

ADVANCES IN MICROBIAL ECOLOGY

Edited by M. Alexander

— Volume 3 —

Advances in MICROBIAL ECOLOGY

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M. Alexander

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Preface

We are most gratified by the response to the initiation of this series of volumes presenting recent developments and new concepts in microbial ecology. Favorable reactions have been expressed in both oral and written communication, and *Advances in Microbial Ecology* thus seems to be providing a worthwhile outlet in a rapidly growing field of microbiology and environmental sciences.

The growing importance of microbial ecology is evident in many ways. University personnel are expanding their programs and increasing the number of research topics and publications. Substantial numbers of industrial scientists have likewise entered this field as they consider the microbial transformation of chemicals in waters and soils and the effects of synthetic compounds on natural microbial communities. Agricultural, medical, dental, and veterinary practitioners and scientists have also been increasing their activity in microbial ecology because of the importance of the discipline to their own professions. In addition, governmental agencies have expanded regulatory and research activities concerned with microbial ecology owing to the importance of information and regulations focused on the interactions between microorganisms in nature and particular environmental stresses.

The present volume maintains the approach formulated originally by the International Commission on Microbial Ecology. The reviews thus deal with both basic and applied microbiology and are concerned with aquatic, oral, rumen, and food ecosystems. Moreover, diverse groups of organisms are the subject of the several reviews, and the approaches of the authors differ substantially according to the professional interests, requirements, and scope appropriate for the various disciplines. An international group of authors likewise contributes to the present volume. It is the hope of the Editorial Board that future volumes will continue to reflect this breadth: both basic and applied topics, diverse ecosystems, various groups of microorganisms, and an international group of authors.

In this light, we encourage our colleagues in various aspects of microbial ecology and environmental microbiology to submit titles and outlines for prospective reviews to members of the Editorial Board. Now that the series is well

established, we welcome unsolicited manuscripts but hope that prospective authors will consult us before preparing full manuscripts so that an assessment of the approach and relevancy of the manuscript can be made. We thus hope that the *Advances* will continue to serve a useful function and will be a vehicle not only for the dissemination of current information but also for the promotion of the further development of microbial ecology.

The Editor and Editorial Board are appointed by the International Commission on Microbial Ecology for fixed terms. Moshe Shilo has now completed his term on the Editorial Board, and the Commission, the Editor, and his colleagues on the Editorial Board express to him their sincere gratitude for his cooperation, professional advice, and willingness to help in initiating *Advances in Microbial Ecology*.

M. Alexander, Editor
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M. Shilo
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Impact of Facultatively Anaerobic Photoautotrophic Metabolism on Ecology of Cyanobacteria (Blue-Green Algae)

E. PADAN

1. Introduction

This review attempts to evaluate the ecological importance of a recently discovered physiological character in cyanobacteria (blue-green algae), anaerobic photoautotrophic metabolism, by considering the possible expression of the character in the natural environment and its selective value to the organism. In striving for clarity and emphasis, this analysis must concentrate on major factors and may be oversimplified. Nevertheless, as in literature, theater, and other fields of human endeavor, if the ideas put forward are understood and elicit a response, the effort will have been worthwhile.

Cohen *et al.* (1975a) demonstrated that a cyanobacterium, *Oscillatoria limnetica*, is capable of anoxygenic CO₂ photoassimilation with sulfide as an electron donor in a photosystem-I-driven reaction. This reaction has since been thoroughly investigated (Cohen *et al.*, 1975b; Oren *et al.*, 1977; Oren and Padan, 1978; Belkin and Padan, 1978). More recently, additional cyanobacteria were shown to possess this physiological character (Castenholtz, 1976, 1977; Garlick *et al.*, 1977).

2. Aquatic Systems with Alternating Photoaerobic-Photoanaerobic Conditions

A light-dependent sulfide-utilizing metabolic mechanism is most likely to be expressed in sulfide-rich ecosystems with light penetration. As sulfide is readily oxidized by O_2 , the maintenance of a particular sulfide concentration in a habitat is determined by the ambient O_2 tension. Thus, a gradient of O_2 is often accompanied by a gradient of sulfide under natural conditions. Furthermore, sulfide accumulation occurs frequently under anaerobic conditions when biological and chemical activities decompose organic material and/or reduce oxidized sulfur compounds. With the enrichment in sulfide, there is a sharp discontinuity in the redox potential between the aerobic and sulfide-containing habitats. The redox potential of the latter can reach -200 mV and even lower values (Baas Becking and Wood, 1955; Fenchel and Riedl, 1970; Fenchel, 1971; Gest, 1972; Pfennig, 1975; Cohen *et al.*, 1977a). The photic sulfide-rich semianaerobic to anaerobic situation is very characteristic of transparent water bodies which, with limited mixing, can become closed systems with respect to air.

2.1. Hot Sulfur Springs

Hot sulfur springs provide a familiar example of a gradient in sulfide concentration. Castenholtz (1976) described alkaline and neutral hot springs in New Zealand, with particular attention to some from the central volcanic zone of North Island with up to 2 mM sulfide at the source and to other springs from southwest Iceland with lower sulfide concentrations of up to 0.3 mM. In the Yellowstone area of the United States (Castenholtz, 1977) (Fig. 1), the source waters of the Upper Terrace of Mammoth Springs have pH values ranging between 6.2 and 6.8 with a mean sulfide concentration of $56 \mu\text{M}$ and a maximum concentration of 0.13 mM. Acidic hot springs containing sulfide are widely distributed (Castenholtz, 1969). As sulfide is readily oxidized by O_2 , the sulfide concentration in hot springs decreases with distance from the source; there is a decrease in temperature with a concomitant increase in O_2 content and pH (Castenholtz, 1977; Fig. 1). Hence, sulfur springs provide a gradient of conditions from the photoanaerobic sulfide-rich source waters to the photoaerobic waters downstream.

2.2. Stratified Lakes

The photoanaerobic sulfide-rich situation is exemplified in many lakes which undergo thermal stratification. [The limnological terminology is that of Hutchinson (1967).] The stratification pattern in lakes varies with different latitudes, altitudes, lake depths, and solutes. However, the summer stratification

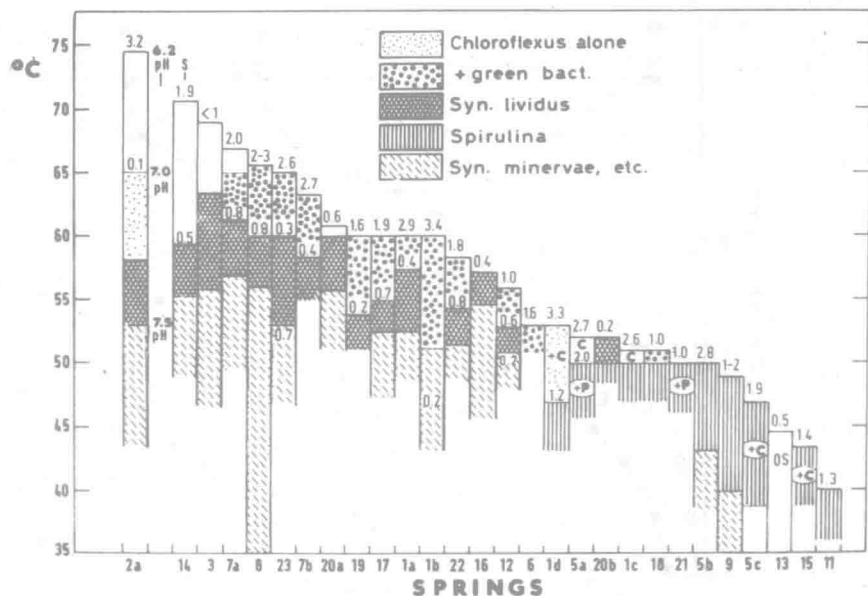


Figure 1. Predominant phototrophs in various temperature zones of springs in the Upper Terrace, Mammoth (Yellowstone National Park, U.S.A.). Each vertical rectangle represents a spring with the source at the top, declining in temperature (toward base) as in the drainway, and along the edges and vertically in hot pools. The sulfide concentration in mg/liter is indicated for each source and also at some species borders at lower temperatures. The pH range at the sources was from 6.2 to 6.7 except for nos. 14 and 11 (pH 6.8), no. 20b (6.9), and no. 20a (7.0). The specific conductance ($\mu\text{mhos/cm}$, 25°C) of these waters ranged from about 2200 to 2600. The species key: C, *Chromatium* sp.; P, *Phormidium* sp.; Os, *Oscillatoria* sp. The blank areas near some sources lack phototrophs but may include nonphotosynthetic bacteria. From Castenholz (1977).

cycle in temperate lakes may serve as an example of the stratification process. After the spring overturn, warming of the upper water layers yields an upper layer (epilimnion) of less dense, freely circulating waters, an intermediate layer (metalimnion) with a temperature gradient (thermocline), and a noncirculating colder, denser bottom layer (hypolimnion). The thermal gradient causes a density stratification resulting in isolation of the hypolimnion. In shallow eutrophic lakes, photoanaerobic conditions may develop both in the stagnant water layer and in the mud. Density stratification in lakes may also be due to a chemical gradient (chemocline) (Hutchinson, 1967; Cohen *et al.*, 1977a,b) (Fig. 2).

Inherent to the physical parameters governing the lake system, the stratified situation is very often unstable with time. Aerobic and anaerobic conditions alternate in accordance with changes in the stratification. A few lakes do not

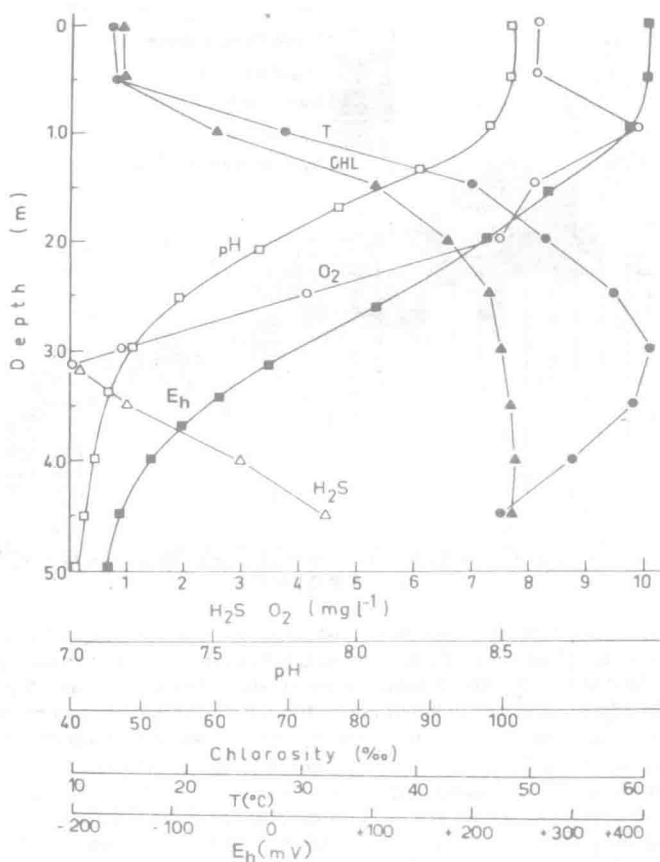


Figure 2. Vertical distribution of temperature, chlorosity, H_2S , O_2 , pH, and E_h at height of stratification, April 4, 1974, in the Solar Lake (Israel). From Cohen *et al.* (1977a).

undergo overturn (amictic lakes); however, most lakes mix partly (meromictic lakes) or completely (holomictic lakes) once or twice yearly. In lower latitudes, mixing may occur more frequently (oligomictic lakes). In the equatorial region's shallow eutrophic lakes undergoing daily overturn (polymictic lakes), there is a daily cycle of stratification and holomixis with daily fluctuations in C_2 tensions (Baxter *et al.*, 1965; Talling *et al.*, 1973; Viner and Smith, 1973; Ganf and Viner, 1973; Ganf and Horne, 1975; Reynolds and Walsby, 1975; Greenwood, 1976).

The O_2 regime in Lake George (Uganda), a polymictic lake, has been thoroughly studied (Burgis *et al.*, 1973; Viner and Smith, 1973; Ganf and Viner, 1973; Ganf, 1974a,b; Ganf and Horne, 1975; Greenwood, 1976) (Fig. 3). At dawn the water column of Lake George is isothermal; from 10.00 hr onward

there is a progressive build-up of thermal stratification which breaks down in the evening, so that at 18.00 hr the water column is isothermal again (Fig. 3a). There is a stratification in O_2 tension corresponding to the thermostratification of the water column (Fig. 3b). With the frequent fluctuations in O_2 tension imposed by this daily cycle, O_2 levels fall below saturation value, but usually not to the anaerobic level. However, Ganf and Viner (1973) have shown that the O_2 budget of the water column is very delicately balanced. The diurnal changes in conditions may cause anaerobiosis and resultant fish mortality. The mean O_2 content of the water column during the night is 13 g/m^2 . The mean O_2 consumption of the upper 5 cm of a 1-m^2 area of bottom mud is 5 g during the first hour of restored contact with O_2 . If wave action at the sediment-water interface is sufficient to suspend this surface mud in the water column even for an hour, a

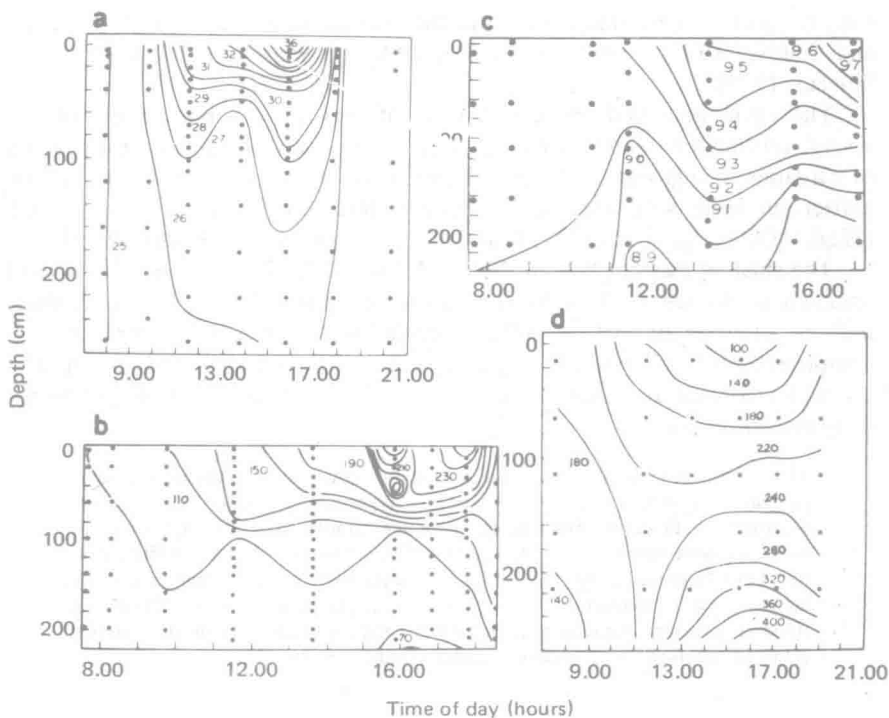


Figure 3. Diurnal vertical distribution of temperature, oxygen, pH and chlorophyll 'a' in Lake George (Uganda), March 26, 1968. a: Temperature—isopleth intervals are 1°C ; dots mark the points at which measurements were taken. b: Percentage oxygen saturation—isopleth intervals are 1–10%. c: pH—isopleth intervals are 0.1. d: Chlorophyll a—isopleth intervals are 40 mg/m^3 . From Ganf and Horne (1975).

significant proportion of the available O_2 in the water will be consumed. Sediment disturbance to 5 cm and greater depths is not uncommon, and if this sediment remains in suspension during the subsequent night, anoxia develops. Thus, whenever the thermocline persists for several days, the hypolimnion is completely deoxygenated, resulting in photoanaerobic conditions the following dawn.

2.3. Aquatic Systems with Photoaerobic to Dark Anaerobic Alternations

In many aquatic systems, as in polymictic lakes, anaerobic sulfide-rich conditions are often established during the night. These are separated in time from the daily aerobic photic conditions. However, an interval of photic anaerobiosis may be expected at dawn. Thus, the photosynthetic community is exposed to frequent anaerobic conditions. In stratified eutrophic lakes, fluctuating anaerobic conditions are not uncommon even in the epilimnion (Hutchinson, 1967; Fogg and Walsby, 1971; Sirenko, 1972; Reynolds and Walsby, 1975; Whitton and Sinclair, 1975).

The cycle described above is typical of very shallow bodies of water of several centimeters' depth, covering large areas of the world, i.e., sea marshes of estuaries, mangroves, and rice paddies. These systems, often rich in organic matter, undergo very marked O_2 tension fluctuations within a daily cycle (Singh, 1961; Fogg *et al.*, 1973; Brock, 1973a; Reynolds and Walsby, 1975).

The shallow marshes behind the beach line of the Texas coast, with limited connections to the Gulf of Mexico, are an example (Odum, 1967). In these millions of acres of shallow polluted marine waters, the living community is compressed into a film which may be less than 10 cm deep. The shallowness of the water column amplifies the diurnal ranges of properties responding to the daily insolation cycle.

Thus, the shallower the water, the greater becomes the diurnal range of temperature, oxygen, and pH. . . . There is a hyperbolic relation of these ranges decreasing with depth. High ranges produce almost anaerobic conditions at night, oxygen being used as fast as it diffuses into the film. Since films cannot have large radii for their eddies, mixing even in strong winds is more laminar, and consequently rates of reaeration per area are small. Thus, one finds an apparent paradox that the thinner the water film, the more tendency it has to function anaerobically at night. (Odum, 1967)

2.4. Aquatic Systems with Very Short Anaerobic Exposures

Contiguous aerobic and anaerobic water layers are not completely separable from each other. Thus, short-term exposures to anaerobic conditions can be expected for communities living mainly under photoaerobic conditions, while

organisms of photoanaerobic layers can also be exposed to temporary aerobic conditions. Changes in conditions may be due to vertical movements of the thermocline (Serruya, 1975), affecting populations living in the metalimnion, lower parts of the epilimnion, or upper parts of the hypolimnion. Vertical migration of the organisms, such as those of cyanobacteria, may have similar effects (Fogg and Walsby, 1971; Burgis *et al.*, 1973; Reynolds and Walsby, 1975; Walsby, 1975).

2.5. Sediments

Alternations in O_2 conditions described above for the water layers are commonly found in the mud bottoms (Baas Becking and Wood, 1955; Wood, 1965; Fenchel and Riedl, 1970; Fenchel, 1971; Sirenko, 1972; Burgis *et al.*, 1973; Jørgensen and Fenchel, 1974; Pfennig, 1975; Viner, 1975; Whitton and Sinclair, 1975; Cohen *et al.*, 1977c; Jørgensen, 1977; Jørgensen and Cohen, 1977). The extent of light penetration into the mud layer appears to be a

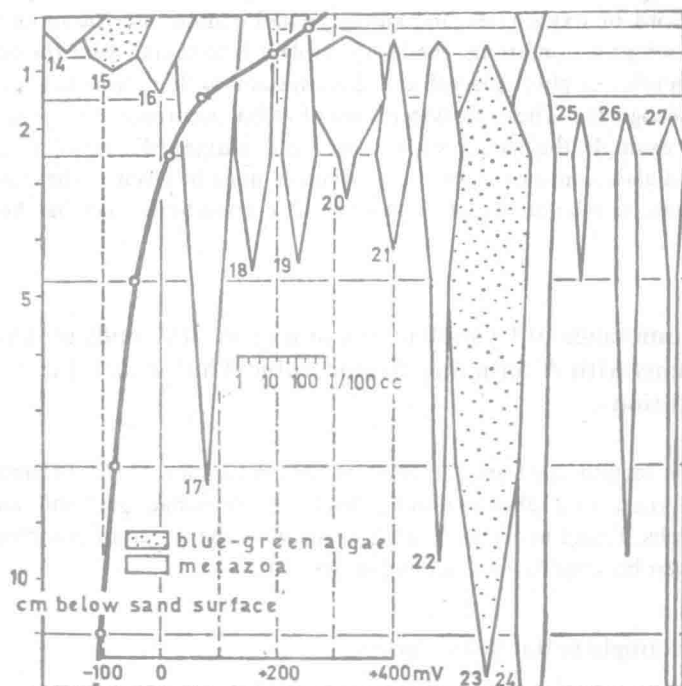


Figure 4. Vertical distribution of blue-green algae and metazoan species from Wrightsville (McCrary's) mudflats (North Carolina, U.S.A.), October. From Fenchel and Riedl (1970).

significant factor with respect to the upper surface layer (Fenchel and Straarup, 1971) and the undisturbed mud-water interface of shallow water bodies. Recently, Fenchel and Riedl (1970) (Fig. 4) described a "thiobiosis" with sulfide concentrations of 10 mM, with occasional exposure to light penetration possible. This habitat is found below an oxidizable surface layer of sand in the littoral zone of many seas. Alternation of O_2 tensions in the benthic habitats occurs in cycles similar to those of the water body (Fenchel and Riedl, 1970; Fenchel, 1971; Serruya *et al.*, 1974). Phototactic or photophobic vertical movements of organisms through the benthic substrate expose them to a steep gradient of redox potential as in the water column (Castenholtz, 1969; Sournia, 1976).

2.6. Summary

Two extremes of light and O_2 conditions in aquatic systems have been described. Permanent photic aerobic conditions are found, as in the epilimnion of many lakes or the waters of the open seas. In contrast, stable sulfide-rich photoanaerobic conditions are found, as in the source waters of hot springs and the monimolimnion of meromictic lakes. In addition, there is a spectrum of combinations of oxygenated and anoxygenated conditions. The more frequent the alternations in conditions, the less possible it is to characterize the ecosystem as photoaerobic or photoanaerobic, and ecosystems with intermediate conditions must be recognized. These ecosystems are of global occurrence and of vast dimensions; for example, the mangroves, estuaries, and marine sediments ("thiobioses") mentioned above. In the future, more attention must be given to these important intermediate combinations of photoanaerobic conditions than has been done previously.

3. Predominance of Cyanobacteria among Phototrophs in Aquatic Systems with Alternating Photoaerobic-Photoanaerobic Conditions

In this section, data are compiled on the distribution of the different phototrophic types, i.e., photosynthetic bacteria, cyanobacteria, and eucaryotic phototrophs, found in the selected habitats with the different combinations of photoanaerobic conditions described in Section 2.

3.1. Phototrophs in Hot Sulfur Springs

The distribution of phototrophic organisms in neutral and alkaline hot sulfur springs of New Zealand, Europe, and the United States has been described