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Photosynthetic bacterial production in lakes: The effects of light intensity¹

T. B. Parkin and T. D. Brock

Department of Bacteriology, University of Wisconsin, Madison 53706

Abstract

Primary production was measured in six lakes supporting populations of photosynthetic sulfur bacteria. Bacteriochlorophyll concentrations (Bchl *a* + Bchl *d*) ranged from 11.1 to 630 mg · m⁻³. The photosynthetic sulfur bacteria accounted for 0.26–6.3% of the total daily production in the lakes. The percentage of photosynthetic bacterial production of total production in the lakes was not correlated with either sulfide concentration or bacteriochlorophyll concentration but was related to light intensity.

Many measurements of carbon fixation by photosynthetic sulfur bacteria have been reported and estimates of the importance of these organisms as primary producers in lakes vary widely. Culver and Brunskill (1969) reported that the phototrophic bacteria accounted for 83% of the annual primary production in Fayetteville Green Lake and Cohen et al. (1977) that the photosynthetic sulfur bacteria in Solar Lake accounted for up to 91% of the primary production. Other estimates of photosynthetic bacterial production are also available (e.g. Lawrence et al. 1978; Takahashi and Ichimura 1968; Czezuga 1968; Sorokin 1965). The two environmental factors which have been most commonly invoked to interpret production patterns of these bacteria are sulfide and light. These parameters have been incorporated into a model designed to predict photosynthetic bacterial production (Takahashi and Ichimura 1970). The purpose of our study was to measure photosynthetic bacterial productivity in lakes of varying light penetration, to more clearly describe the role of light intensity in influencing photosynthetic bacterial production in lakes.

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Materials and methods

Study areas—Productivity was measured in six lakes chosen because all contained populations of photosynthetic bacteria during their stratification periods. Lakes Peter and Paul (in Michigan near the Wisconsin state line) were separate basins of a single body of water until 1951 when an earthen barrier was built between the two basins and hydrated lime applied to Peter Lake (Johnson and Hasler 1954). The lime treatment was repeated in later years until fall 1976 (G. Gallepp pers. comm.). Lakes Mary and Rose (in northern Wisconsin: Vilas Co.) have been the subject of a number of studies. They are small, dystrophic bog lakes connected by a shallow channel and are highly colored by dissolved organic material. Lake Rose is dimictic and Lake Mary is a biogenically meromictic lake (Weimer and Lee 1973). Mirror Lake (in central Wisconsin in the town of Wau-paca) is a small, eutrophic lake; information on its general limnology is given by Parkin (1978). Fish Lake is relatively large and slightly eutrophic (in the northwest corner of Dane Co., Wisconsin). Stauffer (1974) gives information on its limnology.

Sampling techniques and field measurements—Water samples were collected with a peristaltic pump (Horizon Ecology Co.). Water was pumped through latex tubing (0.48-cm i.d.) which was weighted at one end. The weighted end

was attached to a chain which was used to regulate sampling depth and to prevent stretching of the tubing. This procedure allowed accurate sampling at very narrow intervals and minimized exposure of the anoxic water to oxygen. Samples were collected from positions over the deepest areas of the lakes.

Temperature and oxygen were measured in situ with a combination temperature-oxygen probe (Yellow Springs Instr. Co.), light intensity with a Li-Cor model 185 quantum meter combined with an underwater silicon photodiode quantum sensor (Lambda Instr. Corp.).

Chemical assays—Samples for chlorophyll analysis were collected in polyethylene bottles, transported to the laboratory on ice, and filtered through Whatman GF/C glass-fiber filters. The filters were extracted with 90% acetone and refrigerated overnight for chlorophyll analyses. Chlorophyll *a* was determined as described by Vollenweider (1969), bacteriochlorophylls as described by Takahashi and Ichimura (1968). Absorbances were determined on a Beckman DB-G or a Bausch and Lomb spectrophotometer equipped with a red-sensitive phototube. The glass-fiber filters retained >95% of the chlorophyll retained by membrane filters from the same water samples.

Water samples (10 ml) for sulfide analysis were collected in screwcap test tubes containing 0.5 ml of a 2% solution of zinc acetate in 0.2% acetic acid. Sulfide was determined by the methylene blue method of Pachmayr (Brock et al. 1971) modified so that only 1 ml of the amine reagent and 0.5 ml of the ferric iron reagent was added to a 10-ml water sample.

Dissolved inorganic carbon (DIC = $\text{CO}_2 + \text{HCO}_3^- + \text{H}_2\text{CO}_3$) was measured by a modification of the gas stripping technique of Rudd et al. (1974). Water (5 ml) was collected by inserting a 10-ml glass syringe (without needle) into the outlet of the sampling pump. The syringe was held pointing down to prevent any degassing bubbles from escaping and then fitted with a 23-gauge needle; the

water was injected into a butyl rubber-stoppered anaerobic tube. In the laboratory, tubes were assayed for CO_2 on a Packard 419 gas chromatograph after first being acidified with 0.5 ml of 6 N H_2SO_4 . DIC was calculated from the Bunsen absorption coefficients for dissolved CO_2 .

Productivity measurements—Productivity was measured in situ by the ^{14}C method. Water samples were collected in 60-ml BOD bottles (Wheaton Glass Co.), which were flushed with about 180 ml of lake water by inserting the outflow tubing from the pump to the bottom of the bottle so that the flushing water could overflow the top. The glass stoppers were then quickly fixed into place so that no air bubbles remained. Algal and bacterial photosynthesis were distinguished with the inhibitor 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU) (final concn: 10^{-5} M). After a 30-min preincubation period in the dark at 15°C, 0.5 ml of a $\text{NaH}^{14}\text{CO}_3$ solution ($8 \mu\text{Ci}\cdot\text{ml}^{-1}$) was added to each bottle and the glass stoppers were quickly replaced.

The bottles were then suspended in the lake at the depths where the samples were collected. Two light bottles, two light + DCMU bottles, one dark, and one bottle containing Formalin were incubated at each depth. The bottles were incubated for half a day (sunrise to solar noon), then were transported to the laboratory in the dark, on ice (travel time did not exceed 3 h). In the laboratory the contents of the bottles were filtered through 0.45- μm membrane filters (Gelman Metricel GN-6 GD), washed three times with distilled water, placed in HCl fumes for 4 h, dried, and counted in toluene-based scintillation cocktail with a Packard Tricarb liquid scintillation counter.

Results

Some limnological characteristics of the six lakes are shown in Fig. 1. When sampled, each lake was stratified and supported an anaerobic, sulfide-containing hypolimnion. Thermocline depths ranged from 2.5 to 8.5 m. At the depths where bacteriochlorophyll maxima were observed (see Fig. 3 for chlorophyll val-

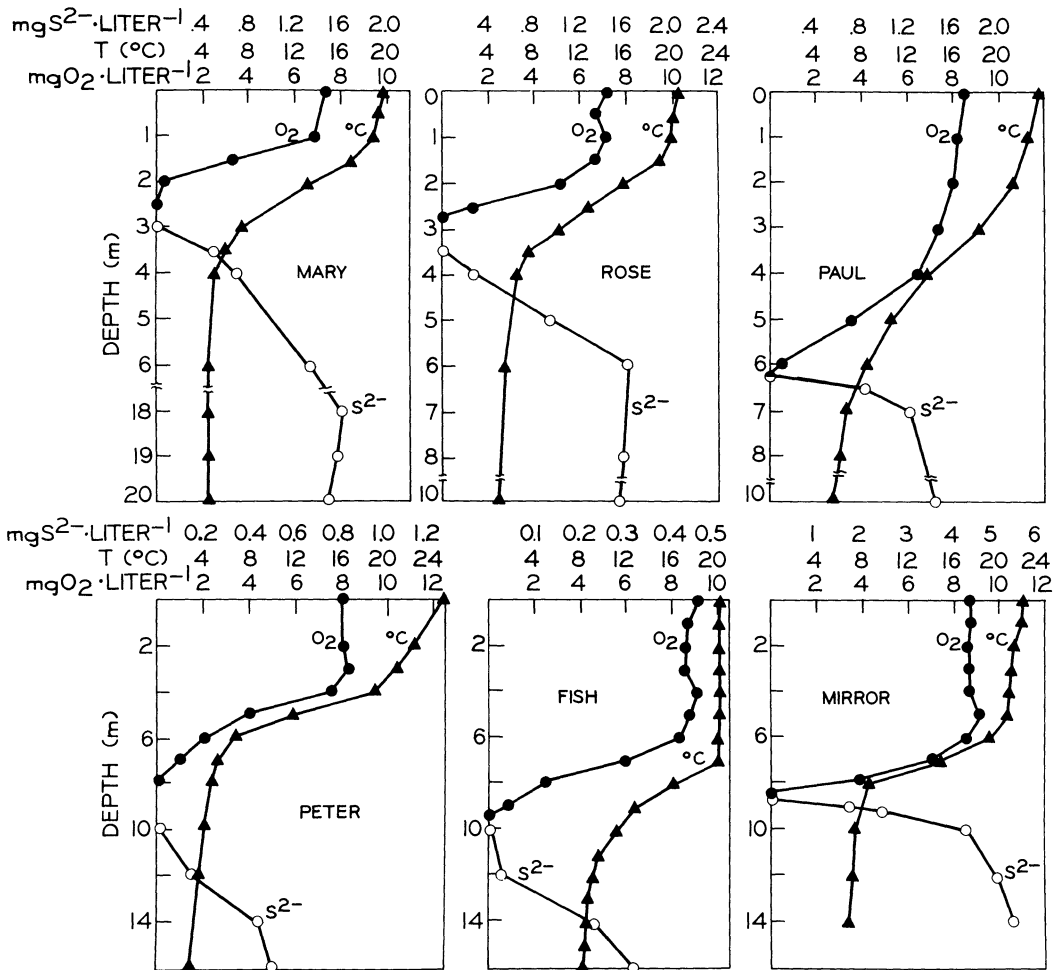


Fig. 1. Some limnological characteristics; S²⁻ includes S²⁻ + HS⁻ + H₂S.

ues), sulfide concentrations were low (<2 mg·liter⁻¹).

In each lake, light was detected at the sulfide-containing waters (Fig. 2). Arrows indicate the uppermost depths at which bacteriochlorophyll was measured in the water column of each lake. Light intensities reaching these bacteria were generally very low (0.30–0.015% of surface light intensities). Light penetration is affected by two factors: the color of the water and the presence of particulate material. Lakes Mary and Rose are very highly stained with humic and tannic materials; their waters are yellow-brown, and light is rapidly extinguished as it

passes down the water column. The dense phytoplankton populations in these lakes are also partly responsible for the sharp light extinction. Paul Lake is only slightly colored with humic materials and light is not absorbed to as great an extent as in Lakes Mary and Rose. Fish, Mirror, and Peter Lakes are uncolored and light penetrates to greater depths: however, because the sulfide-containing waters of these lakes are also at greater depths, the light intensities are still low. Chlorophyll *a* and bacteriochlorophyll concentrations along with productivity profiles for the lakes are plotted in Fig. 3.

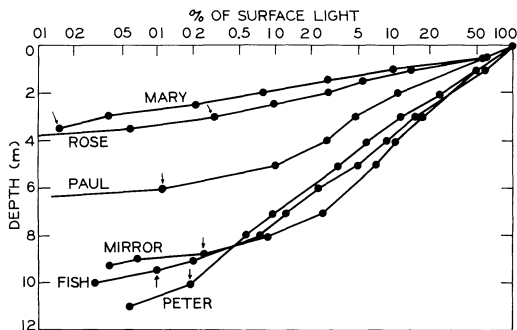


Fig. 2. Light penetration expressed as percentage of zero-depth light intensity. Arrows indicate depths at which photosynthetic sulfur bacteria were first observed in water column of each lake.

Chlorophyll *a* concentrations in the epilimnetic waters of Lakes Mary and Rose showed similar trends, being generally lower in the surface waters and increasing with depth down to the anoxic hypolimnion. Bacteriochlorophyll *d* was the only type of bacteriochlorophyll detected in Lakes Mary and Rose, with the highest concentrations at 3.5 and 4.0 m. The photosynthetic bacterial populations in both lakes were of similar composition and consisted primarily of the genera *Pelodictyon*, *Clathrochloris*, and *Chlorobium* (*Chlorochromatium aggregatum*). Although the chlorophyll *a* and bacteriochlorophyll *d* profiles in the two lakes were similar, the profiles of carbon fixation rates were somewhat different. In Lake Mary carbon fixation essentially followed the profile of light extinction in the lake, with the highest rates near the surface and the lowest in the deeper portions of the epilimnion; production by the phototrophic bacteria was very low. In Lake Rose, phytoplankton production was lower in the surface waters and increased to a maximum at 2.5 m. Production by phototrophic bacteria in Lake Rose was slightly higher than in Lake Mary.

Chlorophyll *a* and bacteriochlorophyll profiles in Mirror and Paul Lakes are also similar. Chlorophyll *a* concentrations are low in the surface waters and increase slightly with depth, bacteriochlorophyll

increased sharply at the depths where sulfide was present. Bacteriochlorophylls *a* and *d* were detected in Mirror Lake, only bacteriochlorophyll *d* in Paul Lake. The photosynthetic bacterial population in Mirror Lake was composed of both purple and green sulfur bacteria with *Lamprocystis*, *Chromatium*, *Pelodictyon*, and *Chlorobium* as the predominant genera. Only green sulfur bacteria were observed in Paul Lake, with *Prosthecochloris* and *Pelodictyon* predominating. In Paul Lake phytoplankton production was highest in the surface waters and decreased with depth. In Mirror Lake, phytoplankton production was lower in the epilimnion and showed a slight metalimnetic peak at a depth at which a bloom of *Oscillatoria* was also observed. Photosynthetic bacterial productivity in these two lakes was also similar. Production was low at the depths where sulfide was first detected in the water column, increased to a maximum value, and then decreased sharply with increasing depth. The bacterial production maxima in these lakes occurred at the same depths as the bacteriochlorophyll maxima.

Epilimnetic chlorophyll *a* concentrations fluctuated in Peter and Fish Lakes. Bacteriochlorophylls *a* and *d* were found. Productivity profiles in these lakes are similar, with phytoplankton productivities fluctuating in the surface waters and showing a metalimnetic maximum. Productivity by the photosynthetic bacteria in these lakes was low.

In all of the lakes, DCMU completely inhibited photosynthesis at the depths where chlorophyll *a* was detected and did not affect photosynthesis where bacteriochlorophyll was present. Since chlorophyll *a* was not detected in the hydrogen sulfide-containing waters of these lakes, primary production in these waters was due to photosynthetic sulfur bacteria and not to anoxygenic photosynthesis by cyanobacteria.

Table 1 summarizes the results of the productivity measurements for the six lakes. Total production values ranged from 293 to 1,570 mg C fixed \cdot m⁻² \cdot d⁻¹ and

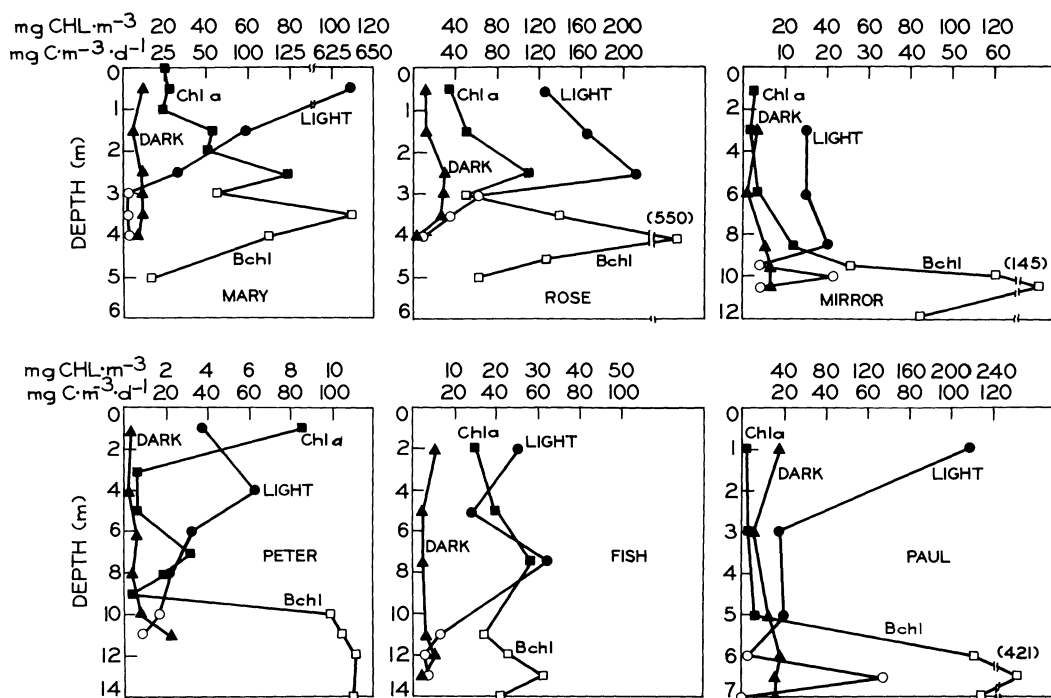


Fig. 3. Chlorophyll and production profiles; dark bottle values have already been subtracted from light bottle values. Bacteriochlorophyll includes Bchl *a* + Bchl *d*. ●—Algal photosynthesis (DCMU-sensitive); ○—bacterial photosynthesis (DCMU-resistant); ▲—dark carbon fixation.

the photosynthetic sulfur bacteria accounted for 0.26–6.3% of these values.

Discussion

Diverse values have been reported for the importance of photosynthetic sulfur bacteria as primary producers. Cohen et al. (1977) estimated that the photosynthetic sulfur bacteria contributed 91% of the total primary production in Solar Lake. Culver and Brunskill (1969) cal-

culated that photosynthetic bacteria accounted for 85% of the total annual primary production in Fayetteville Green Lake. The phototrophic bacteria in Lake Waldsea were found to contribute about 46% to the annual production (Lawrence et al. 1978). All of these values and even those of Takahashi and Ichimura (1970), who reported that photosynthetic bacteria were responsible for 3–25% of the annual primary production in several Jap-

Table 1. Primary production in the lakes studied.

Conditions	PhAR*	Production (mg C m ⁻² ·d ⁻¹)			% bacterial
		Algal	Bacterial	Total	
Mary	Cloudy	1,370	1.98	776	0.26
Rose	Sunny	2,380	32.9	525	6.3
Paul	Cloudy	684	16.8	293	5.7
Mirror	Cloudy	756	59.8	1,570	3.8
Peter	Cloudy	540	10.5	357	2.9
Fish	Sunny	1,950	13.4	1,220	1.1

* Incident photosynthetically available radiation (μEinst m⁻²·s⁻¹).

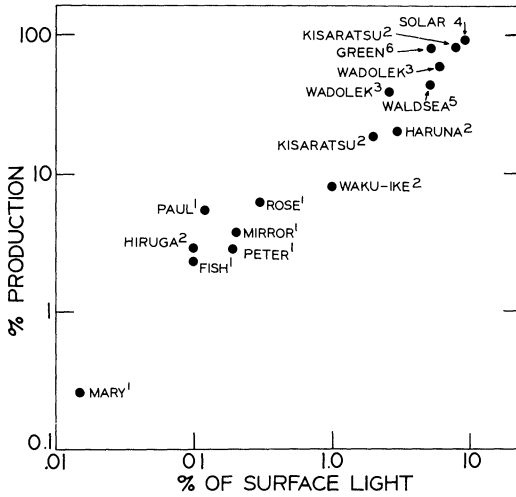


Fig. 4. Contribution of photosynthetic sulfur bacteria to total primary production in several lakes in relation to light intensity. Superscripts: 1—this study; 2—Takahashi and Ichimura 1968; 3—Cze-czuga 1968; 4—Cohen et al. 1977; 5—Lawrence et al. 1978; 6—Culver and Brunskill 1969. Productivity estimates are daily values, except for Green Lake and Lake Waldsea which are yearly.

anese lakes, exceed the estimates presented here.

Among the basic growth requirements of the photosynthetic sulfur bacteria (low Eh, moderate pH, H_2S , and light), it appears that in most aquatic systems, sulfide concentration and light intensity are likely to be most important in controlling the production of these organisms. Little has been done to evaluate the effect of sulfide concentration on CO_2 fixation rates of natural populations of phototrophic bacteria. Takahashi and Ichimura (1970) found that rates of photosynthesis increased with increasing sulfide concentrations up to $1.5 \text{ mg} \cdot \text{liter}^{-1}$ and then leveled off. The effect of sulfide concentration on the photosynthetic rate of a species of *Chromatium* was also tested: rates increased linearly up to a sulfide concentration of $40 \text{ mg} \cdot \text{liter}^{-1}$.

The different responses of pure cultures of photosynthetic sulfur bacteria and natural populations to increasing sulfide concentration can be explained in two ways. In a natural population containing photosynthetic sulfur bacteria

and sulfate- or sulfur-reducing bacteria, sulfide concentration is unimportant if the rate of sulfide supply is sufficiently rapid. Also, photosynthetic bacteria growing in close association with the source of sulfide (such as a sulfate-reducing bacterium) might be experiencing a higher sulfide concentration than that measured in a homogeneous sample. Syntrophic growth of mixed cultures of sulfate-reducing bacteria and photosynthetic bacteria has been studied. Van Gernerden (1967) found that with a two-membered system consisting of pure cultures of *Desulfovibrio* and *Chromatium*, total sulfur concentration was unimportant in the growth of either organism. Photosynthetic sulfur bacteria in nature have often been observed growing in close association with sulfate-reducing bacteria. Biebl and Pfennig (1978) have suggested that green sulfur bacteria may find it advantageous to associate with the sulfur-reducing bacterium *Desulfuromonas acetoxidans* in nature.

To evaluate the role of light in determining photosynthetic bacterial productivity, we plotted light and productivity values for several lakes (Fig. 4). A linear relationship seems to exist between the contribution that photosynthetic bacteria make to the productivity of a given system and the light intensity to which they are exposed. Among the lakes with higher photosynthetic bacterial productivities, both low and high sulfide lakes are represented (Wadolek and Kisaratsu). However, in most of the lakes included, at the depths of maximal phototrophic bacterial productivity, measured sulfide concentrations are low ($<5 \text{ mg} \cdot \text{liter}^{-1}$). It seems, then, that light intensity at the thermocline (chemocline) may be the major factor controlling photosynthetic bacterial production in lakes.

If light is the major parameter controlling the contribution of photosynthetic bacteria to total lake production, one must consider the factors which influence light penetration in lakes (Fig. 5). Hydrogen sulfide-containing lakes can be arranged in a series with respect to the amount of light reaching the sulfide-con-

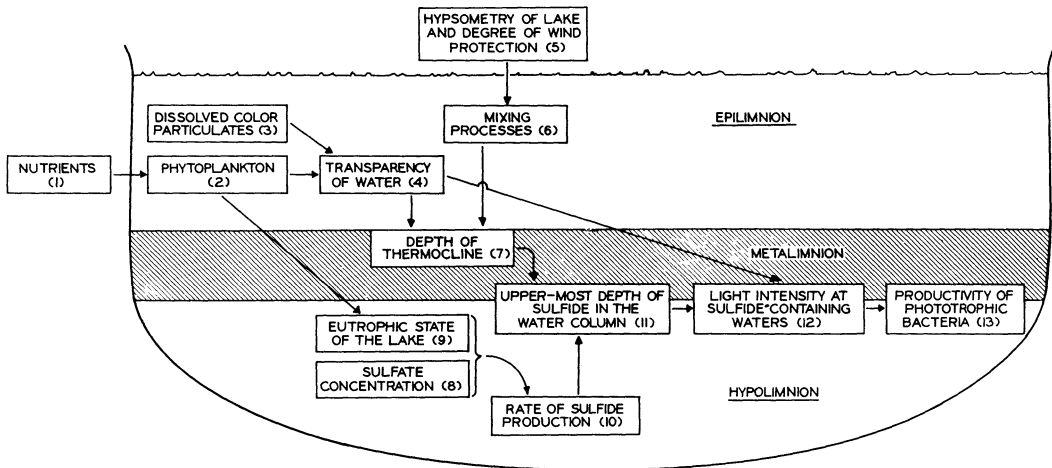


Fig. 5. General outline of factors that determine light intensity penetrating to sulfide-containing waters. Inorganic nutrient concentrations (1) affect phytoplankton growth (2) which, with other particulates and dissolved "color" (3), determine transparency (4). Morphometry of basin and degree of wind protection (5) determine degree and intensity of mixing (6). Mixing processes together with transparency determine thermocline depth (7). Mixing process will also influence nutrient concentrations by thermocline migration during stratification periods and degree of sediment resuspension during turnover. Rate of sulfide production (10) in hypolimnion is influenced by sulfate concentration (8) and, since sulfate reduction is driven by organic matter, eutrophic state (9). Net rate of sulfide formation determines upper depth at which sulfide is present, with thermocline defining upper limit (11). Upper depth of sulfide and transparency of water serve to demarcate light intensity at sulfide-containing waters (12) which, as suggested by Fig. 4, is the major factor influencing primary production by photosynthetic sulfur bacteria.

taining waters. Those of interest are lakes in which no light penetrates to the sulfide waters, lakes in which only very low light intensities ($<0.5\%$ of surface light) penetrate to the sulfide waters, and lakes in which high light intensities ($>5\%$ of surface light) do so.

An example of the first type of lake is Mendota (Wisconsin), a eutrophic, dimictic lake that supports a hydrogen sulfide-containing hypolimnion during its summer stratification period. Due to the dense populations of blue-green algae that develop during summer, the photic zone is limited to the top 6 m of the lake. However, because of Lake Mendota's large surface area in relation to mean depth, wind turbulence extends the oxygenated epilimnetic waters below the 6-m depth so that the thermocline is established at 10–14 m (T. D. Brock unpubl.). The morphometry of the basin and the dense cyanobacterial bloom thus serve to isolate the photic zone from the H_2S -containing hypolimnion and, as a re-

sult, photosynthetic sulfur bacterial blooms are never observed.

The second group, those in which very low light intensities are available to the photosynthetic sulfur bacteria, encompasses the lakes of this study which include not only dimictic lakes but biogenically meromictic lakes. Surface areas are relatively small in relation to mean depths so that in these lakes the bottom of the thermocline approximates the maximum depth of light penetration. Thus, in these lakes photosynthetic bacteria develop at the top of the hypolimnion, where sulfide is present and light intensities are low.

Lakes of the third type, with relatively high light intensities in the H_2S -containing waters, include crenogenically meromictic Fayetteville Green Lake (Culver and Brunskill 1969), Solar Lake (Cohen et al. 1977), and Kisaratsu Reservoir (Takahashi and Ichimura 1968). The epilimnetic waters of these lakes are strongly chemically stratified and are relatively

clear. The chemical stratification prevents mixing of the oxygenated epilimnetic waters with the sulfide-containing hypolimnetic water despite the occurrence of inverse temperature profiles at the thermocline (chemocline). Thus, the photosynthetic sulfur bacteria in these lakes develop in an environment where sulfide is present and light intensities are high.

Because it is questionable what the measured sulfide concentration of a system means in relation to photosynthetic bacterial production, we propose that light intensity is the primary factor influencing photosynthetic bacterial production in lakes. However, measurements of sulfate reduction rates and sulfide turnover rates in the water column might yield information which would enable us to describe more clearly the interplay of light and sulfide in affecting photosynthetic sulfur bacterial production.

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