



6-30-1978

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Recommended Citation

Axler, R. P.; Gersberg, R. M.; and Paulson, L. J. (1978) "Primary productivity in meromictic Big Soda Lake, Nevada," *Great Basin Naturalist*: Vol. 38 : No. 2 , Article 4.

Available at: <https://scholarsarchive.byu.edu/gbn/vol38/iss2/4>

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PRIMARY PRODUCTIVITY IN MEROMICTIC BIG SODA LAKE, NEVADA

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ABSTRACT.— *In situ* radiocarbon uptake measurements conducted at Big Soda Lake, Nevada, indicate that (i) bacterial photosynthesis comprises an important fraction (30 percent) of the lake's total primary production and (ii) bacterial chemosynthesis contributes significantly to organic particle production. The results of nutrient enrichment bioassay experiments support Hutchinson's prediction that availability of inorganic nitrogen, rather than phosphorus, limits primary production in the mixolimnion. Nutrient additions of NO₃-N with Fe⁺³ most stimulated ¹⁴C uptake.

Big Soda Lake was described hydrologically as early as 1885 (Russell 1885) and has received considerable limnological attention by virtue of its meromixis (Hutchinson 1937, 1957, Kimmel et al., in press). However, little biological data has been accumulated on the lake. Hutchinson, in 1933, found a thermally stratified mixolimnion with an oxygen depleted hypolimnion, overlying an anoxic monimolimnion. He measured concentrations of a number of nutrients and deduced that phosphorus was much less likely to limit primary production in the mixolimnion than inorganic combined nitrogen (Hutchinson 1937). Koenig et al. (1971) reported on the limnological status of the lake and noted a stratum of pink-colored water located in the deep hypolimnion. Photosynthetic purple sulfur bacteria were identified in this water (*Rhodotheca sp.* and *Thiotheca sp.*). However, primary productivity measurements were not made.

In a meromictic lake with high concentrations of sulfide in the chemocline region and an anoxic (but photic) hypolimnion, bacterial photosynthesis may comprise a significant fraction of a lake's primary production (Wetzel 1975, Cohen et al. 1977a, b). We have utilized inorganic ¹⁴C to estimate the magnitude of algal and bacterial photosynthesis at Big Soda Lake and have conducted nutrient enrichment experiments

to investigate the possible nitrogen limitation suggested by Hutchinson.

METHODS

Temperature, pH, and dissolved oxygen were measured *in situ* with a calibrated Hydrolab water quality analyzer. Light penetration was measured with a Whitney LMD photometer. Total alkalinity was determined by potentiometric titration with 0.1N HCl. Chloride concentrations were determined by the argentometric method (Am. Public Health Assoc. 1971). Total phosphorus, reactive iron, and nitrate were determined by the methods of Strickland and Parsons (1968) as modified by Fujita (see Goldman 1974). Ammonia was determined as per Solórzano (1969) as modified by Lidicoat et al. (1975). *In situ* incubations of water samples with ¹⁴C for determination of primary productivity and nutrient stimulation followed the procedures developed and modified by Goldman (1963). Filtered samples were acid fumed (Wetzel 1965) to remove precipitated and adsorbed ¹⁴C. Solar insolation was recorded with a Belfort pyrheliometer. Dissolved inorganic carbon (DIC) available for photosynthesis was approximated from temperature, pH, and alkalinity data using the data of Saunders et al. (1962). This method probably over-

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estimates available DIC in alkaline Big Soda Lake samples (see Hutchinson 1957, Talling 1973), and thereby results in some overestimation of primary productivity.

RESULTS AND DISCUSSION

On 23 April 1977 the thermocline and chemocline were located at about 5 m and 37.5 m, respectively (Fig. 1). The vertical extinction coefficient was 0.35 m^{-1} and measurable light penetrated to 26 m.

The vertical distribution of primary productivity (Fig. 2) was bimodal with peaks at

5 and 25 m. The zone below 17.5 m was oxygen deficient ($<1 \text{ mg O}_2 \cdot \text{f}^{-1}$) and presumably, could only support photosynthetic growth by anaerobic bacteria.³ The areal productivity for this zone was calculated to be $317 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. Similar calculations for the upper, aerobic zone yielded a value of $717 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ (phytoplankton photosynthesis). Therefore, the bacterial contribution to the total photosynthetic productivity in the water column was 31 percent.

At all depths inorganic carbon uptake in dark bottles represents a large percentage of that in light bottles, thus indicating sig-

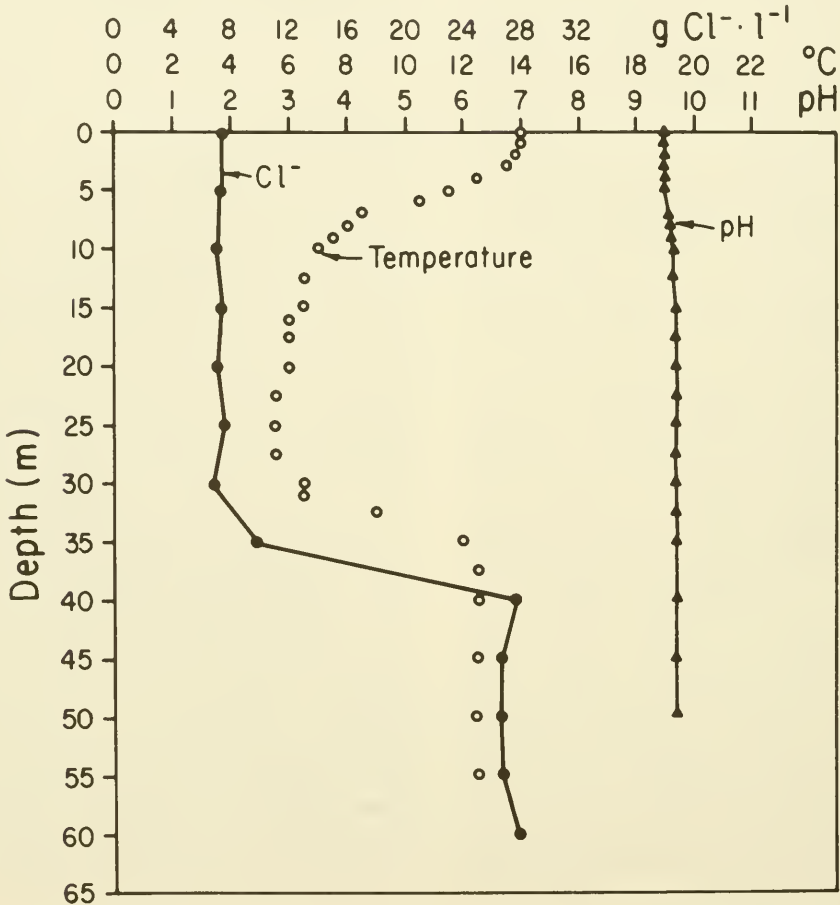


Fig. 1. Depth profiles of temperature, pH, and chloride for Big Soda Lake, 23 April 1977.

³Recent evidence indicates that some species of *Oscillatoria* are able to photosynthesize anaerobically by using H₂S as a source of electrons for photosystem II (Cohen et al. 1975).

nificant chemosynthetic activity. In the mixolimnion this is probably due to both nitrifying bacteria (which utilize electrons from NH_4^+ to reduce CO_2) and sulfur oxidizing bacteria (which utilize electrons from H_2S to reduce CO_2). Concentrations of sulfide (from Koenig et al. 1971) and ammonia (Fig. 3) in the region of the chemocline are $400 \text{ mg S}\cdot\text{l}^{-1}$ and $4\text{--}34 \text{ mg N}\cdot\text{l}^{-1}$, respectively, and therefore, the gradual entrainment of monimolimnetic water (see Kimmel et al., in press) must introduce appreciable quantities of these nutrients into the mixolimnion during the fall-winter overturn. Conditions in the deep hypolimnion are also suitable for chemosynthetic denitrifying sulfur bacteria, such as *Thiobacillus denitrificans*. The concentration of nitrate in the oxygen depleted hypolimnion does decline

from 55 to $9 \text{ }\mu\text{gN}\cdot\text{l}^{-1}$ (see Fig. 3). In the strictly anoxic monimolimnion, high dark uptake rates may be due to the presence of anaerobic sulfate reducing bacteria (e.g., *Delsulfovibrio desulfuricans*) which are facultatively autotrophic and use molecular hydrogen as an electron donor (Doelle 1975).

Our data for total phosphorus, ammonia, and iron (Fig. 3) are similar to those reported by Hutchinson (1937). A series of nutrient enrichment experiments on epilimnetic water collected on 24 April 1976 provided evidence to support Hutchinson's suggestions concerning phosphorus and nitrogen limitation of primary productivity. Maximum stimulation of ^{14}C uptake occurred in water samples enriched with both nitrate and iron (Fig. 4). Phosphate additions, either singly or together with nitrate or iron,

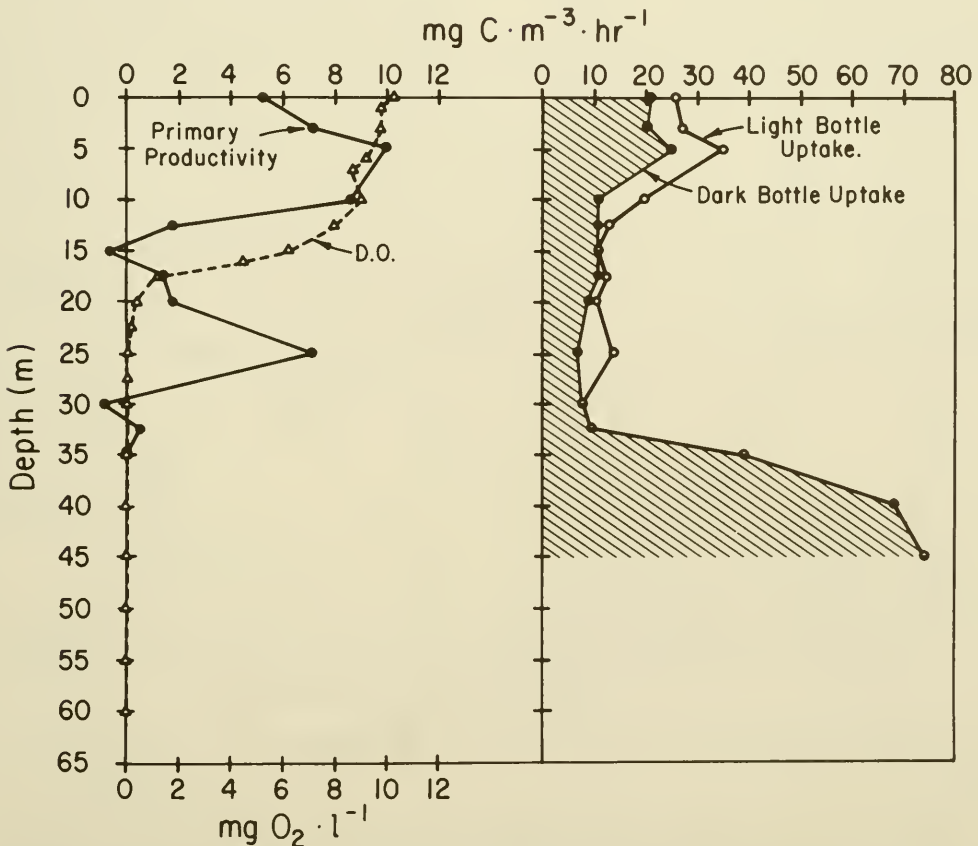


Fig. 2. Depth profiles of dissolved oxygen and primary productivity, 23 April 1977 (1000-1400 hrs). Productivity data represents the difference in uptake between light and dark sample bottles where each has been corrected for dark-uptake during the time between removal from the lake and filtration.

produced a small effect. Similarly, trace metal additions provided little stimulation unless added in concert with nitrate and iron.⁴

Primary production in many types of lakes has been shown to be limited by inorganic nitrogen concentration and, in a number of hardwater calcareous lakes, by available iron (Wetzel 1975). Goldman (1972) reported that on water samples from Lake Tahoe, California, nitrate and iron acting in concert produced a greater stimulation of primary productivity than either one added singly. Such an effect may be

due to the role of iron in the assimilatory reduction of nitrate by microorganisms. After reduction to nitrite via the enzyme nitrate reductase, further reduction to ammonium is catalyzed by nitrite reductase. Iron appears to be an integral component of both nitrite reductase and of ferredoxin, the immediate electron donor (Morris 1975, Healey 1973).

The data we have accumulated on Big Soda Lake are of a preliminary nature and certainly insufficient to fully delineate the microbial processes occurring in the water column. However, they do indicate a very

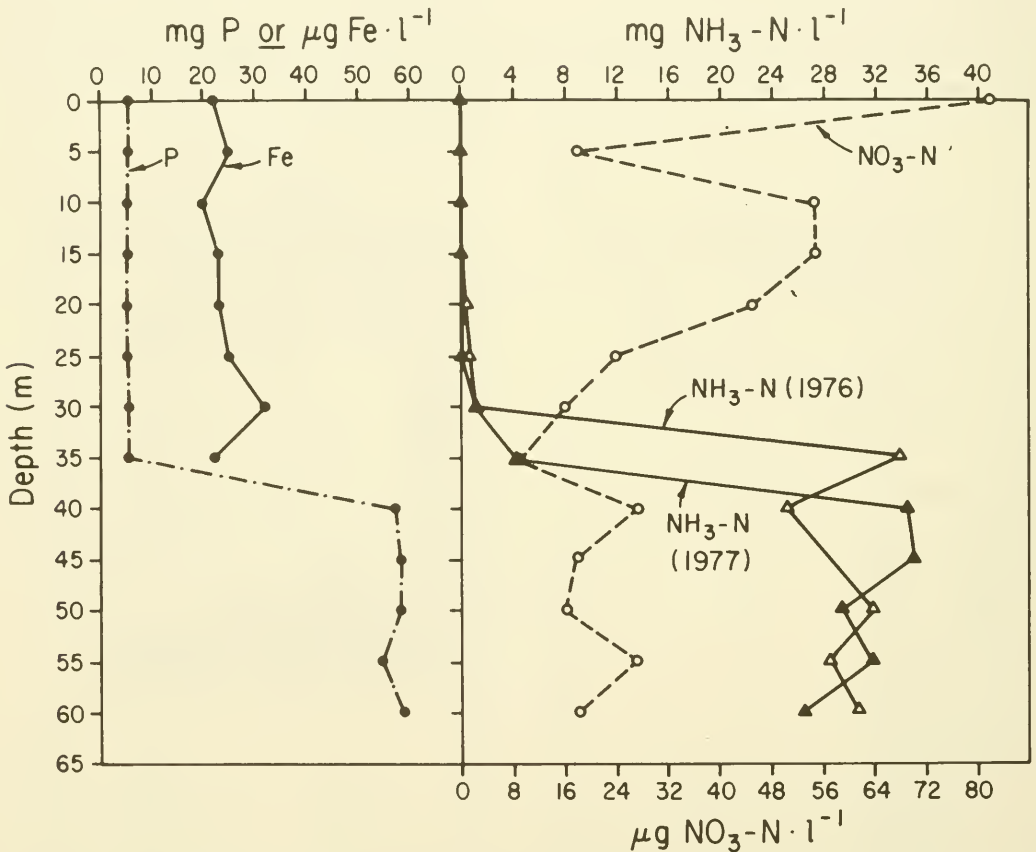


Fig. 3. Depth profiles of NO₃-N and NH₃-N (24 April 1977); total phosphorus, reactive iron, and NH₃-N (24 April 1976).

⁴Unfortunately, the variance in our primary productivity data from April 1976 was generally too high to include in this report (presumably this was due to precipitation of carbonates during the sample filtrations with subsequent clogging of the filtration apparatus). However, the limnological condition of the lake, as determined by vertical profiles of temperature, dissolved oxygen, light attenuation, alkalinity, pH, and chloride and ammonium concentrations was virtually identical in 1976 to 1977. Furthermore, the primary productivity at 0 m and 5 m (23 April 1976) was 4.5 mg C·m⁻³·hr⁻¹ and 9.3 mg C·m⁻³·hr⁻¹, respectively, which were similar to the rates measured at these depths in 1977.

interesting system in which bacterial photosynthesis is an important fraction of the total primary productivity, and bacterial chemosynthesis contributes significantly to organic particle production. There was no obvious pink color in deep hypolimnetic water when our measurements were made and, therefore, one might expect the rate of bacterial photosynthesis to be much higher later in the growing season (as when Koenig et al. collected samples in October 1970). However, the fraction of total primary productivity contributed by the sulfur bacteria seasonally remains to be investigated.

We are especially indebted to Dr. Bruce L. Kimmel from the University of Oklahoma Biological Station, who helped with the field and laboratory work and data analysis and interpretation, and who critically reviewed the manuscript. We acknowledge the field and laboratory assistance of the University of California (Davis) 1976 and 1977 limnology laboratory classes and the financial assistance of the Division

of Environmental Studies. Some of the equipment used in this investigation was purchased under the auspices of National Science Foundation grants NSF BM 74-02246 A01 and NSF DEB 76-19524 to C. R. Goldman. J. Coil contributed significantly with the laboratory analyses. M. Smith and G. Malyj aided in manuscript preparation.

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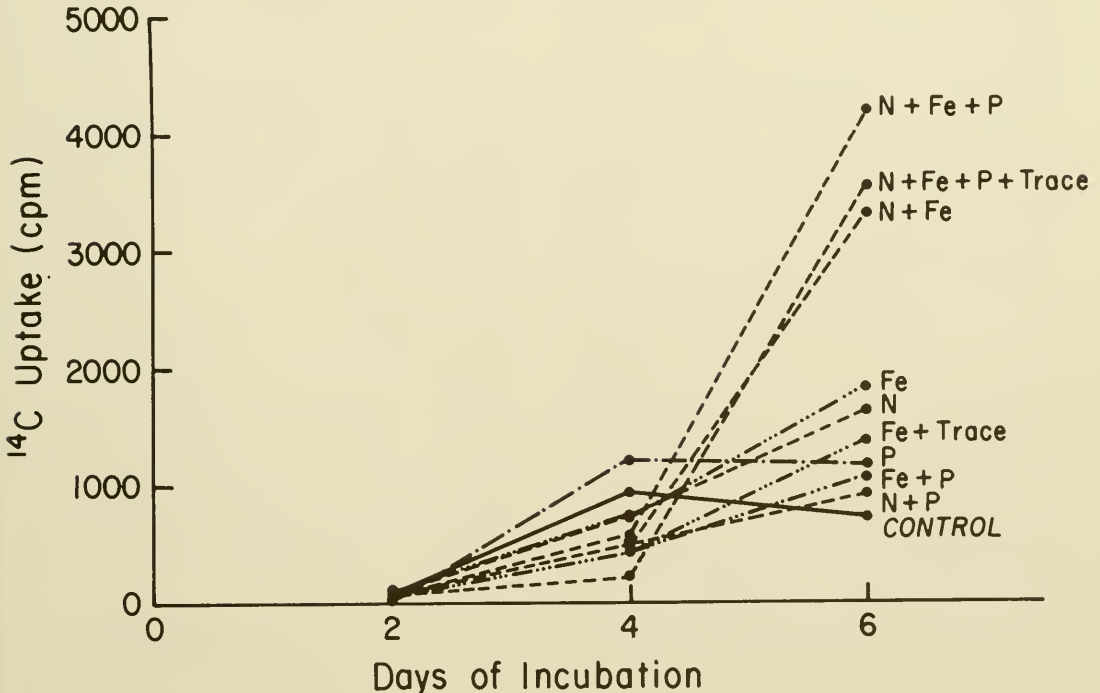


Fig. 4. Results of nutrient enrichment bioassays on water collected 24 April 1976. Enrichment concentrations were: N = 50 $\mu\text{g NO}_3\text{-N}\cdot\text{l}^{-1}$; P = 50 $\mu\text{g PO}_4\text{-}^3\text{-P}\cdot\text{l}^{-1}$; Fe = 25 $\mu\text{g Fe}^{+3}\cdot\text{l}^{-1}$; Trace = 3 $\mu\text{g}\cdot\text{l}^{-1}$ each of Co, Mo, Zn, Mn.

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