream invertebrate communities, and phytoplankton assemblages have all been used as empirical tests of the IDH.

Fill in the blank: The intermediate disturbance hypothesis predicts that species diversity is highest at ________ levels of disturbance, because neither competitive exclusion (at low disturbance) nor stress-tolerance filtering (at high disturbance) eliminates most species from the community.

5.4.2 Resilience, resistance, and ecological recovery

Resistance is the ability of an ecosystem to withstand disturbance without significant change in structure or function. A highly resistant system absorbs perturbation with minimal displacement from its pre-disturbance state. Resilience is the ability to recover to the pre-disturbance state after displacement; a highly resilient system returns quickly. These two properties often trade off: highly resistant systems (e.g. stable, species-rich tropical lakes) may recover slowly once displaced, while less-resistant systems (e.g. seasonal floodplain pools) recover rapidly because their species are adapted to frequent perturbation.

Alternative stable states describe the situation in which an ecosystem can exist in two or more distinct community configurations. A shallow lake may switch between a clear-water state (dominated by macrophytes) and a turbid state (dominated by phytoplankton) depending on nutrient level and disturbance history, and may not spontaneously return to the clear-water state even if nutrient inputs are reduced. Hysteresis, the phenomenon where the path of recovery differs from the path of degradation, means that ecosystem restoration often requires more intervention than simply removing the original stressor. Recovery after oil spills in Niger Delta mangroves, for example, requires decades even after pollution ceases.

Fill in the blank: The phenomenon in which an ecosystem can exist in two distinct community states and may not return spontaneously to its original state after disturbance is called ________ stable states; restoration therefore requires active intervention beyond simply removing the stressor.

5.4.3 Applications: biomonitoring and ecological restoration

Biomonitoring uses the composition, abundance, and diversity of biological communities as indicators of environmental quality. Biological indicators (bioindicators) are organisms whose presence, absence, or condition reflects specific environmental conditions. Macroinvertebrate communities are widely used in freshwater biomonitoring: pollution-sensitive taxa (Ephemeroptera mayflies, Plecoptera stoneflies, Trichoptera caddisflies; collectively EPT taxa) decline or disappear in organically polluted or oxygen-depleted waters, while pollution-tolerant taxa (Chironomus, Tubifex oligochaetes) increase. The BMWP (Biological Monitoring Working Party) score and the South African Scoring System (SASS) assign scores to taxa by tolerance, summing them to give a water quality index.

Diatoms are used as bioindicators of nutrient status and pH; fish assemblage indices (IBI: Index of Biotic Integrity) assess overall riverine health. Ecological restoration aims to return a degraded ecosystem to a trajectory toward its natural state. Key principles include: identifying and removing stressors (source control); restoring physical habitat (re-meandering channelised rivers, removing weirs, reattaching floodplains); re-establishing lost species through transplanting and reintroduction; controlling invasive species; and monitoring recovery over time. In Nigeria, restoration priorities include mangrove replanting in the Niger Delta, remediation of oil-contaminated sediments, and rehabilitation of channelised urban streams in Lagos and Ibadan.

Fill in the blank: The EPT taxa used in freshwater biomonitoring consist of three pollution-sensitive macroinvertebrate orders: Ephemeroptera (mayflies), Plecoptera (stoneflies), and ________ (caddisflies); their abundance and richness decline rapidly in organically polluted or oxygen-depleted water.

Interaction	**Effect on Species A**	**Effect on Species B**	**Aquatic Example**
Predation	Positive (food gain)	Negative (death)	Shark preying on fish
Competition	Negative (reduced resources)	Negative (reduced resources)	Different fish species competing for plankton
Mutualism	Positive	Positive	Cleaner fish removing parasites from larger fish
Parasitism	Positive (nutrients gained)	Negative (host harmed)	Copepods parasitizing marine fish gills
Commensalism	Positive (benefit gained)	Neutral (no effect)	Remora attaching to a shark for transport
Herbivory	Positive (food gain)	Negative (plant tissue loss)	Sea urchins grazing on kelp

Box 5.1: Summary of key biological interrelationships in aquatic ecosystems with aquatic examples

Pilot questions 5.4

6. State the intermediate disturbance hypothesis and explain its prediction for species diversity.
7. Distinguish between resistance and resilience in aquatic ecosystems and give one example of each.
8. Explain what alternative stable states are and describe the turbid-water and clear-water states of a shallow eutrophic lake.
9. Define biomonitoring and explain how EPT taxa are used to assess freshwater quality.
10. State four principles of ecological restoration and give one example of a restoration activity relevant to Nigeria.

Series Summary

Colonisation is the establishment of organisms in new habitats via wind, water currents, birds, active movement, or human transfer. Pioneer species are r-selected, broadly tolerant, and effective dispersers; the priority effect gives early colonisers a competitive advantage over later arrivals. Ecological succession is the directional change from pioneer communities to climax states; primary succession starts on bare substrate while secondary succession begins on disturbed but previously colonised ground. The hydrosere progresses from open water through submerged macrophytes, floating-leaved plants, emergent reeds, sedge fen, shrub swamp, to climax forest. Estuarine and rocky shore succession follow analogous sequences driven by sediment accretion and substrate modification.

Biological interrelationships include predation (top-down control of lower trophic levels), competition (for nutrients, light, and space), herbivory (zooplankton on phytoplankton; insects on periphyton), parasitism (trematodes, lice, fungi), and mutualism (Azolla-Anabaena; cleaner fish). Keystone species such as Lates niloticus exert disproportionate effects; trophic cascades propagate top-down effects through food webs. The intermediate disturbance hypothesis explains maximum diversity at intermediate disturbance levels. Resilience and resistance govern ecosystem recovery; alternative stable states and hysteresis complicate restoration. Biomonitoring using EPT taxa, diatoms, and fish indices provides water quality assessment; ecological restoration requires stressor removal, habitat rehabilitation, species reintroduction, and long-term monitoring.

Glossary of Terms

- **Alternative stable states:** the condition in which an ecosystem can exist in two or more distinct community configurations; once shifted to an alternative state, it may not return spontaneously to its original state even after the stressor is removed.
- **Biomonitoring:** the use of living organisms and their communities as indicators of environmental quality; commonly employs macroinvertebrate (EPT), diatom, or fish assemblages in freshwater quality assessment.

- **Climax community:** the relatively stable, self-sustaining community that represents the end point of ecological succession under a given set of environmental conditions.
- **Colonisation:** the process by which organisms disperse to and establish viable populations in a previously unoccupied or cleared habitat; the first stage in succession.
- **Disturbance:** any discrete event that disrupts ecosystem structure, community composition, or resource availability; examples in aquatic systems include floods, pollution events, dredging, and drought.
- **EPT taxa:** Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies); pollution-sensitive macroinvertebrate orders used as bioindicators of clean, well-oxygenated freshwater.
- **Hydrosere:** the successional sequence that begins in open water and progresses through aquatic and semi-aquatic seral stages toward a terrestrial climax community; driven by organic matter accumulation raising the lake bed.
- **Hysteresis:** the phenomenon in which the path of ecosystem recovery from disturbance differs from the path of degradation; restoration requires more intervention than simply removing the original stressor.
- **Intermediate disturbance hypothesis (IDH):** Connell's (1978) hypothesis that species diversity is maximised at intermediate levels of disturbance frequency and intensity, because neither competitive exclusion nor stress-tolerance filtering eliminates most species.
- **Keystone species:** a species whose effect on the ecosystem is disproportionately large relative to its abundance; its removal causes dramatic restructuring of community composition at multiple trophic levels.
- **Mutualism:** a symbiotic relationship in which both species benefit; aquatic examples include the Azolla-Anabaena nitrogen-fixing partnership and cleaner fish removing ectoparasites from larger fish.
- **Parasitism:** a symbiotic relationship in which the parasite benefits at the expense of the host; aquatic examples include trematode flukes using fish or snails as hosts, Argulus fish lice, and Saprolegnia fungi on fish.
- **Pioneer species:** the first organisms to colonise a new or disturbed habitat; characterised by broad environmental tolerance, effective dispersal, and rapid reproduction (r-selected strategy).

- **Priority effect:** the competitive advantage held by species that arrive first in a new habitat; early colonisers modify conditions and pre-empt resources, suppressing or excluding later-arriving species.
- **Resilience:** the ability of an ecosystem to recover to its pre-disturbance state after displacement; a highly resilient system returns quickly after perturbation.
- **Resistance:** the ability of an ecosystem to withstand disturbance without significant change in structure or function; a highly resistant system absorbs perturbation with minimal displacement from its pre-disturbance state.
- **Succession:** the directional, non-seasonal change in species composition of a community over time; proceeds from pioneer communities through a series of seral stages toward a climax community.
- **Trophic cascade:** a top-down effect in which a change at one trophic level propagates through multiple lower levels; the freshwater example involves piscivore reduction releasing planktivores, which suppress Daphnia, causing algal blooms.

Concept Check Questions [Series 5]

Objective Questions

1. The competitive advantage that early-arriving colonisers hold over later species by pre-empting resources is called the ________ effect. (Linked to SLO 5.1)
2. The successional sequence from open water to terrestrial climax vegetation is called the ________. (Linked to SLO 5.2)
3. A species whose removal causes disproportionately large changes in community structure is called a ________ species. (Linked to SLO 5.4)
4. The three pollution-sensitive macroinvertebrate orders used in freshwater biomonitoring are collectively called ________ taxa. (Linked to SLO 5.6)
5. The intermediate disturbance hypothesis predicts that species diversity is highest at ________ levels of disturbance. (Linked to SLO 5.5)

Short-Answer Questions

1. Name four dispersal mechanisms by which organisms colonise new freshwater habitats. (Linked to SLO 5.1)

2. Distinguish between primary and secondary succession and explain why secondary succession is faster. (Linked to SLO 5.2)
3. Name three types of biological interrelationship and give one aquatic example of each. (Linked to SLO 5.3)
4. Distinguish between resistance and resilience in aquatic ecosystems and explain why they often trade off. (Linked to SLO 5.5)
5. State four principles of ecological restoration and give one example relevant to Nigeria. (Linked to SLO 5.6)

Long-Answer Questions

1. Explain the process of colonisation in aquatic ecosystems, describe the role of pioneer species, and discuss the factors that determine colonisation success, using Nigerian examples where appropriate. (Linked to SLO 5.1)
2. Distinguish between primary and secondary succession, describe the hydrosere in detail, and explain succession on a West African estuarine mudflat. Describe three biological interrelationships in aquatic systems and explain the concept of the trophic cascade with a freshwater example. (Linked to SLOs 5.2, 5.3, 5.4)
3. Explain the intermediate disturbance hypothesis and discuss its implications for aquatic biodiversity management. Distinguish between resilience and resistance, explain alternative stable states and hysteresis, and describe how biomonitoring and ecological restoration are applied to degraded freshwater and estuarine systems in Nigeria. (Linked to SLOs 5.5, 5.6)

Answers to Concept Check Questions [Series 5]

Objective Questions

1. Priority.
2. Hydrosere.
3. Keystone.
4. EPT.
5. Intermediate.

Short-Answer Questions

1. Wind transport of spores and resting stages; waterbird transport on feathers, feet, and in gut; passive drift via water currents; active swimming (fish); human-mediated transfer via ballast water or stocking.
2. Primary succession starts on bare substrate with no prior biological legacy (e.g. new volcanic lake); secondary succession starts after disturbance removes an existing community but leaves substrate, organic matter, and propagules intact (e.g. pond after dredging). Secondary succession is faster because organic matter, nutrients, and viable seed or spore banks are already present, allowing rapid regrowth without the slow build-up phase.
3. Predation (+ / -): Lates niloticus eating haplochromine cichlids in Lake Victoria. Mutualism (+ / +): Azolla-Anabaena nitrogen-fixing partnership. Parasitism (+ / -): Schistosoma mansoni using Biomphalaria snails as intermediate hosts.
4. Resistance is the ability to withstand disturbance without significant change; resilience is the speed of recovery after disturbance. They often trade off: highly resistant systems (e.g. stable, species-rich tropical lakes) may be slow to recover once displaced, while less resistant systems (seasonal floodplain pools) recover quickly because species are adapted to frequent perturbation.
5. Identify and remove the stressor (source control); restore physical habitat (re-meandering, weir removal, floodplain reconnection); reintroduce lost species through transplanting; control invasive species; monitor recovery over time. Nigerian example: mangrove replanting using locally sourced Rhizophora propagules in the Niger Delta following oil spill remediation.

Long-Answer Questions

1. Colonisation: organisms disperse to unoccupied habitats via wind (spores), water currents, waterbirds (feathers, feet, gut), active swimming, or human transfer (ballast water, stocking). New habitats include newly impounded reservoirs (Kainji, Jebba), crater lakes, oxbow lakes, and floodplain pools. Rate depends on dispersal ability, habitat connectivity, distance from source, and abiotic suitability. Pioneer species: r-selected; rapid reproduction; broad tolerance; effective dispersal; examples include small chlorophytes and cyanobacteria (phytoplankton), chironomid larvae and rotifers (invertebrates), small cyprinids and cichlids (fish). Factors for success: abiotic (temperature, dissolved oxygen, pH, salinity, substrate, nutrients, light); biotic (competition from established species; predation on arriving colonisers; food availability; mutualists). Priority effect: early colonisers pre-empt resources and modify habitat, suppressing later arrivals; explains difficulty of displacing invasive

species such as Eichhornia crassipes once established. Connectivity: isolated water bodies colonise more slowly than connected river-lake systems.

2. Primary vs secondary succession: primary starts on bare substrate (no legacy); secondary starts after disturbance with intact substrate and propagules; secondary faster. Hydrosere stages: (1) open water, phytoplankton and submerged macrophytes; (2) floating-leaved plants (Nymphaea) as sediment rises; (3) emergent reed swamp (Typha, Phragmites); (4) sedge-rush fen as litter raises substrate; (5) shrub swamp (Raphia, Alchornea); (6) climax tropical riverine forest. Estuarine mangrove succession (West Africa): bare mudflat colonised by bacterial and diatom biofilm; polychaetes and bivalves stabilise sediment; Rhizophora (seaward pioneer) establishes on accreting mudflat; Avicennia and Laguncularia succeed it in higher intertidal zones; terrestrial forest replaces mangrove on highest ground. Biological interrelationships: predation (Lates eats cichlids; planktivores control Daphnia); competition (phytoplankton compete for phosphorus and light); mutualism (Azolla-Anabaena; cleaner fish). Trophic cascade: reduction of piscivorous fish (over-fishing) releases planktivorous fish; planktivores graze down Daphnia; without Daphnia, phytoplankton bloom; water becomes turbid. Biomanipulation reverses cascade by restocking piscivores or removing planktivores, restoring Daphnia and clearing water.
3. IDH (Connell, 1978): diversity is maximised at intermediate disturbance; at low disturbance, competitive exclusion reduces diversity to a few dominants; at high disturbance, only stress-tolerant pioneers survive; at intermediate levels, regular habitat resetting prevents competitive exclusion and allows coexistence of many species. Implications for management: maintaining natural flood regimes and seasonal variability in rivers and floodplains preserves diversity; suppressing all disturbance (e.g. full flow regulation by dams) can reduce biodiversity by allowing competitive exclusion. Resilience vs resistance: resilience is speed of recovery; resistance is ability to avoid change; trade-off because resistant systems store complexity that makes rapid recovery after threshold crossing difficult. Alternative stable states: shallow lake can exist as clear-water (macrophyte-dominated) or turbid (phytoplankton-dominated) state; nutrient reduction alone may not restore clear water due to hysteresis (legacy phosphorus from sediment; absence of macrophyte seed bank); active restoration needed (macrophyte transplanting; sediment capping). Biomonitoring: EPT taxa (mayflies, stoneflies, caddisflies) sensitive to organic pollution; BMWP or SASS scoring assigns water quality index; diatom indices assess nutrient status; IBI assesses fish community health for rivers. Restoration in Nigeria: mangrove replanting in Niger Delta (stressor: oil spills; activity: propagule collection and planting); urban stream rehabilitation in Lagos and Ibadan (remove concrete channels;

restore riparian vegetation; control effluent discharge); river flow restoration below Kainji Dam to reactivate floodplain nutrient cycling and fish spawning migration; long-term monitoring essential for adaptive management.

Answers to Pilot Questions [Series 5]

Part 5.1

1. Colonisation: establishment of organisms in a previously unoccupied or cleared habitat. Four mechanisms: wind transport of spores and resting stages; waterbird transport on feathers, feet, and in gut; passive drift via water currents; active swimming and migration of fish; human transfer via ballast water or deliberate stocking.
2. Three characteristics: broad environmental tolerance; effective dispersal ability; rapid reproduction (r-selected). Freshwater example: chironomid (midge) larvae, which tolerate low dissolved oxygen and high organic matter and rapidly colonise soft sediments of newly formed ponds and reservoirs.
3. Priority effect: early colonisers pre-empt space and resources and may modify habitat conditions to favour their own persistence, suppressing or excluding later arrivals. In a newly formed lake, the first phytoplankton species to establish consume available nutrients and shade the water, making it harder for later-arriving competitors to grow; the first macrophytes to root stabilise sediment and absorb nutrients, preventing other plant species from establishing in those patches.
4. Temperature; dissolved oxygen concentration; pH; salinity; substrate type; nutrient concentration; light availability.
5. Fish communities were established in Kainji primarily by immigration from the parent Niger River system through the newly flooded valley before the dam closed, and by active inward migration via any remaining connections. Phytoplankton and zooplankton assembled rapidly from waterborne inocula carried by inflowing rivers and by waterbirds. Government fisheries agencies also deliberately stocked the reservoir with Tilapia species, catfish, and other economically important species to accelerate the development of harvestable fish populations.

Part 5.2

1. Primary succession: starts on bare substrate with no prior biological legacy; example: colonisation of a newly formed volcanic crater lake. Secondary succession: starts after

disturbance removes an existing community but leaves the substrate and propagule bank intact; example: recovery of a seasonal floodplain pool after drying.

2. Stage 1: open water with phytoplankton and submerged macrophytes. Stage 2: floating-leaved plants (Nymphaea) as sediment fills the margin. Stage 3: emergent reed swamp (Typha, Phragmites) as the margin becomes shallower. Stage 4: sedge-rush fen as reed litter raises the substrate above the water table. Stage 5: shrub swamp (Raphia palm, Alchornea) on drier ground. Stage 6: climax tropical riverine forest.
3. Secondary succession is faster because organic matter, mineral nutrients, and viable propagules (seeds, spores, resting eggs) are already present in the substrate. Pioneer biofilms and macrophytes regrow from retained propagules within weeks to months, bypassing the slow initial colonisation phase required in primary succession where bare rock or sediment must first be biologically modified.
4. Bare mudflat is colonised by bacterial and diatom biofilm, then polychaetes and bivalves stabilise the sediment surface. Rhizophora racemosa establishes on the pioneer seaward mudflat, its prop roots trapping more sediment and raising the substrate. As the surface rises, Avicennia germinans colonises the middle intertidal zone with its pneumatophores. Laguncularia racemosa occupies the higher intertidal. On the highest, least-flooded ground, terrestrial forest species eventually replace the mangrove community.
5. A climax community is the relatively stable endpoint of succession under a given set of environmental conditions. In tropical African freshwater systems, a true climax may never be reached because seasonal flooding, annual drought, fire in riparian zones, and human land use continuously reset or interrupt the successional trajectory, maintaining persistent semi-aquatic or early-successional communities rather than allowing development of mature forest.

Part 5.3

1. Dragonfly larvae (Anisoptera) prey on mosquito larvae and small Daphnia. Chaoborus (phantom midge) larvae prey on small zooplankton including rotifers and nauplii. Predatory copepods (Cyclops) prey on rotifers and smaller copepods and cladocerans.
2. Parasitism: one species (parasite) benefits and the other (host) is harmed; example: Schistosoma mansoni uses Biomphalaria snails as intermediate hosts in West African rivers, completing its life cycle in the snail before infecting humans. Mutualism: both species benefit; example: Azolla water fern and Anabaena cyanobacterium, where Anabaena fixes nitrogen for the plant and receives photosynthate in return.
3. Lates niloticus (Nile perch) was introduced into Lake Victoria in the 1950s to 1960s. As a top piscivore, it preyed intensively on the diverse haplochromine cichlid species that dominated

the lake. Its predation pressure, combined with eutrophication and overfishing, caused the extinction or near-extinction of over 200 endemic cichlid species, fundamentally restructuring the lake food web from a diverse, multi-species system to one dominated by Lates and the introduced Nile tilapia.

4. Removal of piscivorous fish by over-fishing releases planktivorous fish from top-down control; planktivore abundance increases; planktivores intensively graze large-bodied Daphnia; Daphnia populations collapse; without Daphnia grazing, phytoplankton biomass increases, causing algal blooms; lake water becomes turbid; submerged macrophytes decline as light is blocked; benthic habitats degrade. Biomanipulation reverses this by restocking piscivores or removing planktivores, restoring Daphnia and clearing the water.
5. Schooling behaviour (dilution effect and confusion of predators; e.g. sardines); diel vertical migration (Daphnia descends to deep dark water by day to avoid visual predators); development of spines or helmets (Daphnia develops a neck spine or head helmet in the presence of chemical cues from Chaoborus predators).

Part 5.4

1. IDH (Connell, 1978): species diversity is maximised at intermediate levels of disturbance frequency and intensity. At low disturbance, a few competitive dominants exclude most species, reducing diversity. At high disturbance, only stress-tolerant pioneers survive, reducing diversity again. At intermediate disturbance, regular habitat resetting prevents any species from dominating indefinitely, allowing coexistence of many species.
2. Resistance: ability to withstand disturbance without significant change in structure or function; example: a species-rich, structurally complex tropical lake that maintains its water quality and community composition despite moderate agricultural runoff. Resilience: ability to recover quickly after disturbance; example: a seasonal floodplain pool that dries completely each year but rapidly recolonises from retained eggs and seeds within weeks of refilling, because its species are adapted to annual perturbation.
3. Alternative stable states: an ecosystem can exist in two distinct configurations and may not revert to its original state spontaneously once shifted. Clear-water state: dominated by submerged macrophytes; macrophytes absorb nutrients from sediment, outcompeting phytoplankton; water transparent; Daphnia abundant. Turbid state: dominated by phytoplankton; dense algal blooms block light; macrophytes absent; Daphnia suppressed by planktivores and cyanobacterial toxins. Hysteresis: reducing external nutrient inputs alone may not restore clear water because internal phosphorus loading from sediment and the

absence of macrophyte propagules sustain the turbid state; active intervention (macrophyte transplanting, sediment capping) is needed.

4. Biomonitoring: using biological communities to assess environmental quality. EPT taxa (Ephemeroptera, Plecoptera, Trichoptera) are assigned high scores in the BMWP index; their presence indicates clean, well-oxygenated water; as pollution increases (organic enrichment, low dissolved oxygen), EPT taxa disappear and are replaced by Chironomus and Tubifex (tolerant taxa with low BMWP scores); the summed BMWP score gives a water quality band from very good to bad.
5. Principles: (1) identify and remove the stressor causing degradation; (2) restore physical habitat structure; (3) reintroduce lost species; (4) control invasive species; (5) monitor recovery adaptively. Nigerian example: mangrove replanting in the Niger Delta; the stressor (oil spills) is addressed through remediation and pipeline repair; Rhizophora propagules are collected locally and planted on cleared mudflats; progress is monitored by tracking canopy cover, invertebrate recolonisation, and water quality over at least five years.

References and Attributions [Series 5]

Textual References (Books and External Sources)

- Wetzel, R. G. (2001). Limnology: Lake and river ecosystems (3rd ed.). Academic Press.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. Science, 199(4335), 1302–1310.
- Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. Nature, 413, 591–596.
- Moss, B. (2010). Ecology of fresh waters: A view for the twenty-first century (4th ed.). Wiley-Blackwell.
- Magurran, A. E., & May, R. M. (Eds.). (1999). Evolution of biological diversity. Oxford University Press.

Figures, Plates, Tables, and Boxes

- Figure 5.1: The hydrosere showing six seral stages from open water to tropical riverine forest. Attribution: AI generated. Suggested OER search string: "hydrosere succession stages open water reed swamp fen woodland diagram OER".
- Figure 5.2: A trophic cascade in a freshwater lake showing the effect of piscivore removal. Attribution: AI generated. Suggested OER search string: "trophic cascade freshwater lake piscivore planktivore Daphnia phytoplankton diagram OER".
- Box 5.1: Summary of key biological interrelationships in aquatic ecosystems. Attribution: AI generated. Suggested OER search string: "biological interrelationships table predation competition mutualism parasitism aquatic examples OER".