DWR-753

Limnology

Lake and River Ecosystems

Third Edition

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ACADEMIC PRESS
An Imprint of Elsevier

San Diego San Francisco New York Boston London Sydney Tokyo

This book is printed on acid-free paper. ♾

Academic Press
An Imprint of Elsevier
525 B Street, Suite 1900, San Diego, California 92101-4495, USA
http://www.academicpress.com

Academic Press
32 Jamestown Road, London NW1 7BY, UK
http://www.academicpress.com

Library of Congress Catalog Card Number: 00-110178

ISBN-13: 978-0-12-744760-5
ISBN-10: 0-12-744760-1

PRINTED IN THE UNITED STATES OF AMERICA
10 11 EB 14 13

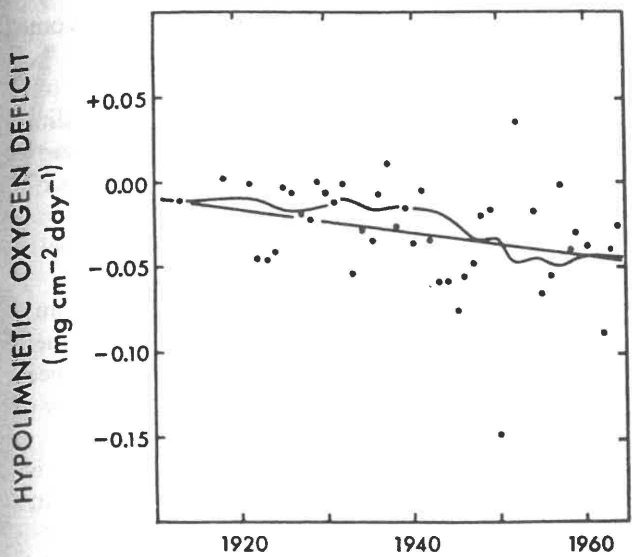

FIGURE 9-13 Change in estimated annual hypolimnetic oxygen deficits over a 53-year period in Douglas Lake, Michigan (negative values in all except two cases indicating a progressively greater rate of hypolimnetic oxygen reduction). The straight line represents the line of best fit by linear regression; the smooth curve represents an exponentially smoothed 1-year forecast at each year. (Modified from data of Bazin and Saunders, 1971.)

1980). Other indices of eutrophication and its reversal will be discussed in other chapters. Hypolimnetic oxygen deficits are but one index and must be used with great caution and careful consideration of differences in hypolimnetic temperatures and thicknesses.

VII. SUMMARY

1. Dissolved oxygen is essential to the respiratory metabolism of most aquatic organisms. The dynamics of oxygen distribution in inland waters are governed by a balance between inputs from the atmosphere and photosynthesis and losses from chemical and biotic oxidations. Oxygen distribution is important for the direct needs of many organisms and affects the solubility and availability of many nutrients and therefore the productivity of aquatic ecosystems.
2. Solubility of oxygen in water decreases as temperature increases. The solubility of oxygen decreases somewhat with lower atmospheric pressures at higher altitudes and increases with greater hydrostatic pressures at depth within lakes. Oxygen solubility decreases exponentially with increases in salt content.
3. Because diffusion of oxygen from the atmosphere into and within water is a relatively slow process, turbulent mixing of water is required for dissolved oxygen to be distributed in equilibrium with that of the atmosphere. Although oxygen content within small, turbulent streams is near saturation, marked variations occur spatially and temporally in larger rivers and are often coupled to variations in discharge and loadings of organic matter. Ground water is often largely or completely devoid of oxygen as a result of chemical and biological oxidations.
4. Distribution of oxygen in the water of thermally stratified lakes is controlled by a combination of solubility conditions, hydrodynamics, inputs from photosynthesis, and losses to chemical and metabolic oxidations.
   a. In unproductive oligotrophic lakes that stratify thermally in the summer, the oxygen content of the epilimnion decreases as the water temperatures increase. The oxygen content of the hypolimnion is higher than that of the epilimnion because the saturated colder water from spring turnover is exposed to limited oxidative consumption. Such a vertical distribution is called an ***orthograde oxygen profile*** (Fig. 9-2).
   b. The loading of organic matter to the hypolimnion and sediments of productive eutrophic lakes increases the consumption of dissolved oxygen. As a result, the oxygen content of the hypolimnion is reduced progressively during the period of summer stratification, usually most rapidly at the deepest portion of the basin where strata of less volume are exposed to the more intensive decomposition in surficial sediments. The resulting vertical distribution is termed a ***clinograde oxygen profile*** (Fig. 9-2).
   c. Oxygen saturation at existing water temperatures returns to all water strata during fall circulation.
   d. The exchange of oxygen with the atmosphere ceases for all practical purposes with the advent of ice formation. The oxygen content and saturation levels are reduced at lower depths in productive lakes, but not to the extent observed during summer stratification, because of prevailing colder water temperatures (greater solubility, reduced respiration).
   e. ***Metalimnetic oxygen maxima*** are often observed, in which the oxygen content in the metalimnion is much greater than, and often supersaturated in relation to, levels in the epilimnion and hypolimnion. The resulting ***positive heterograde oxygen curve*** is usually caused by photosynthetic oxygen production by algae in excess of oxidative consumption in the metalimnion.

openwater areas) and seasonally when utilization or losses exceed inputs. Concentration of a nutrient is important to growth and phytoplanktonic community structure but so is the supply rate of one nutrient relative to other potentially limiting nutrients. Competitive dominance of species populations will develop along nutrient gradients according to the species' maximal growth rates, their half-maximal growth rates (half-saturation constants of nutrient uptake), and their species-specific mortality rates (Kilham and Kilham, 1978; Tilman, 1978, 1980; Kilham and Tilman, 1979). For example, *Asterionella* is a successful competitor at high Si/P ratios, *Fragilaria* can dominate at intermediate ratios, and *Stephanodiscus* grows well when Si/P ratios are low.

6. The ***latter part of summer stratification*** exhibits conditions of high temperatures, high water column stability but a progressive erosion and deepening of the metalimnion, high but declining light availability, and low nutrient availability. Herbivorous zooplankton become food-limited, and their collective biomass declines precipitously from decreased fecundity and greatly increased fish predation. The greatly reduced grazing pressures and increasing nutrient availabilities from processes such as erosion of the metalimnion and parts of the hypolimnion result in a more diverse phytoplanktonic community. Chrysophytes, cryptophytes, and colonial green algae frequently become abundant, and their growth often reduces availability of phosphorus and commonly also combined nitrogen (NO_3^- and NH_4^+) to limiting concentrations.

If silica is abundant, the green algae are often replaced by large diatoms. Commonly, however, silica levels are reduced in the trophogenic zone in late summer. Under these circumstances of silica depletion (<0.5 mg SiO_2^- liter^{-1}), dinoflagellates and cyanobacteria dominate (Fig. 15-9). As summer algal growth utilizes combined nitrogen to very low concentrations, filamentous cyanobacteria capable of fixing molecular nitrogen often dominate, a very common sequence in temperate lakes (cf. earlier discussion; Dokulil and Skolaut, 1986; many others). The ability of many cyanobacteria to migrate by buoyancy alterations (cf. p. 347) between lower depths of relative nutrient abundance and upper strata of light abundance (e.g., Gamf and Oliver, 1982), as well as the ability to fix molecular nitrogen from atmospheric sources, results in a superior competitive position in relation to other species of phytoplankton. Certain cyanobacterial species can be recruited from the sediments, particularly during midsummer. For example, a significant portion of the bloom-forming cyanobacterial populations of a small reservoir was gained by migrations from the sediments into the overlying waters (Trimbee and Harris, 1984).

In shallow lakes where inputs of nutrients, such as silica and/or combined nitrogen, from the sediments or external sources exceed microbial utilization, faster-growing chlorophytes or diatoms can become superior competitors compared with the relatively slow-growing cyanobacteria (Hecky *et al.*, 1986; Jensen *et al.*, 1994). Nutrient turnover rates and availability to biota can be very high in shallow lakes, even when inorganic nutrient concentrations are low and the pH high.

The spring maximum of phytoplanktonic biomass is generally short-lived, usually less than one to two months in duration. This maximum often is followed by a period of low algal numbers and biomass that may extend throughout the summer. Among more eutrophic lakes of the temperate region, the summer minimum is often brief and phases into a late summer profusion of cyanobacteria that persists into the autumn, until thermal stratification is disrupted. Populations of phytoplankton are often low throughout the summer in temperate oligotrophic lakes but may develop a second maximum in the autumn period (Fig. 15-9). This second maximum of the autumn, which often consists predominantly of diatoms, is generally not as strongly developed as that of the spring period (e.g., Diaz and Pedrozo, 1993). The decline of the autumnal populations into the winter minimum is often abrupt and more irregular than the decline after the spring development. The limited growing season of lakes of high altitudes and in polar regions often is reflected in a conspicuous, single, summer maximum of phytoplanktonic biomass.

As silica concentrations are reduced in productive lakes, diatom populations are often succeeded by a preponderance of first green algae and later cyanobacteria (e.g., Fig. 15-9). Growth in these eutrophic lakes can be so intense that combined nitrogen ($NO_3^-$and NH_4^+) sources are reduced to below detectable concentrations in the trophogenic zone (e.g., Wintergreen Lake, Chap. 12). When this happens, often by midsummer when the warmest epilimnetic temperatures occur, cyanobacteria with efficient capabilities for fixing molecular nitrogen have a competitive advantage and can predominate (cf. Chap. 12). These lakes require, as a general rule, a reasonably sustained and heavy loading of phosphorus (cf. e.g., Moss, 1973c).

Gradients in nutrient ratios are commonly observed during and after the spring diatom outburst in eutrophic lakes because phosphorus and nitrate concentrations decline at different rates (e.g., Pechlaner, 1970). As a result, the Si/P ratio increases and the N/P ratio decreases markedly. At high Si/P ratios, diatoms can effectively outcompete cyanobacteria (e.g., Holm and Armstrong, 1981). As concentrations of silica are reduced, and later combined nitrogen declines, green