Solar Lake (Sinai). 4. Stromatolitic cyanobacterial mats

Wolfgang E. Krumbein
Geoscience, University of Oldenburg, Oldb. P.O. Box 943, D-2900 Oldenburg, Germany

Yehuda Cohen
Department of Microbiological Chemistry, Hebrew University, P.O. Box 1172, Jerusalem, Israel

Moshe Shilo
Department of Microbiological Chemistry, Hebrew University

Abstract

Cyanobacterial mats of Solar Lake, studied in the field and by microscopic methods, are classified into four types: flat shallow-water mat, pinnacle mat on the upper slope, cyanobacterial and other photosynthetic bacterial films on the lower slope, and flocculose mat at the bottom. The annual cycle and development of the four types are described. Measurements of photosynthesis by the flat shallow-water mat in the field and the laboratory yielded an average value of 10 g C m⁻² d⁻¹. In the flocculose anaerobic bottom mat 5 g C m⁻² d⁻¹ was measured. Total accretion rates including organogenic material for the four mat types range between 5 and 50 cm 100 yr⁻¹; aerobic and anaerobic degradation of the organic production of the shallow-water mat remineralizes more than 99% of the biomass. In the deeper parts of the mat, organic matter is transformed into carbonates. The role of bacteria in this process is demonstrated by ultramorphological analyses and by comparison to laboratory experiments with bacterial isolates.

The zonation of benthic communities in mesothermal, hypersaline Solar Lake is caused by the rapidly changing environmental conditions (Cohen et al. 1977a). Several different types of cyanobacterial and bacterial mats carpet the entire bottom of the lake. We here report on the spatial distribution, accretion rates, degradation, and ultimate transformation into solid rock material of the cyanobacterial mats.

The development of cyanobacterial mats and the calcification within such environments have been described from various intertidal environments (e.g. the Persian Gulf: Golubic 1973; Shark Bay, Australia: Davies 1970; the Bermudas and Bahamas: Monty 1972; Africa: Walter et al. 1973). Park (1976) commented on the significance of laminations in recent and ancient stromatolites.

With the exception of the thermal environments (Brock and Brock 1967) in most cases the geological setting and the sediment trapping were studied more extensively than productivity and degradation pathways in the mats. Similarities between recent mats of stromatolitic environments and ancient stromatolites and stromatolitic rocks have been described by Awramik (1971), Monty (1967), and Owen (1973). Several possibilities have been proposed for the sometimes still debated carbonatization in such environments: trapping of carbonate grains on cyanobacterial mucus; precipitation of carbonates via photosynthetic CO₂ uptake and consequent carbonate precipitation by HCO₃⁻ shifts; inorganic precipitation from seawater supersaturated for Ca, Mg, and bicarbonate; precipitation by chemoorganotrophic and chemolithotrophic bacterial activities during degradation and decay of cyanobacterial material. Biogeochemical reactions leading to carbonate precipitation have been proposed by several workers, sometimes without substantial biological or biogeochemical data (e.g. Friedman et al. 1973; Kitano et al. 1970; Mitterer 1972; Suess and Fütterer 1972). It

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2 Present address: H. Steinitz Marine Biology Laboratory, P.O. Box 469, Elat, Israel.
is also of interest whether cyanobacteria can be fossilized during the process of degradation and transformation into carbonates (Krumbein 1975; Krumbein and Cohen 1974). We have therefore studied productivity, accretion rates, degradation of organic matter, and lithification processes of the benthic cyanobacterial mats by morphological, biological, and chemical methods.

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**Material and methods**

The benthic cyanobacterial mats were studied from a boat, by walking on the shallow mats, and in frequent SCUBA dives. In winter during stratification few diving observations were possible because the water temperature was too high (50°-60°C) and visibility was restricted by suspended bacteria and the floculose mats. In summer during holomixis, the whole slope and bottom area were easily observed and samples were taken at several places.

Samples for sediment analyses were taken by SCUBA diving as well. Altogether three long cores from the bottom, two cores from the slope, and 12 cores from the shallow mats were taken. Chemical and bacterial analyses were done on five of them. Two cores were analyzed completely, the others used for random subsamples and for counting laminae. Subsamples for transmission and scanning electron microscopy were fixed in 4–6% glutaraldehyde in Solar Lake water immediately after sampling, to avoid osmotic shock. The samples were then washed in cacodylic buffer and dried in alcohol series, by critical point drying, or both.

**Determination of accretion rates**—Accretion rates were determined by five different methods which were correlated and compared. 1. Laminae of the cyanobacterial mats were counted. 2. Measurements of actual and potential primary productivity of the upper parts of the mats were transformed into total organic matter production. 3. Inorganic compounds in the mat were determined by ignition of samples. 4. Deposition and accretion of gypsum, carbonates, and organic matter on objects placed into the lake were observed from 1969–1974. 5. Five selected samples were dated by 14C (courtesy of M. A. Geyh). The ages obtained were correlated with counted laminae and sampling depth.

**Determination of productivity**—Oxygen method. Slices (20 × 20 × 1 mm) of the surface layer of the algal mat were put into a 2-liter incubation vessel and illuminated under 2,000 lux at a distance of 150 cm with constant stirring. Changes in oxygen concentration, pH, and temperature were recorded continuously under light (12 h) and dark (12 h) conditions for several 24-h periods. Ingold pH and Hydrobios oxygen electrodes were used. They were controlled by oxygen titrations every 4 h. Organic carbon production was then calculated according to Lund and Talling (1957) and Schramm (1966).

Primary production was also measured by covering parts of the mats in situ with domes of acrylic plastic. We tried to avoid penetration of the domes into the mat material to prevent changes in oxygen concentration by increased H₂S migration from the layers below.

The O₂ and H₂S concentrations were determined by taking water samples from the domes after stirring with a device fixed to the domes. O₂ and H₂S were determined according to Standard methods (Am. Public Health Assoc. 1971).

14C-method. As described by Brock and Brock (1967), cores from the mats were
sliced into 1.5-2-mm slices of known diameter (medical syringes were used for sampling). The slices were homogenized and aliquot samples were incubated with $[^{14}\text{C}]\text{NaHCO}_3$ in the light and in the dark. Alkalinity measurements were controlled by dissolved inorganic carbon measurements (Cohen et al. 1977b). Other subsamples were extracted three times with acetone, and chlorophyll a and pheophytin were determined in a spectrophotometer. Protein was determined by the modified method of Lowry et al. (1951) from Brock and Brock (1967).

**Bacteriology**—Bacteriological inocula were prepared by cutting pieces from the central parts of the long cores (5-cm diam) with scalpels sterilized in portable Bunsen burners. All inoculations were made with media and methods described by Krumbein (1971). The media were prepared with aged Gulf of Elat water (41%) and Solar Lake water (150%) and the cultures were incubated at 35°C. Sulfate reducers, anaerobic heterotrophic bacteria, and bacteria producing H$_2$S from organic sulfur compounds were cultivated in solid media in completely filled tubes, sealed with paraffin.

Experiments on carbonate precipitation were done according to Krumbein (1973, 1974). Isolates from the mats were incubated in media of different salinities made up from seawater, with one specific carbon compound serving as carbon and energy source. We used amino acids, lactate, polysaccharides, and sterilized mat material. All compounds that we used generally occur in such environments. NaNO$_3$ was added to some of the media to test denitrification. We used the same media for aerobic, anaerobic, and sterile incubations.

Organic nitrogen and carbon were determined on decalcified samples in a CHN-analyzer (catalytic oxidation and reduction, gas chromatography, and heat conduction detector: Hewlett-Packard). For decalcification we used 7.5% phosphoric acid to minimize losses of volatile organic compounds. Chlorophyll a and pheophytin were determined according to Strickland and Parsons (1968). Inorganic carbon (carbonate) was determined by two different methods. In the first, samples were dried and mixed with hydrochloric acid in a gas vessel; CO$_2$ evolution was measured by a manometer. In the second, Ca and Mg were determined by EDTA titration with calconcarbonic acid and murexide as indicators on HCl extractions and CO$_2$ was calculated, assuming that only CaCO$_3$ and MgCO$_3$ were dissolved by HCl. The two methods gave values within 4%.

Samples of the mats and of the bacterial carbonate precipitates obtained in the laboratory were fixed in glutaraldehyde (the laboratory precipitates after slow filtration on Nuclepore 0.15-μm filters), washed in cacodylic buffer, and dried in alcohol or by critical point drying. The samples then were coated with carbon for energy dispersive X-ray analyses and with gold-palladium or gold for SEM micrographs.

**Results**

**Productivity measurements in the flat shallow-water mat**—The potential CO$_2$ photoassimilation and dark CO$_2$ uptake were measured in the shallow-water mat (Fig. 1). The highest photoassimilation (1.5 mg C cm$^{-2}$ d$^{-1}$) is recorded at 2-mm depth. The surface slice shows significantly lower CO$_2$ photoassimilation, which may indicate photoinhibition at the surface of the mat. Four major peaks of po-
potential CO₂ photoassimilation recorded in the whole 1.8-cm core alternate with peaks of dark CO₂ uptake, demonstrating the nature of the lamination of the core. Layers predominantly composed of cyanobacteria yield high photoassimilation rates, while layers consisting mainly of chemoorganotrophic bacteria yield high dark CO₂ incorporation rates; these are winter and summer layers, respectively. The layers with high dark CO₂ incorporation values must contain more material from the summer laminae, more susceptible to bacterial decay than the resistant filamentous cyanobacteria in winter laminae. The distance between the different CO₂ assimilation peaks decreases with depth, probably indicating increased consolidation of the laminae.

The vertical distributions of chlorophyll a and protein along a 1.8-cm core of the shallow-water mat are given in Fig. 2. The four major peaks of chlorophyll a alternate with four peaks of protein. These peaks can be correlated with the peaks of CO₂ photoassimilation and dark CO₂ uptake described in Fig. 1. In general, chlorophyll and protein decrease with depth; this is most pronounced in the upper 5 mm where mineralization causes a 54% decrease in protein. In the lower 0.8 cm of the core, mineralization stabilizes at a lower level with a mean decrease of about 22% in chlorophyll and about 49% in protein (Krumbein and Cohen 1974).

Figure 3 represents the distribution of specific CO₂ photoassimilation (in terms of chlorophyll) and specific dark CO₂ uptake (in terms of protein) in the upper (1.8 cm) part of the shallow-water mat. As in Figs. 1 and 2, alternating peaks of photosynthetic capacity and dark CO₂ uptake appear. Surprisingly, values of specific CO₂ photoassimilation increase with depth, indicating a higher potential photosynthetic activity per unit of chlorophyll a at deeper layers.

Figure 4 represents chlorophyll a:protein and photoassimilation:protein ratios in the upper 43 mm of the shallow-water mat core. Eleven layers, consisting mainly of cyanobacteria and diatoms which retain their photosynthetic capacity, can be distinguished along this section. Though specific photoassimilation decreases by more than three orders of magnitude, some activity can still be determined at the 43-mm depth, which corresponds to about 80 years of burial.

Primary production measurements by
14C (Brock and Brock 1967) for the uppermost layer of the shallow-water mat yielded a net primary production of 12 g C m⁻² d⁻¹. Dissection of the uppermost part of the mat and measurements of O₂ uptake and evolution in the laboratory (Schramm 1966) yielded a net primary production of 8 g C m⁻² d⁻¹. In situ measurements in December 1974 with transparent and dark acrylic plastic domes placed on top of the mat for 4 to 7 h (Jørgensen and Cohen 1977) yielded a primary production calculated from oxygen uptake and evolution of only 0.4 g C m⁻² d⁻¹. These low in situ measurements can be explained by the escape of oxygen and interference by H₂S. The minimal primary production required for balancing organic carbon oxidation via sulfate reduction measured by the [³⁵S]SO₄ method is 1.5 g C m⁻² d⁻¹ (Jørgensen and Cohen 1977). Thus, primary production of the shallow-water mat should lie between a minimum value of 1.5 and a maximum of 12 g C m⁻² d⁻¹. This is astonishingly high productivity.

Estimates of primary production by the oxygen method exclude bacterial-type photosynthesis, which uses H₂S as the electron donor. The shallow-water mat includes several types of photosynthetic bacteria in addition to Oscillatoria limnetica, a major constituent of the mat which has been shown to be capable of bacterial photosynthesis (Cohen et al. 1975a). We thus assume that the total primary production should be close to the maximal potential value recorded by the 14C method.

Temperatures—Many degradation processes depend on sediment temperature. Temperature profiles for different seasons are given in Fig. 5. Temperatures within the mats range from 25.6°-40°C and are related to the development of the thermocline within the water column in contact with the sediments. The temperature distribution in the sediments undergoes an annual cycle, governed by the limnological cycle of the lake. In spring and early summer the thermocline is at 2.8-3 m and the mat has a relatively uniform temperature. In fall and winter, with the thermocline rising closer to the surface, temperature gradients in the mat are pronounced (Cohen et al. 1977a).

Oxidation-reduction potential and pH—pH and Eh values show a steep gradient in the upper 20 cm of the mats, where pH changes from 7.7 to 6.6, and Eh from −155 to −215 mV (Fig. 6). In the zone below (20-35-cm depth), which is charac-
terized by numerous borings of the coleopteran *Berosus*, pH and redox potentials increase considerably, down to the densely packed cyanobacterial material (35–80 cm) which is a more reducing environment. Near the bottom of the core (80 cm), pH (6.95) and Eh (−222 mV) reach minima; at 90 cm, immediately above the gypsum layer, both increase slightly.

**Water content**—The average water content of the mat material from the surface to about 70–80-cm depth is around 70%, with a decrease to about 63% observed for the bored zone between 15 and 35 cm. The water content decreases to a minimum of 31% in the gypsum sediments below the mats (below 85 cm).

**Chemical analyses of cyanobacterial mat cores**—Gypsum sediments are not found in the shallow-water mat itself; they underlie the mat and belong to a different era in the history of the lake (85–115 cm: Fig. 7). Gypsum precipitating in or on the mats would be reduced immediately by *Desulfovibrio*. The distribution of carbonates is summarized in Fig. 8. The carbonate content within the cyanobacterial laminites increases with depth. Three different areas can be defined. From 0–10 cm, the average concentration is <10% of the dry weight. Between 10 and 35 cm, CaCO$_3$ increases to average values of 50%, which remain more or less stable down to a 5-cm layer, between 75 and 81 cm, that contains up to 80% CaCO$_3$. Analyses of selected laminae reveal CaCO$_3$ layers with concentrations even higher than 85%, alternating with layers containing a high percentage of organic matter. This reflects the lamination of the mats (Fig. 7).

The high average concentration of calcium carbonate at the bottom of the mats may be caused by seepage of seawater, replenishing calcium and magnesium ions along this interface. Calcium carbonate concentrations in the gypsum sediments below the mats are about 10%. Thus the development of high CaCO$_3$ concentrations in Solar Lake sediments is intimately linked with the organic fraction of the mats.

**Organic material**—The concentration of organic matter in the shallow cyanobacterial mats of Solar Lake is very high. The concentrations of organic carbon and nitrogen are shown in Fig. 9.

Organic C and nitrogen decrease rapidly in the first 10 cm. A clearly discernible layer of clastic sediments (from a flash flood) is embedded in the mats at about 13 cm and contains very low amounts of org C (0.35%) and org N (0.02%); these values were not included in the average curves. A further decrease is seen at about 35 cm, corresponding to the lower end of the bored zone (Fig. 7). In the deeper highly compacted cyanobacterial mats (35–80 cm) the values fluctuate according to sampling and lamination, but do not exceed 5% org C and 0.4% org N.

The separation into three distinct parts is even more pronounced with respect to carbon:nitrogen ratios (Fig. 9). The carbon:nitrogen ratios are low in the topmost 10 cm and decrease to about 6.5 at the lower end of the highly reducing zone (see Fig. 7). Throughout the boring zone the C:N ratios remain fairly constant (about 8.5). The ratios then continuously increase in the deeper compacted layers to a final value of 12.3.

Chlorophyll $a$ and pheophytin (Fig. 10)
rapidly decrease in the first 13 cm of the core. As expected, chlorophyll $a$ is degraded faster than its derivative. The concentrations of both, as well as their ratios, are quite constant from 20 cm downward. The preservation of some chlorophyll $a$ to a depth $>80$ cm within the sedimentary column is probably a result of the highly reducing conditions in the compacted cyanobacterial mats (Fig. 6).

**The distribution of bacteria in Solar Lake sediments**—Viable counts for different physiological groups of bacteria were obtained from mat sediments of the shallow and deep parts of the lake; those of a core from the shallow-water mats are presented in Table 1.

Aerobic heterotrophic bacteria were extremely abundant in the surface layer, reaching numbers of $10^8$ g$^{-1}$ wet wt, and decreased sharply with increasing depth. Viable counts at 40-cm depth were of the order of $5 \times 10^2$ g$^{-1}$ wet wt. Aerobic heterotrophic bacteria in the deeper parts of the core consisted mainly of bacilli, as indicated by the relatively high numbers obtained on freshwater medium. At 80 cm (the lowermost part of the cyanobacterial layers), in contact with loose clastic and gypsum deposits, numbers again increased to $10^4$ g$^{-1}$ wet wt.

Viable counts of anaerobic heterotrophic bacteria were relatively low: $8 \times 10^4$ g$^{-1}$ wet wt at the surface, $5 \times 10^2$ at 40 cm, and an increase to $16 \times 10^8$ at 80 cm. These low counts for anaerobic bacteria, including *Desulfovibrio*, may be partly due to exposure to oxygen during inoculation. The increase in counts of heterotrophic bacteria on all the different media at the lowermost part of the cyanobacterial layers can be explained, like the increase in

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**Fig. 7.** Typical laminated core of shallow mats. Upper portion is black due to sulfate reduction and sulfide precipitation. Light bands are silt layers (9 cm, 11 cm). From 13–30 cm: bored zone with alteration of laminae; 30–65 cm: condensed cyanobacterial laminites with increasing carbonate inclusions (white layers and spots indicate carbonate laminae and spherules); 65 cm: thick carbonate layer; 70–80 cm: increasing gypsum; 83–115 cm: pure evaporates of mainly gypsum (96–99%) and some carbonate.
CaCO₃, by seepage of seawater along this layer. Seawater seeping through the bar into Solar Lake is under artesian pressure. It is highly probable that nutrients, oxygen, and possibly also bacteria are transported continuously along the interface between the cyanobacterial laminae and gypsum deposits. Viable counts of sulfate-reducing bacteria in the core amounted to $2 \times 10^4$ g⁻¹ wet wt at the surface and $7 \times 10^2$ g⁻¹ at 40 cm. No sulfate reducers were cultured from deeper layers. In another core, viable counts of $4 \times 10^8$ g⁻¹ wet wt were obtained close to the surface and none below 20 cm. Viable counts of bacteria producing H₂S from organic compounds were higher in general than those of Desulfovibrio and were obtained as well at 80 cm ($3 \times 10^2$ g⁻¹ wet wt). Chromatium ($10^8$ g⁻¹ wet wt) and thiobacilli ($2.3 \times 10^3$ g⁻¹ wet wt) were cultured only from the upper 2 mm of the core. No representative viable counts were obtained for cyanophytes, Beggiatoa, or a highly abundant colorless sulfur bacterium classified as Achromatium volutans (Buchanan and Gibbons 1974; la Rivière pers. comm.). Scanning electron microscope surveys of the uppermost cyanobacterial mat layers showed the presence of numerous filamen-
Table 1. Viable counts of bacteria from core d (SE edge of lake).

<table>
<thead>
<tr>
<th>depth in sediment (cm)</th>
<th>aerobic heterotrophic proteolytic bacteria*</th>
<th>anaerobic carbonate reducers</th>
<th>Chromatium</th>
<th>sulfatereducers</th>
<th>H₂S producers (sulfur-ating)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FW</td>
<td>SW</td>
<td>SL</td>
<td>FW</td>
<td>SW</td>
<td>SL</td>
</tr>
<tr>
<td>0.0 - 0.3</td>
<td>2.0 x 10⁴</td>
<td>1.1 x 10⁹</td>
<td>2.9 x 10⁸</td>
<td>8.0 x 10⁴</td>
<td>1 x 10³</td>
</tr>
<tr>
<td>2.0</td>
<td>2.2</td>
<td>4.5 x 10⁴</td>
<td>3.5 x 10⁷</td>
<td>4.0 x 10⁷</td>
<td>7.5 x 10⁴</td>
</tr>
<tr>
<td>5.0</td>
<td>5.2</td>
<td>1.7 x 10⁴</td>
<td>2.2 x 10⁵</td>
<td>1.8 x 10⁵</td>
<td>1.4 x 10⁴</td>
</tr>
<tr>
<td>12.0 - 12.3</td>
<td>3.0 x 10⁴</td>
<td>3.3 x 10⁴</td>
<td>2.7 x 10⁵</td>
<td>1.5 x 10⁴</td>
<td>0</td>
</tr>
<tr>
<td>13.0</td>
<td>13.3</td>
<td>6.0 x 10⁴</td>
<td>7.0 x 10⁴</td>
<td>2.7 x 10⁴</td>
<td>6.5 x 10³</td>
</tr>
<tr>
<td>40.0 - 40.3</td>
<td>500</td>
<td>100</td>
<td>100</td>
<td>500</td>
<td>0</td>
</tr>
<tr>
<td>80.0 - 80.3</td>
<td>1 000</td>
<td>3 000</td>
<td>8 000</td>
<td>6.0 x 10³</td>
<td>0</td>
</tr>
</tbody>
</table>

* FW = freshwater medium; SW = seawater medium; SL = Solar Lake water medium.

Toxous bacteria, with cell diameters between 0.3 and 0.7 μm, resembling those described by Walter et al. (1973), Bauld and Brock (1973), and Castenholz (1973a).

Biogenic carbonates within the mats and from laboratory experiments—The cyanobacterial mats contain no detrital marine carbonates, and only negligible amounts of other detrital sediments are washed into the lake by flash floods from the surrounding metamorphic mountain ridges (e.g. the layer of clastic sediments at ca. 13 cm). The carbonates within the laminites therefore are exclusively autochthonous. We will here discuss only the biogenic carbonates within the mats, not the evaporitic carbonate and gypsum sediments below the mats.

Though carbonate aggregates occur in the first few millimeters, they are more prominent in the deeper parts of the mats. Precipitation of carbonates in the water column above the stromatolites has not been observed, and trapping of the carbonate mud as described by Walter et al. (1973) can be disregarded here because carbonate mud was not found in the uppermost millimeter of the mats during 1968-1974. The surrounding rocks are metamorphic and contain no carbonate minerals. On the other hand, the growth of carbonate aggregates occurs in the uppermost layers within the laminites; this process increases with increasing depth within the sediment: A comparison of CaCO₃ and org-C and org-N values in the cores suggests a direct relationship between the decrease in organic carbon and increasing carbonate within the mats.

Carbonate precipitation as a consequence of CO₂ photoassimilation can play only a minor role in the Solar Lake mats because CaCO₃ is precipitated mainly in the aphotic zone, not in the uppermost productive layers. The microbial degradation of organic matter and biogeochemical reactions leading to CaCO₃ precipitation thus govern the carbonate equilibrium in these mats. Carbon dioxide released by metabolic activity may however migrate through the mats to places where precipitation has been initiated. Aerobic decay, sulfate reduction, denitrification, and fermentation processes are involved in cyanobacterial mats of this lake. Measurements of SO₄ reduction (Jørgensen and Cohen 1977) as well as bacterial counts and pH and Eh curves (Fig. 6, Table 1) indicate that about 10% of the
Fig. 11. Carbonate formation in the laboratory and in the natural mat environment (bar is 1 μ). a—Heterotroph bacterial culture from Solar Lake (24 h); b—same culture after 36 h; c—rods settling on *Nitzschia* sp. (mat); d—same as c; e—enlargement of d; f—microcolony from the mat; g—crystallized rod from mat on hexagonal big crystal and noncrystallized coccus as revealed by EDAX analysis.
organic matter produced by the shallow-water benthic cyanobacteria undergoes sulfate reduction by *Desulfovibrio*.

Ca and Mg carbonate aggregates develop in close morphological relationship to the decaying algae and the bacteria involved in decay processes (Figs. 11, 12, 13). This process is initiated in the aerobic zone and increases in the anaerobic parts of the mat. In order to find out whether CaCO$_3$ precipitation is initiated by the bacteria in the mats, we used 20 isolates in laboratory experiments on CaCO$_3$ precipitation. Sixteen of the 20 bacterial cultures, including *Desulfovibrio*, caused carbonate to precipitate when grown in seawater of different Ca and Mg concentrations with carbon and energy sources such as lactate, acetate, aspartic acid, alanine, peptone, and homogenized cyanobacteria from the lake itself (Krumbein 1973, 1974). No precipitation was observed in sterile controls. Precipitates were formed with different isolates, under aerobic and anaerobic conditions, and at initial pH values from 6.8–8.7, with only minor variations in the results.

X-ray analyses of the precipitates showed that their bulk consisted of aragonite; Mg calcite and monohydrocalcite were obtained in the experiments with lactate and alanine (*see also* Kitano et al. 1970). When Mg salts were added to the culture media, most of the Mg taken out of solution was found in the organic fraction (by treatment with H$_2$O$_2$).

In cultures we found that precipitation of CaCO$_3$ started on the bacterial cell surfaces (Figs. 11, 12) and not within the cells, and that bacteria were destroyed within 96 h by the crystallites surrounding them. The carbonate aggregates obtained varied in size and shape. Some of them resembled the wheat grain type, others formed spherulites, oncoids and oncoidal flakes, and ooidal structures. Similar precipitates frequently occur together with bacteria in the mat environment itself (Figs. 11, 12, 13). Usually the first precipitates developing in the bacterial cultures were dumbbell-shaped aragonite bunches surrounding the cells (Figs. 11, 12). Aragonite needles surrounding a bacterial cell often were later transformed to large pseudohexagonal crystals by recrystallization; the focus of crystallization in these cases was only detectable by the fibrous ends and mucus protruding through cracks in the crystal. The bacterial cell in the interior is first deflated and later completely destroyed (Krumbein 1973).

The various stages of CaCO$_3$ deposition on bacterial and algal material were also studied by SEM techniques. In order to define early stages of CaCO$_3$ precipitation and the type of carbonate developing, we analyzed several SEM samples with energy dispersive X-ray equipment. Bacterial cells initially showed high peaks for potassium, while calcium and magnesium increased in later stages. In this way the transformation of bacterial cells into an aragonite bunch could be followed in laboratory experiments as well as in samples taken from the natural environment (Figs. 11 and 13).

The precipitation of dolomite occurring later is an indirect result of concentration changes in the interstitial brine and the subsequent release of large amounts of magnesium formerly adsorbed to the organic matter.

**Morphology, distribution, and accretion rates of benthic cyanobacterial mats**

The development of different types of benthic mats in Solar Lake, and their accretion rates, is controlled by water depth, the annual limnological cycle, and exposure to different light, temperature, oxygen, H$_2$S, and salinity conditions. Drastic changes in temperature and all other parameters during the annual cycle of this mesothermal monomictic lake (maximum $t = 60.5^\circ$C; summer holomixis and winter stagnation with maximum H$_2$S concentrations of 39 ppm, absence of O$_2$ during stagnation; hypersaline conditions) can also influence the bottom communities (Cohen et al. 1977a).

The benthic cyanobacterial and diatom mats in the lake were classified according to the terminology of Golubic (1973). I—Flat shallow-water mat (0–1.25-m water
Fig. 12. Carbonate development in laboratory cultures and in Solar Lake mats (single bar is 1 μ; double bar is 10 μ). a—Culture as in Fig. 11a,b after 96-h cultivation. Bacteria are crystallized either by aragonitic needles or micritic coating (observe cap at lower right); b—aragonite bunches (same size as in a) from mat with cracks and slime penetrating; c—aragonitic aggregates from labora-
depth); II—pinnacle mat (1.0–2.5-m depth); III—cyanobacterial and other photosynthetic bacterial films on the evaporitic gypsum crusts of the lower slope (1.5–4-m depth); IV—flocculose cyanobacterial mat of the bottom (4–5 m depth).

I—Flat shallow-water mat—An extended strip of laminated cyanobacterial mats surrounds the lake, covering the broad shallow-water region (Fig. 14: I). Parts of this mat dry up in summer because the water level is lowered during the period of maximum evaporation (Friedman et al. 1973). The mat consists of finely laminated layers, 0.5–1.5 mm thick, compacted in extremely flexible form with a leathery appearance. The uppermost 15–20 cm of freshly removed cores are black because of iron sulfides precipitated within the mats (Jørgensen and Cohen 1977). When this layer becomes partially oxidized the original colors return.

In summer the surface of this type of mat is brownish-red with a green underlayer. In winter during stagnation a brilliant green layer appears at the surface, above the brownish-red layer, consisting of filamentous cyanobacteria, mainly Microcoleus sp., accompanied by Oscillatoria limnetica and Oscillatoria salina, Spirulina labyrinthiformis, and an additional Spirulina sp. (Fig. 15). The coccolid cyanobacteria Aphanothece halophytica and Aphanoocapsa littoralis are also found, together with Entophysalis sp. and the diatoms Nitzschia sp., Amphora coffeaeformis, and Navicula sp., but these are rare in winter when the mat is dominated by the filamentous forms. A great variety of photosynthetic sulfur bacteria, filamentous bacteria, colorless sulfur bacteria, and heterotrophic bacteria is found in both types of mats (Fig. 15). The brownish-red summer mat consists of patches of the coccolid A. halophytica and A. littoralis (20–70%), and of the diatoms Nitzschia thermalis, A. coffeaeformis, and Navicula sp. The diatoms produce a granular surface while the surface is slimy where Aphanothece predominates. The production of light-protecting carotenoids by both Aphanothece and the diatoms in summer results in the brownish-red appearance of the summer mat; the filamentous cyanobacteria in the pond are sensitive to photooxidative stress and are overgrown by the coccolid cyanobacteria and diatoms. Thus, a summer mat of diatoms and coccolid forms alternates with a winter mat consisting mainly of filamentous forms.

Because Oscillatoriaceae are capable of both phototaxis and photophobotaxis (Cas-tenholz 1973b; Drews 1959; Nultsch 1962) they can glide rapidly in changing light conditions. The winter mat can be initiated experimentally in summer by shading parts of the mat for a day or two. The filamentous layer below the Aphanothece-diatom community then rapidly covers the red layer with a thin brilliant green film. In addition, part of the green color developing upon shading is caused by greening of the coccolid forms under the reduced light.

This flat shallow-water mat resembles the flat "low" algal type which Golubic (1973, p. 460) described from the Persian Gulf. It is also highly productive and the simultaneously occurring decay processes do not destroy the mat (see p. 652). The accretion rate is low mainly because gypsum precipitates are minimal in the shallow-water mat due to bacterial sulfate reduction. Clastic sedimentation occurs only sporadically when winter flash floods enter the lake. High production combined with decay processes result in a relatively low accretion rate of about 5 cm 100 yr⁻¹.

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tory culture of different heterotrophic bacterial isolate. d—enlargement of c (cf. b); e—Aphanothece, deflated, hollow, encrusted with aragonite (no Mg peak found using ORTEC equipment); f—non-encrusted and encrusted Oscillatoria sp. from shallow mat. Large crystals may be crystallized Chromatium. To left of 10-μ bar small microcolony of rods (no Ca peak); star-shaped aggregate in middle left consists of aragonite.
Fig. 13. Sequence of crystallization of bacteria into aragonite crystal aggregates on *Nitzschia* sp. as noticed in single SEM sample from 4-cm depth (single bar is 1 \( \mu \)m; double bar is 10 \( \mu \)m). a—Note different species of bacteria; b—enlargement of a; c–f—sequential stages of crystallization of aragonite bunches developing in bacterial microenvironment.
A total of 120 cm of shallow-water mats has accumulated in the lake in the last 2,400 years (Figs. 7, 14).

II—Pinnacle mat—The pinnacle mat (Fig. 14) is situated below the flat shallow-water mat at water depths between 1.0 and 2.5 m (Golubic 1973: figures 15, 21, p. 461). The gentle slope is covered throughout the year by a slow-growing, irregularly shaped, loose mat, composed mainly of diatoms and coccolid cyanobacteria. The species composition is almost identical to that of the surface layer of the shallow-water mat in summer. The mat looks rough and shows a pinnacle profile pattern; it is well aerated because of the high surface:volume ratio. It grows on top of a gypsum crust. Seawater under artesian pressure, flowing between the shallow-water mat and the underlying sediments, enters the lake at this level (Cohen et al. 1977a) and supplies additional oxygen (5–6 ppm). The mat thus undergoes rapid aerobic degradation by exposure to dissolved oxygen from both above and below. Trapped oxygen bubbles produced by photosynthesis enhance the mechanical rupture of the mat by floating large portions of it.

The net rate of accretion in this mat is low, because aerobic decay and mechanical disruption counteract primary production. The degradation of organic matter is high because reducing conditions do not develop in lower parts of the mat as they do in the flat shallow-water mat. Sediment accumulation and growth of the gypsum crust are faster than in type I but slow in comparison to type III (see below) owing to low salinities at this water depth in winter; accretion rates reach about 15–20 cm 100 yr⁻¹. At the beginning of stratification the pinnacle mat is exposed to a combination of high salinities and high temperatures. During this time the transient gypsum precipitation produces a “blister-mat” appearance (Golubic 1973: figures 16, 21) which may also contribute to the
development of pinnacles. Vertical growth of cyanobacterial laminites (stromatolites) is well known and pinnacle mats develop frequently in many marine environments (Golubic 1973). Brock (1973) described similar forms for siliceous pinnacle mats in Yellowstone Park (USA).

III—Cyanobacterial and photosynthetic bacterial films—The deeper slope of the lake is covered by a hard crust of gypsum and carbonate (Fig. 14) precipitating from the supersaturated brines (Aharon 1974; Krumbein and Cohen 1974). The precipitation of sulfates and carbonates in this section of the lake is high because salt concentration is high throughout the year at this depth. Temperatures as high as 40°–50°C and minimal sulfate reduction via Desulfovibrio at low organic matter concentrations favor high gypsum accumulation rates. An object placed on the slope from 1968–1973 accumulated a crust of 5–6 cm.

Microorganisms developing here contribute very little to the annual accumulation of sediments. When the gypsum crust forms in summer during holomixis, it is covered by a thin layer of filamentous and unicellular cyanobacteria. In winter, when both carbonate and gypsum precipitation occur, the crust surface is overgrown mainly by the sulfur photosynthetic bacterium, Chromatium violescens, contiguous with the dense metalimnetic Chromatium plate developing at this time (Cohen et al. 1977b). The algal and bacterial films developing during stratification are well preserved within the laminated gypsum crusts down to a depth of about 10 cm. Although organic matter accretion is low compared to that in the shallow-water mat, the highest sediment accumulation in the lake was observed here, reaching values of about 50 cm 100 yr⁻¹.

Several factors may explain the poor development of the microbial community in this mat type. Gypsum and carbonate precipitation occur at maximal rates owing to the generally high salinities and temperatures maintained throughout the year. The gradual descent of the metalimnion and thermocline along the steep slope leads to continuously changing environmental conditions (salinity, temperature, pH, Eh, O₂, and H₂S content) along this section and precludes development of a stable community. Finally, the population of Artemia salina—the major grazer in the lake—is concentrated immediately above the thermocline and moves down with it along
this region of the slope; the grazing of this organism reduces to some extent the accumulation of organic matter. We deduce this from the fact that Artemia is concentrating at the interface of the thermocline with the benthic mat which forms a rim along the lake bottom at this depth.

IV—Flocculose cyanobacteria mat—The term flocculose mat is used to describe the soft flocculose layers formed by cyanobacteria developing in nutrient-rich, aerobic, sheltered marine environments with little sedimentation (Golubic 1973). This layer is frequently lifted from the bottom by oxygen bubbles to float on the water surface.

In Solar Lake a flocculose carpet of *O. limnetica* and *O. salina* develops at the bottom (Fig. 14) during winter under high H₂S concentrations (up to 39 ppm). The occurrence of a dense and highly productive *Oscillatoria* mat under these conditions implied a special physiological adaptation. It was shown that *O. limnetica* is capable of both oxygenic (plant type) and anoxygenic (bacterial-like) photosynthesis using H₂S as electron donor (Cohen et al. 1975b). In winter during stratification the flocculose mat develops into a dense, demersal bloom located between 4.5- and 5-m water depth; productivity then reaches a maximum of 4.9 g C m⁻³ d⁻¹.

Only 0.2% of the surface light reaches the bottom at this time. This corresponds to a value integrated over the visible light spectrum of 10¹⁶ quanta cm⁻² s⁻¹, so that these organisms grow under limiting light conditions (Cohen et al. 1977b). Although the cyanobacteria tend to migrate upward toward higher light intensities, their special type of anoxygenic photosynthesis requires high H₂S concentrations, above a threshold of 0.5 mM H₂S (Cohen et al. 1975b), so that the flocculose mats are restricted to the lower layers of the hypolimnion which provides the suitable H₂S concentrations. The loose form of this mat minimizes the self-shading effect and provides more efficient light absorbency. These species of *Oscillatoria*, so sensitive to photooxidative conditions in the highly irradiated shallow-water mat, thrive well under the limited light prevailing in the deep section. Irradiation at this depth increases at the beginning of overturn and in early phases of holomixis, while H₂S content decreases. Oxygen evolution is then initiated by a switch from anoxygenic photosynthesis to oxygenic photosynthesis. Now the flocculose mat condenses to a layer 0.5–1 cm thick. Large patches of the mat with entrapped oxygen bubbles become detached and float upward, where they are exposed to high irradiation and undergo rapid photooxidative death. Other parts of the flocculose mat are degraded in situ by myxobacteria, forming macroplaques. Myxobacteria isolated from these macroplaques lyse axenic cultures of *O. limnetica* and *O. salina* (Miriam Shilo pers. comm.). Filamentous bacteria, *Beggiatoa* spp., and other nonphotosynthetic sulfur bacteria develop in masses in the lower parts of the mat, forming a white layer on top of it. Thus the greater part of the cyanobacterial mat formed during stratification decays either in situ or after floating up during holomixis.

The accumulation rate is about 10 cm 100 yr⁻¹. The remaining organic matter of the decaying mat contributes not more than 4% of the total accretion and accumulates, without discernible development of laminites, in close mixture with gypsum precipitates.

This type of filamentous cyanobacterial mat can be placed at the extreme end of the scale of cyanobacterial environments with respect to adaptation to low O₂ concentrations and low redox potentials, conditions similar to those described by Brock (1973) and Fogg et al. (1973). The capacity to carry out anoxygenic photosynthesis and to switch to oxygen-evolving photosynthesis allows classification of the *Oscillatoria* strains of the flocculose mat as active participants in the "sulfide system" proposed and described by Fenchel and Riedl (1970).

**Discussion**

The development and preservation of laminated sediments in marine and hyper-
saline environments has been studied from various points of view in many places. Monty (1972, p. 779) wrote, although without substantial analytical data,

All the small scale processes and factors responsible for the given features and behaviour of a stromatolitic flat, as well as the complex flow of biological, social, chemical phenomena within a single algal dome or mat have always frightened me when I consider the simple (too simple!) resulting laminated structures that the paleontologist has to study; I wonder then how much of the natural history of a stromatolite is left in the thin compacted residual laminae found in the base of a recent deposit; how much then in a fossil stromatolite? Well, very little most probably.

Our own analysis of the Solar Lake cyanobacterial mats in terms of morphology, productivity, the decay processes which follow, and the lithification of the mat material allows some general speculation on the lithification and development of stromatolitic rocks. With our data we can try to quantify some of the steps involved in the transformation from the present mats to the analogous, or perhaps homologous, past. The sequence of formation and transformation in the cyanobacterial mat environment begins with production of organic matter by unicellular and filamentous cyanobacteria, and some diatoms. From the productivity data presented here and from the counting and 14C-dating of laminae, we derive the following arguments.

If an average production of 10 g organic carbon m⁻² d⁻¹ is generalized from the summer and winter measurements by the oxygen and 14C methods, we can calculate a productivity of about 25 g dry organic matter m⁻² d⁻¹, using a ratio of organic matter:organic C of 2.5 for the mats. This ratio seems probable from carbon, nitrogen, and hydrogen analyses of surface material. This adds up to 8,000–9,000 g dry organic matter m⁻² yr⁻¹. We will continue our calculation with the lower value, in view of fluctuations in productivity in the lake and its cyanobacterial mats. The water content of the upper layers of the mats averages 70% for the first 70 cm. In the topmost layers it reaches 75–80%. Therefore the total wet weight of the annual production may reach values as high as 26,000–40,000 g m⁻² yr⁻¹. If we use a value of 75% water content we may take a figure of 32,000 g m⁻² yr⁻¹. If we assume a density of 1 for the wet algal material, this would correspond to an annual total accretion of 32 mm of organic material if no degradation processes occurred simultaneously. Since the average depth of the lake is only 1.2 m it would then be completely filled with organic material within about 40 years.

However, the observed accretion rate is only 0.5 mm yr⁻¹ and the age of the organic mat material at 80-cm depth is 2,465 ± 155 years according to 14C-dating. Even in the recent mats, the water content decreases from 75–80% at the surface to 30% in the deepest layers; the final stromatolitic rock has an average water content <5%. The transformation of organic material into carbonates does not bring about major losses or gains in volume. Thus the final rock volume will be about 25–30% of the original wet material. Since only 0.5 mm of wet organic material is accumulated in the lake in 1 year, this corresponds to 0.125–0.15 mm of rock material per annum. From these calculations, which still include sources of error of the order of 10–20%, we see that for the production of 0.125–0.15 mm of a stromatolitic carbonate rock roughly 26–32 mm of wet organic matter (i.e. cyanobacterial biomass) must have been produced. A 1-mm layer of an ancient laminated stromatolitic rock must then have necessitated the production of some 180–250 mm of cyanobacterial biomass, gradually reduced to fossil rock by the processes described: degradation by bacteria, transformation to carbonate minerals, compaction, and dehydration. Keeping this in mind we will discuss in broader terms the processes of degradation and lithification involved.

In his thesis on recent and ancient stromatolites, Monty (1965) observed spherulites and oncolites which he called pellets, probably due to bacterial action. Park (1976, p. 379) summarized several attempts to explain the structural relations and sig-
The significance of laminations in stromatolites and concluded that "millimetre-scale lamination may be produced on a number of interacting processes but as yet no one has been able to determine with any great assurance whether it represents daily, monthly, annual or some other regular periodic growth."

We have seen in Solar Lake the annual accretion of two different layers of the order of magnitude of 0.5 mm, which may be reduced to 0.15 mm in the sequence of fossilization. Therefore we assume that the lamination on the millimeter scale frequently found in stromatolitic rocks is not related to the annual lamination occurring in recent stromatolites. In some cases, many years of algal production may be transformed into clusters of laminae on the centimeter scale, which then may alternate with laminae of gypsum or carbonates not originating from algal material (Cohen et al. 1977a; Park 1976). The data we have accumulated here, and from which we derive the conclusion that lamination patterns in the millimeter scale in ancient stromatolites may not really represent annual layers, are important since to our knowledge nowhere else in the world have laminated algal mats 120 cm thick been found. Also, productivity measurements and taxonomic analyses of different summer and winter populations are scarce in the literature. In addition we have found compacted subrecent cyanobacterial mats with well preserved organic matter, but without any discernible cells, below the recent gypsum precipitates of the deep part of the lake (Fig. 14: IV). 

1^4C-dating of these mats yielded an age of formation between 2400 B.P. and 1900 B.P. Therefore these 30 cm represent about 500 years, which is well within the range of the recent accretion data derived from the shallow mat. Since these mats still contain 35% water and have not yet been entirely transformed into carbonates they will be further reduced to some 10–25% of their present thickness. Thus our conclusions above are supported twice within the same lake with reference to different developmental stages (Cohen et al. 1977a).

What bacterial action is involved in the transformation of organic material into carbonates and carbonate cements has always been somewhat obscure. Bricker (1971, p. 3) wrote "Special factors: Several workers suspect, but without real proof, that occult microorganisms or organic coatings may be the villains explaining a lot of the variability in morphology and mineralogy of carbonate cements." He later stated that the role of bacteria needs to be studied in more detail.

Reviewing the influence of cyanobacteria on carbonate precipitation, Golubic (1973) stressed several factors. The first is the trapping of detrital carbonates. This does not occur in Solar Lake because no detrital carbonates enter the lake. The next is CaCO₃ precipitation via photosynthetic CO₂ uptake. This also has no major effect on carbonate development in the mat in Solar Lake, because the bulk of carbonates form in the aphotic zone.

Golubic's last two suggestions, the effect of bacterial and biogeochemical processes on the cyanobacterial filaments, have been studied more intensively in the shallow-water mats of Solar Lake. In the SEM micrographs of the lake sediments we have identified many structures which can be connected to bacterial calcification (Figs. 11–13). Laboratory experiments with bacterial isolates from Solar Lake yielded large amounts of carbonates similar to the aggregates described from the mats (Krumbein and Cohen 1974). The astonishing similarity between the carbonates produced in the laboratory experiments and those found in the mats supports the assumption that carbonate precipitation within the mats is governed by the degradation of organic carbon compounds by bacteria. The carbonate aggregates that replace the organic matter are closely related to the bacterial morphology and distribution within the mats during the initial stages of precipitation (Fig. 11). The bacteria involved in these precipitation processes are aerobic ammonia-producing bacteria in the aerated zone, Desulfovibrio species, facultative anaerobic proteolytic bacteria, and many denitrifying bacteria in
the anaerobic zone. They produce changes in their microenvironment which lead to carbonate precipitation, such as sulfate reduction, denitrification, ammonification, CO₂ release into a semiclosed environment, and the release of large amounts of organic acids. We observed (Figs. 11–13) that carbonate particles form initially on the cell surfaces of the bacteria and that the precipitation of carbonate aggregates is accelerated in decaying and lysing bacterial aggregates when the cytoplasm is released into the environment.

Our findings support the belief that the carbonate equilibrium of seawater is strongly modified by organic substances. Shearman and Skipwith (1965) have reported carbonate deposits on the mucilagenous coatings of algae (sheaths and slime). Mitterer (1972) demonstrated the relation between proteins excreted to the environment and carbonate precipitation. Suess and Fütterer (1972) have produced ooids in the laboratory by mixing seawater with humic acids. Trichet (1968) showed that the excretion of amino acids by cyanophytes leads to carbonate precipitation. McCallum and Gubathakurta (1970) have demonstrated that many bacteria isolated from Bahama Bank sediments precipitate carbonates. Similar results were found by Krumbein (1974). Berner (1969) has shown that carbonate soaps formed from fatty acids may be precursors of carbonate deposits in anaerobic sediments. Smith (1973) and Smith and Key (1975) in discussing the alkalinity changes of seawater also refer to the problems involved in separating calcification from productivity in terms of CO₂ uptake. They saw little change between day and nighttime calcification in coral reef flats with algal influence. Such calcification may be bacterial. Krumbein (1974) used isolates from coral reef flats to demonstrate bacterial calcification in these environments.

We have shown here that the processes studied in laboratory experiments by SEM techniques in combination with electron dispersive X-ray analyses also occur in nature. A variety of biochemical reactions may produce different types of carbonates within cyanobacterial mats. Jørgensen and Cohen (1977) suggest that the overall equilibrium between the original organic matter and ultimate CaCO₃ supports these findings. Many of the fossilized cyanobacterial structures within the mats (micritic coatings on Aphanothece, needle and micritic cement on some of the Microcoleus filaments) indicate that not only heterotrophic bacteria but also organic matter produced from the cyanobacteria during metabolic activity and decay may contribute to CaCO₃ precipitation. However, observations of fossilized cyanobacterial structures in this environment are rare. Generally the cyanobacterial structures and particularly the heterotrophic bacterial structures are destroyed during the process of lithification, as has been shown in Figs. 11–13. Therefore a detailed study of recent environments is necessary to explain the role of microorganisms in the formation of fossil carbonate laminites and biostromes, so often considered fossil cyanobacterial mats by morphological analogy alone.

It is fascinating that while <1% of the recent material of these stromatolitic mats is transformed to carbonate rocks, this small amount still appears to preserve a record of the laminations of the former living organisms. Finally, it should be emphasized that our observations and calculations hold for certain very special types of cyanobacterial mats in which the agglutination of sediment particles plays almost no role because they are formed in a lake only indirectly connected to the open sea, with its clastic carbonate sediments which usually modify such mats.

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