Solar Lake (Sinai). 2. Distribution of photosynthetic microorganisms and primary production[1]

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Abstract

The seasonal and vertical distributions of sulfur photosynthetic bacteria and cyanobacteria in Solar Lake, and their contribution to primary production, are described. During stratification, separate plates of the phototrophic sulfur bacteria *Chromatium violescens* and *Prosthecochloris* sp. develop. A bottom cyanobacterial bloom consisting of *Oscillatoria* spp. and *Microcoleus* sp. develops in H_2S concentrations up to 39 ppm and under light conditions down to 0.5% of surface light. The occurrence of a cyanobacterial bloom in the hypolimnion is explained by the facultative anoxygenic photosynthesis of *Oscillatoria limnetica*. Primary production is extremely high during stratification and reaches a maximum of 8,015 mg C m^{-2} d^{-1}, 91% of which is produced in the metalimnion and hypolimnion. The overall annual production (59.09 g C m^{-2} yr^{-1}) is low, owing to extremely low primary production in the epilimnion throughout stratification and in the whole column during holomixis. Stagnant conditions in a shallow body of water exposed to high irradiation leads to an inverse productivity profile.

The occurrence of sulfur phototrophic bacteria in lakes during periods of stagnation is well known (Kondratieva 1965; Kusnetsov 1959). Their distribution in relation to H_2S concentration and light intensities has been discussed for several lakes (Genovese 1963; Overbeck 1974; Takahashi and Ichimura 1970; Trüper and Genovese 1968). Data on productivity for monomictic and meromictic lakes with a major contribution by photosynthetic sulfur organisms have been reported by Czeczuga (1968*a*,*b*), Culver and Brunskill (1969), and Takahashi and Ichimura (1968). Pfennig (pers. comm.) has compiled more data on these lakes (Table 1) which show that photosynthetic sulfur bacteria are responsible for 20–85% of the total daily production. Table 1 includes monomictic and meromictic lakes according to the classification proposed by Hutchinson (1957); the highest primary production is recorded for the meromictic lakes.

Solar Lake is an extraordinary mesothermal, monomictic lake with extremely high primary production in the anoxic zone. In contrast to normal monomictic lakes of the northern hemisphere, it has a period of holomixis in summer. In fall, seawater seeping in through a bar overlies the concentrated hypersaline brine and allows heliothermal heating of the lower water masses. Stratification builds up with an inverse temperature profile (surface: 16°–20°C; thermocline up to 60.2°C, and bottom around 45°C). Anoxic conditions develop in the hypolimnion. In early summer, with higher evaporation and less seawater supply, overturn occurs. The stratification period lasts from 9–11 months (Cohen et al. 1977*a*; Krumbein and Cohen 1974). Temperature, salinity, and oxygen distribution are homogeneous during holomixis. The results of a detailed study of primary production and the distribution of photosynthetic microorganisms and their pigments in this lake are presented here.

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Table 1. Primary production in monomictic and meromictic lakes and contribution of photosynthetic sulfur microorganisms to total productivity (prepared by N. Pfennig).

Name of water body	Max production A*	Max production B†	Production of photosynthetic sulfur bacteria (% of total)	References
Muliczne	90	145	24	Czeczuga 1968a
Haruna	50	60	20	Takahashi and Ichimura 1968
Wadolek	20	55	63	Czeczuga 1968a, b
Plußsee	35	45	22	Biebl 1973
Beloved'	300	180	40	Lyalikova 1975
Idem	50	110	20	Sorokin 1970
Kisaratsu Reservoir	1,200	800	60	Takahashi and Ichimura 1968
Suigetsu	65	45	20	Idem
Medicine Lake	2,000	190	55	Hayden 1972
Fayetteville Green Lake	1,600	2,470	85	Culver and Brunskill 1969
Solar Lake	4,960	8,015	91	This paper

*mgC m^{-3} day^{-1}. †mgC m^{-2} day^{-1}.

We are greatly indebted to N. Pfennig for allowing us to use the material he prepared (Table 1) and for identifying the sulfur bacteria. We wish to thank I. Dor for identification of cyanobacteria, the staff of the H. Steinitz Marine Biology Laboratory, Elat, for help in carrying out fieldwork, and B. Golek and G. Koch for help in preparing the manuscript.

Materials and methods

Oxygen was determined according to the azide modification of the Winkler method (Am. Public Health Assoc. 1971). Samples were taken with a modified 1-liter Nansen bottle, transferred immediately to duplicate 130-ml BOD bottles, and fixed. Titration was done in the laboratory within 2 h after sampling.

Sulfide was determined according to the titrimetric iodine method (Am. Public Health Assoc. 1971). Samples taken simultaneously with samples for oxygen determinations were put into duplicate 130-ml BOC bottles containing 1 ml of 2% $CdCl_2$ solution and titrated within 2 h after sampling. The results were corrected for pH, temperature, and salinity according to Platpond (1965). When the sulfide was lower than 1 mM the methylene blue visual color matching method (Am. Public Health Assoc. 1971) was applied.

Light penetration was measured by a scanning quantaspectrometer (QSM 2400, UME-Instrument AB, Umea, Sweden) combined with a quanta integrator (UME-Instrument AB) which integrates light intensities between 405 and 710 nm. The scanning quantaspectrometer was fitted into an underwater housing and lowered through the water column by an 80-m coaxial cable. The vertical distribution of light intensity in the visible range between 405 and 710 nm was plotted.

Direct counts of microorganisms—500-ml water samples were taken with a modified 1-liter Nansen bottle and centrifuged at 10,000 rpm for 30 min. The pellets were then resuspended in a known volume of sterile filtered Solar Lake water. Microorganisms were classified morphologically and each type was counted under phase contrast in a Petroff-Hauser cell, in statistically significant numbers.

Primary production—Vertical profiles were measured for primary production according to the Steemann Nielsen method (1952) modified as follows: Sterilized

130-ml BOD bottles were filled completely with water taken at 0.5-m intervals at station A (*see* Cohen et al. 1977*a*: figure 1). To each bottle [^{14}C]$NaHCO_3$ was added to an activity of 65 μCi per bottle. No significant changes of redox potentials were found during sampling and filling the BOD bottles. A pair of light and dark bottles was placed at the original depth. After 3 h of incubation (always from 1000 to 1300 hours), the bottles were recovered and immediately transferred to the laboratory in a cool (4°C) dark box. The water samples were filtered within 30 min after recovery on 0.22-μm-mean-pore-size Millipore filters. The volume filtered depended on the cell density of the samples. The filters were rinsed with 0.01 M HCl prepared in filtered seawater and radioactivity was measured by a gas flow counter (Nuclear Chicago model 1412 B) after drying at room temperature.

Two-liter water samples were taken at the same time and depths for analysis of pigments, protein, and alkalinity.

Alkalinity measurements are highly influenced by the presence of sulfide. Three sets of vertical profiles were acidified and total CO_2 (dissolved inorganic carbon = DIC) was measured by a total carbon analyzer (Beckman). DIC distillation was done with H_2S present and in a parallel set after removal of H_2S by precipitation with 2% $CdCl_2$ solution. The DIC values were then compared with alkalinity measurements of the same samples done according to Strickland and Parsons (1968). This procedure enabled us to correct the alkalinity measurements according to Strickland and Parsons (1968) with reference to the sulfide concentrations of each sample.

Protein—For analysis of protein, 500-ml water samples were filtered through glass fiber filters (Whatman GF/C) after removal of sulfur by washing the filters with absolute ethanol. Protein was then determined according to Lowry et al. (1951).

Biomass was initially calculated from numbers and volumes of the various morphological types of microorganisms obtained by phase microscopy. The biomass values obtained by this method were then compared to total organic carbon determinations (TOC) made with a Beckman carbon analyzer: the correlation was good.

Pure cultures of cyanobacteria, *Chromatium violescens*, and various chemoorganotrophic bacteria isolated from Solar Lake were then analyzed for TOC and protein. Protein content was 50% of the TOC for most bacteria examined, but cyanobacteria had a protein content of 40% of the TOC. On the basis of these findings we could calculate a suitable conversion factor for each sample in terms of the cyanobacteria : other bacteria volume ratios from direct microscopic counts. Biomass was then generally calculated from protein determinations and expressed as organic carbon.

Pigment determinations—One-liter water samples were centrifuged at 10,000 rpm for 30 min. The pellet was then resuspended and the cell suspensions were used for absorption spectra measured on a Cary spectrophotometer using the opaque glass method (Shibata et al. 1954).

Results

Seasonal and vertical distributions of photosynthetic microorganisms in Solar Lake—During holomixis (Fig. 1) the community of photosynthetic organisms was limited and evenly distributed throughout the water. It consisted of low numbers of the cyanobacteria *Aphanothece halophytica, Aphanocapsa littoralis, Oscillatoria salina, Microcoleus* sp., *Spirulina labyrinthiformis*, and *Spirulina* sp. The predominant cyanobacterium was *A. halophytica*. Total numbers of cyanobacteria did not exceed 2×10^3 cells ml^{-1}. Relatively high numbers of diatoms were present, including *Amphora coffeaeformis, Nitzschia thermalis*, and *Navicula* sp. Diatom numbers did not exceed 2×10^4 cells ml^{-1}. During holomixis no photosynthetic sulfur bacteria were detected in the water column (Fig. 1).

During winter stratification, several different layers of phototrophic microorganisms were observed. The epilimnetic community was small and consisted of the

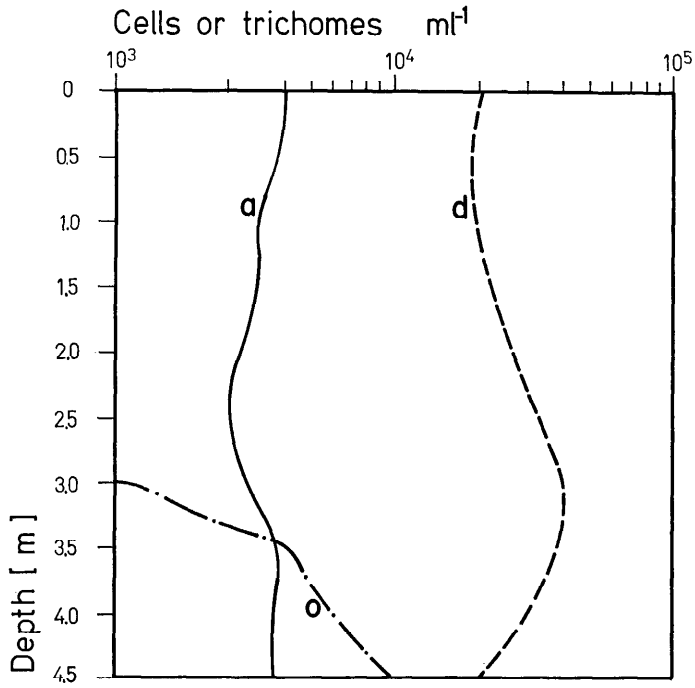

Fig. 1. Vertical distribution of photosynthetic microorganisms during holomixis. Numbers (direct counts) of each group from samples taken on 27 July 1970: d—diatoms (*Nitzschia* sp., *Amphora* sp., *Navicula* sp.); o—filamentous cyanobacteria (*Oscillatoria limnetica, Oscillatoria salina, Microcoleus* sp.); a—unicellular cyanobacteria (*Aphanothece halophytica, Aphanocapsa littoralis*).

same species that appeared during holomixis throughout the water column (Fig. 2). In the metalimnion a dense population of purple sulfur bacteria developed, consisting of *Chromatium violescens* (up to 10^6 cells ml^{-1}), some *Lamprocystis* sp., accompanied by some filamentous cyanobacteria (*O. salina, Oscillatoria limnetica*, and *Microcoleus* sp.). These cyanobacteria occurred in small numbers (2×10^3 filaments ml^{-1}) throughout the metalimnion and the upper hypolimnion. The unicellular coccoid cyanobacteria found in summer were absent from this layer during stratification.

The upper hypolimnion was dominated by a dense population (up to 2×10^6 cells ml^{-1}) of the green sulfur bacterium, *Prosthecochloris* sp., with small numbers of purple sulfur bacteria. The numbers of filamentous cyanobacteria increased with increasing depth. The microbial community of the lower hypolimnion merged into a benthic mat, without definite boundaries. The green sulfur bacteria diminished toward the bottom (to 2×10^5 cells ml^{-1}) and were replaced by a dense bloom of benthic filamentous cyanobacteria (*O. salina, O. limnetica*, and *Microcoleus* sp.). The dense layers of cyanobacteria appeared about 50 cm above the bottom, and formed a loose benthic mat on the bottom (Krumbein et al. 1977). *Prosthecochloris* sp. partially disappeared near the bottom where the H_2S concentration is maximal and light penetration is minimal. Cyanobacteria—mainly *O. limnetica*—then predominated in the bottom layer.

During stratification, light absorption (Fig. 3) was very low for all wavelengths measured throughout the epilimnion (to 2-m depth), whereas at the metalimnion and hypolimnion we found intensive absorption of wavelengths below 515 nm. A peak of very low intensity remained at 565

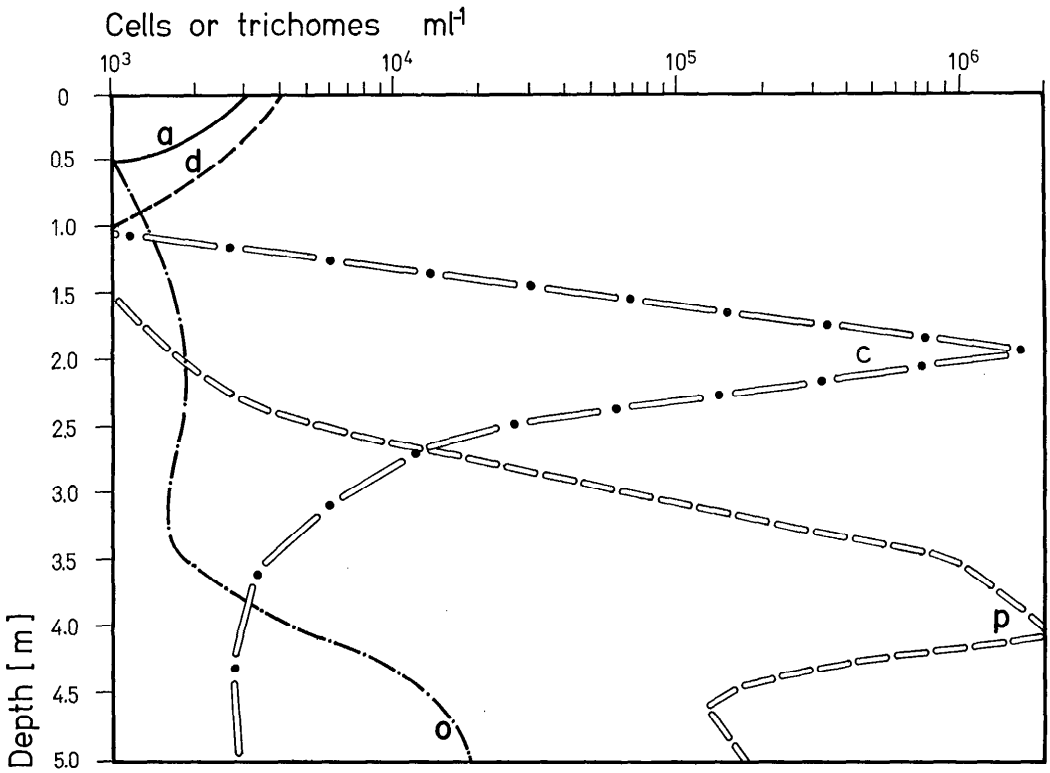

Fig. 2. Vertical distribution of photosynthetic microorganisms during stratification. Numbers (direct counts) of each group from samples taken on 27 March 1971: d—diatoms (*Nitzschia* sp., *Amphora* sp., *Navicula* sp.); a—unicellular cyanobacteria (*Aphanothece halophytica, Aphanocapsa littoralis*); c—*Chromatium violescens*; p—*Prosthecochloris* sp.; o—filamentous cyanobacteria (*Oscillatoria limnetica, Oscillatoria salina, Microcoleus* sp.).

nm. Minima of light transmission in the green and red at depths of 3 and 3.5 m appeared at 630, 665, and 710 nm, corresponding to the absorption maxima of phycocyanin, chlorophyll *a*, and bacteriochlorophyll *c*. At the bottom, light transmission was restricted to a narrow peak at 565 nm and a second increase at 710 nm.

Figure 4 shows the vertical light transmission during summer holomixis. The peak in the green at 565 nm and the relatively high absorption in the blue and red represent the normal absorption of light in relatively clear hypersaline water. The slight absorption at 660 nm in the upper 3 m of the water column may be caused by low concentrations of chlorophyll *a*.

The vertical distribution of integrated values for light transmission in the whole visible range (405–710 nm) during stratification and holomixis is summarized in Fig. 5. The absorption in the epilimnion was relatively low down to a water depth of 1.5–2.0 m. The bacterial plate of the metalimnion caused a high absorption at 2.5–3 m, which was further increased in the hypolimnion by a dense cyanobacterial bloom and the presence of some photosynthetic sulfur bacteria. The total integrated visible light intensity at the bottom (4.5 m) was only 0.5% of the surface light intensity. In summer, light transmission to the bottom was fifty times higher: 25.7% of the integrated surface light intensity in the visible range reached the bottom at that time. A linear decrease was observed for all depths, except the uppermost 50 cm, influenced by

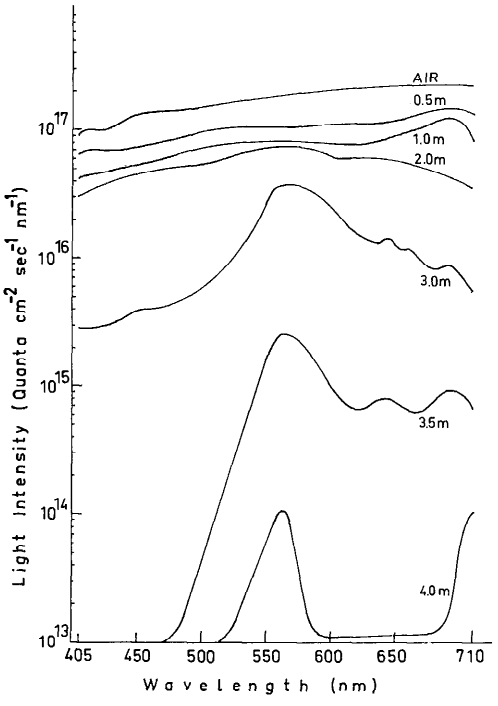

Fig. 3. Vertical light transmission in visible spectrum measured during stratification, 6 June 1974.

convectional mixing of the highly concentrated brine with seawater seeping into the lake.

The development of the photosynthetic sulfur bacteria communities during stratification was closely related to the simultaneous establishment of an anoxic zone with increasing H_2S concentrations toward the bottom (Fig. 6). The two different communities of photosynthetic sulfur bacteria described above were correlated with the concentration of H_2S. The upper community, consisting mainly of *C. violescens*, reached maximum cell densities at the CO_2–H_2S boundary and moved vertically with the seasonal changes of this chemocline during stratification (Fig. 7). The second community, composed mainly of *Prosthecochloris* sp., seemed to be closely correlated to an H_2S concentration of about 15 ppm and moved vertically together with the seasonal changes of this concentration (Fig. 7). Thus, the vertical separation of

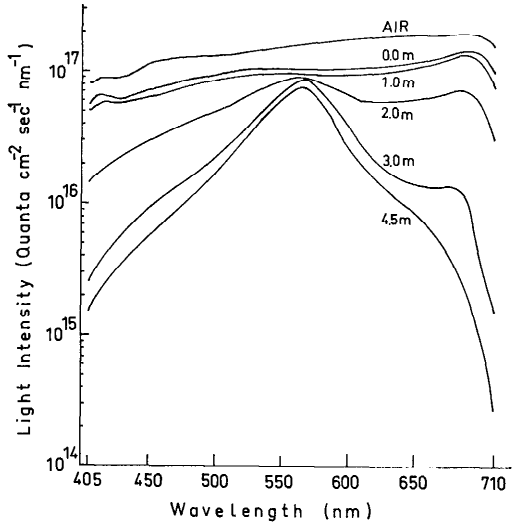

Fig. 4. Vertical light transmission in visible spectrum during holomixis, 9 September 1974.

the two communities became more and more accentuated with the development of stagnation. At maximum stratification the two vertical plates were separated by 2 m (Fig. 2). The *Oscillatoria* plate remains at the bottom throughout stratification. Anoxygenic photosynthesis by this strain was found to require high H_2S concentrations: above 0.5 mM (Cohen et al. 1975*a*).

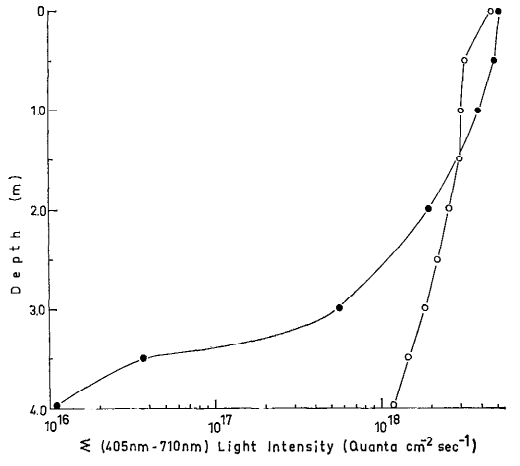

Fig. 5. Vertical integrated light transmission in visible spectrum during stratification, 6 June 1974 (●), and during holomixis, 9 September 1974 (○).

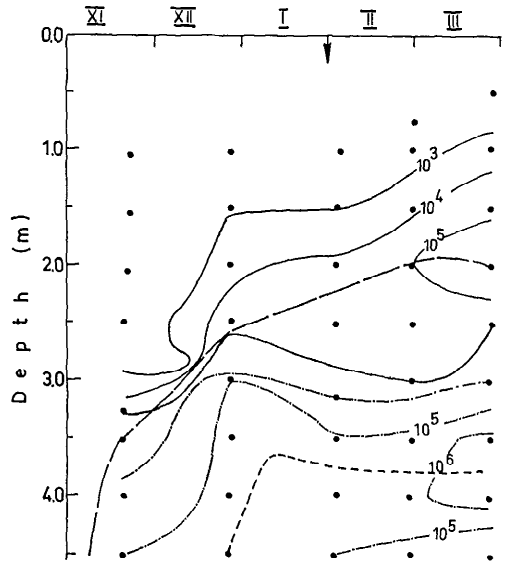

Fig. 6. Seasonal and vertical distribution of *Chromatium violescens* (——) and *Prosthecochloris* (-·-·-) during period of stratification, November 1970–March 1971, in direct counts; O_2–H_2S borderline (— — —) 15 ppm H_2S; chemocline (- - - - -). Arrow—flash flood.

Periodic observations during 1970–1971 showed rapid development of the two photosynthetic sulfur bacteria plates during the early phase of stratification. After a more or less stationary phase (throughout January) a second rapid increase in cell density and in the volume of water occupied by the photosynthetic bacteria followed a partial distortion by a flash flood.

During holomixis the entire water column was oxygenated (Fig. 7). With the establishment of the pycnocline (in September) oxygen quickly disappeared from the deeper parts of the lake. This is related to the development of a dense community of chemoorganotrophic bacteria in this zone (*Cohen et al. 1977b*). From late November, H_2S, produced mainly in the bottom sediment, began to accumulate in the water and reached a maximum concentration of 39 ppm (April 1971). Toward the end of stratification (May 1971), with lowering of the thermocline, dissolved oxygen reached maximum values of 9 ppm above the thermocline; it was produced by development of the coccoid cyanobacterium *A. halophytica* in this zone. With the breakdown of stratification the dense photosynthetic communities were dispersed and the total number of these organisms in the entire column decreased markedly, leading to a reduction in total photosynthetic activity.

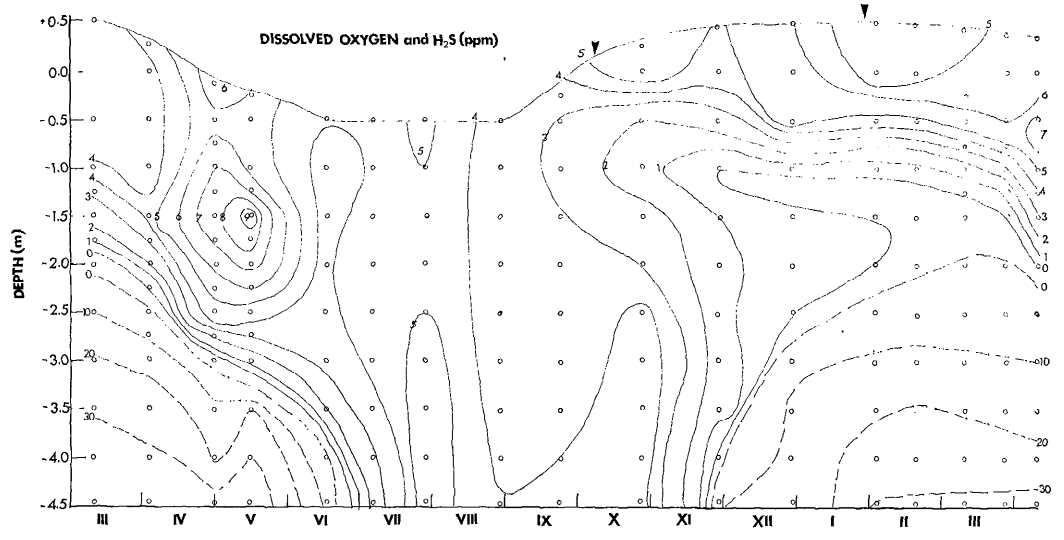

Fig. 7. Seasonal and vertical distributions of dissolved oxygen (——) and H_2S (- - - - -), 1970–1971. Arrows—introduction of freshwater during flash flood.

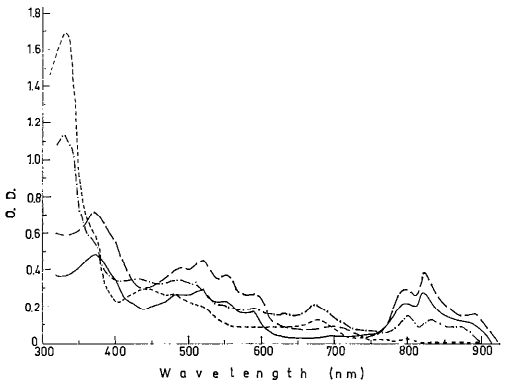

Fig. 8. Absorption spectra of cell suspension from different depths in April 1971 at 1 m (– – – – –), 3 m (–•–•–), 4 m (——), and 4.5 m (—— ——).

Pigments—The absorption spectra of concentrated water samples from different depths were measured periodically during the annual cycle of 1972–1973. The pigment composition determined spectroscopically was in good agreement with the viable counts of the photosynthetic organisms which were isolated simultaneously.

A typical set of in vivo absorption measurements from different water depths is given in Fig. 8. The absorption spectrum recorded at 4 m corresponds almost to that of pure cultures of *Chromatium* (*see* Gest et al. 1963, p. 496); the dominant photosynthetic microorganism was *C. violescens*. A small peak at 675 nm, typical of chlorophyll *a*, represents the presence of some cyanobacteria at this depth. Far red peaks, typical for the bacteriochlorophyll *a* of *Chromatium*, appeared at 3, 4, and 4.5 m. From the optical density it can be calculated that the maximum bacteriochlorophyll *a* concentration occurred at 4 m, corresponding to the O_2–H_2S boundary at that time. In 1972 the maximum H_2S concentration was only 5 ppm, in contrast to 39 ppm in 1971. In 1972 only the *C. violescens* plate was found; the absence of the *Prosthecochloris* plate can be explained by the lower H_2S concentrations in that year.

Primary production and biomass—The seasonal and vertical distribution of primary production calculated from the CO_2 photoassimilation of $[^{14}C]NaHCO_3$ is summarized in Fig. 9. During holomixis (Au-

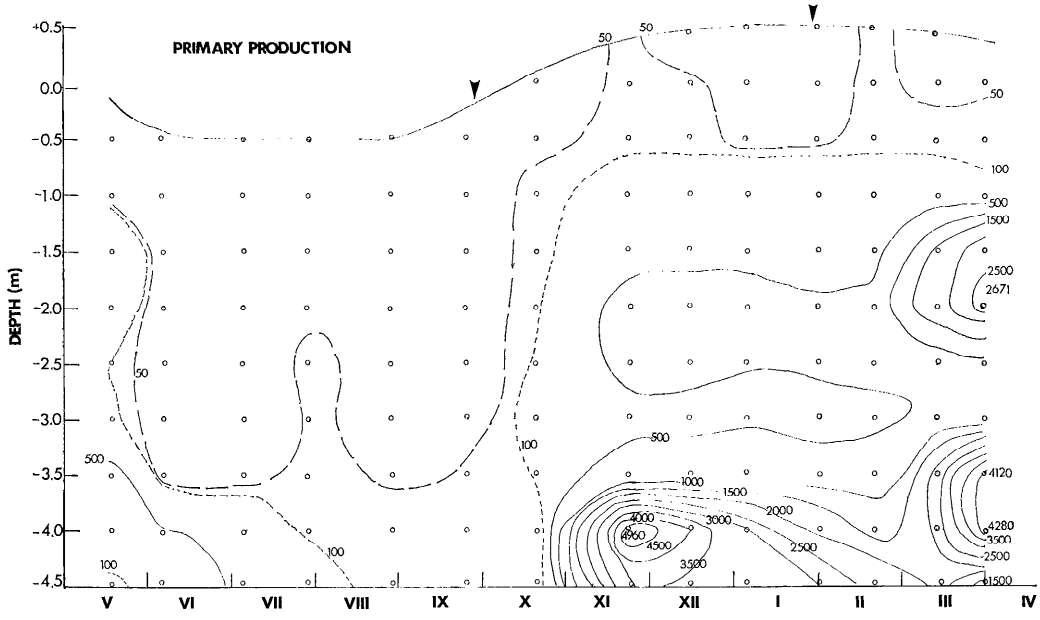

Fig. 9. Seasonal and vertical distribution of primary production, 1970–1971, expressed in mg C m^{-3} d^{-1}. Arrows—introduction of freshwater during flash flood.

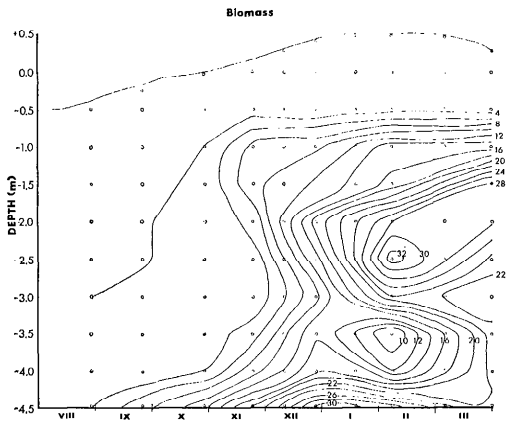

Fig. 10. Seasonal and vertical distribution of biomass during stratification, 1970–1971, expressed in g C m^{-3}.

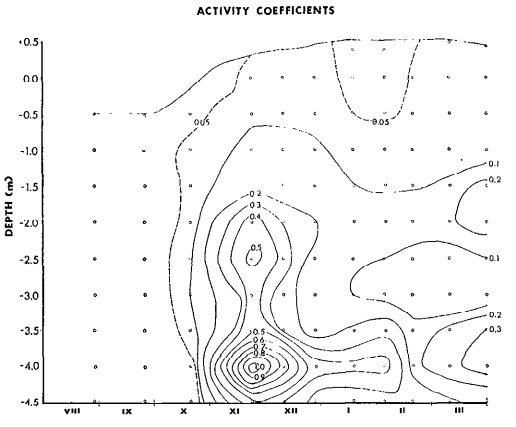

Fig. 11. Seasonal and vertical distributions of activity coefficients, as calculated from Figs. 9 and 10, expressed in C photoassimilated per day per C biomass.

gust to mid-October) the primary production of the whole water column was low; it did not exceed 100 mg C m^{-3} d^{-1} for all depths. During stratification most primary production took place in the metalimnion and hypolimnion; the epilimnion was characterized by extremely low productivity. Thus, primary production in Solar Lake takes place mainly at depths where H_2S is present.

A maximal primary production of 4,960 mg C m^{-3} d^{-1}, measured at 4 m at the beginning of stratification on 20 November 1970, represents one of the highest productivities so far recorded for natural nonpolluted waters. Two distinct productivity zones develop, in the metalimnion and hypolimnion, with advancing stratification.

The stationary phase in stratification mentioned before is accompanied by a decrease of productivity. The partial distortion by the desert flash flood in 1971 (*see Fig.* 9) was followed by high peaks in primary production. At this time three different vertically separated maxima of productivity developed. With the disappearance of H_2S by overturn, the H_2S-dependent photosynthetic communities broke down, and the total production dropped considerably as a consequence.

Vertical and seasonal distributions of biomass are presented in Fig. 10. During holomixis the biomass was low throughout the water column and did not exceed 6 g C m^{-3}. Three separate biomass peaks gradually developed during this period.

Activity coefficients were calculated from primary production and biomass, and their vertical and seasonal distributions are plotted in Fig. 11. They were highest in the early phase of stratification, demonstrating the fast development of the photosynthetic bacterial communities. The maximum value of 1.0, calculated for 4 m on 20 November 1970, represents a theoretical doubling of the biomass within a single day. The stationary period (in January) is represented by drastically decreased values; after the flood distortion a new increase began in the metalimnion and hypolimnion.

Discussion

In Solar Lake, changes in climatic factors and water supply have a great influence on the seasonal development of monomixis, which in turn affects the distribution of H_2S and oxygen. During the period of investigation (1968–1974) maximum H_2S concentrations in the hypolimnion varied between 5 and 39 ppm. These fluctuations seem to be a major factor in controlling the distribution of photosyn-

thetic bacteria. In 1970–1971, there were two separate bacterial plates of *C. violescens* and *Prosthecochloris* sp., and a third distinct layer of cyanobacteria below them in the bottom layer where H_2S concentrations rose to 39 ppm and light intensities were extremely low.

The presence of such a bloom was remarkable since it is generally assumed that cyanobacteria occur only in the presence of oxygen (Zimmermann 1969); however there are reports of cyanobacteria under anoxic conditions (Castenholz 1969, 1973; Stewart 1973). The presence of a cyanobacterial bloom below two photosynthetic sulfur bacteria communities has never before been reported. These cyanobacteria have been isolated in pure culture and their photosynthetic capacity under different conditions has been studied (Cohen et al. 1975*b*). One of these isolates, *O. limnetica*, which dominates the bottom bloom is of special interest. It was found to be able to photoassimilate CO_2 under aerobic conditions with O_2 evolution via both photosystems I and II and to fix CO_2 in anaerobic conditions using sulfide as sole electron donor. Under these conditions only photosystem I was operative, similar to the photosynthetic mechanism of photosynthetic sulfur bacteria. It was shown experimentally that high concentrations of H_2S are required to activate this anoxygenic photosynthesis of *O. limnetica* (Cohen et al. 1975*a*).

The light intensity reaching the bottom of Solar Lake during stratification may be too low (0.5% of the surface light) for oxygenic photosynthesis, but may be sufficient for anoxygenic photosynthesis based on H_2S as electron donor. The light spectrum reaching the bottom has two defined peaks (at 565 and above 710 nm). Both peaks stimulate photosystem I in *O. limnetica*, while wavelengths preferentially stimulating photosystem II (mainly 630 and 675 nm) have been absorbed at the metalimnion. Under these special light conditions, an organism capable of utilizing the high H_2S concentration for photosynthesis has an ecological advantage. Therefore we assume that this type of cyanobacterium is not restricted to Solar Lake and may be found in other sulfur biotopes exposed to light.

The presence of three clearly defined layers of photosynthetic microorganisms in the H_2S zone of the stratified lake seems satisfactorily explained by their different requirements and tolerance of H_2S. Above the cyanobacterial bloom, two separate layers of photosynthetic sulfur bacteria—*Chromatium* above, *Prosthecochloris* below—were recorded for 1970–1971. This vertical distribution of photosynthetic bacteria fits perfectly the description by Van Niel (1963, p. 459).

> The green bacteria have a greater tolerance for H_2S than do the purple sulfur bacteria. The former are therefore apt to occur closer to the source of H_2S, which is usually generated by the biological activity (sulfate reduction) in the bottom sediments. Hence mass developments are frequently stratified with the purple above the green sulfur bacteria.

Gorlenko and Lebeva (1971) have described examples of two different plates of photosynthetic sulfur bacteria. This seems to be, however, a relatively unusual observation; only a single plate of photosynthetic sulfur bacteria has been observed in many stagnant lakes (Culver and Brunskill 1969; Genovese 1963; Overbeck 1974; Takahashi and Ichimura 1968). In most stagnant lakes the light intensity at the O_2–H_2S border is minimal (0.1% and less), and the strata highly enriched with H_2S are completely dark. Thus, in most such lakes only one plate of photosynthetic sulfur bacteria appears; it may be dominated by Chromatiaceae, Chlorobiaceae, or a mixture of both (Culver and Brunskill 1969; Kusnetsov 1959; Pfennig 1967; Takahashi and Ichimura 1970; Trüper and Genovese 1968). In shallow Solar Lake, however, the extremely high irradiation allows efficient light intensities to reach the H_2S-rich layer (4.5–5 m).

Overbeck (1974) stressed the role of phototrophic sulfur bacteria in primary production, which in some meromictic lakes may reach 25% of the total annual production. During phases of low produc-

tivity in the epilimnion of monomictic lakes and in the mixolimnion of meromictic lakes, the contribution of phototrophic sulfur bacteria to the daily production may be as high as 91% (*see Table 1*). Primary production in stratified Solar Lake is almost entirely restricted to the metalimnion and hypolimnion populated by the photosynthetic sulfur microorganisms. The contribution of these microorganisms to the annual production is as high as 82.3%, because the period of stratification lasts for at least 9 months per year. The highest primary production recorded reached 4,960 mg C m^{-3} d^{-1} at 4 m, corresponding to 5,280 mg C m^{-2} d^{-1}. The highest production in terms of surface area, calculated as 8,015 mg C m^{-2} d^{-1} because of the additive effect of the three different peaks (2,671 mg C m^{-3} d^{-1} at 2 m, 4,960 at 4 m, and 1,500 at the bottom), was recorded 3 months later (*see Fig. 9*).

The overall annual primary production of Solar Lake is low, reaching only 59.09 g C m^{-2}. This is related to the bathymetry of the lake. The relatively low average values are caused by the extremely low productivity in the epilimnion during stratification and in the whole water column during holomixis. If annual primary production is calculated only for the water column below the winter epilimnion, a value of 222.43 g C m^{-2} is obtained for the surface area of the metalimnion. The corresponding value for the surface area of the hypolimnion is 923 g C m^{-2}. The annual production of the epilimnion does not exceed 18.24 g C m^{-2}. This unique partition of primary production is contrary to that observed in monomictic lakes with winter overturn and in meromictic lakes with low productivity in the hypolimnion (Culver and Brunskill 1969). The extremely high irradiation throughout the year in the Sinai may inhibit primary production in the oxygenated epilimnion by creating photooxidative conditions to which certain cyanobacteria seem to be especially sensitive (Abeliovich and Shilo 1972).

Holomixis is characterized by low values of primary production (maximum recorded: 136.25 mg C m^{-2} d^{-1}). During this period the communities of phototrophic sulfur bacteria dominating the metalimnion and hypolimnion disappear completely. Parts of the cyanobacterial benthic mats of the hypolimnion float up with the mixing brines and form a temporary peak of primary productivity during mixing (*see Fig. 9*). The photosynthetic cyanobacterial community of the winter epilimnion, consisting of several species of diatoms and coccoid cyanobacteria, is distributed evenly throughout the water body during holomixis. Diatoms, which are most resistant to photooxidation, predominate at this time.

The data presented here stress the contribution of cyanobacteria to primary production in anoxic layers of stagnant lakes. Until now this primary production has been attributed exclusively to photosynthetic sulfur bacteria. The role of possible anoxygenic photosynthesis by cyanobacteria, frequently recorded under anoxic conditions, was neglected. In holomictic lakes, where stagnant (anoxic) periods alternate with oxygenated conditions, an organism capable of switching from oxygenic to anoxygenic photosynthesis has an important ecological advantage.

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