

Seasonal changes in the chemistry and biology of a meromictic lake (Big Soda Lake, Nevada, U.S.A.)

James E. Cloern, Brian E. Cole & Ronald S. Oremland

U.S. Geological Survey, 345 Middlefield Rd., MS96, Menlo Park, CA 94025, U.S.A

Keywords: saline lakes, meromictic, phytoplankton, photosynthetic bacteria, nutrient limitation, nitrogen-fixation, methane

Abstract

Big Soda Lake is an alkaline, saline lake with a permanent chemocline at 34.5 m and a mixolimnion that undergoes seasonal changes in temperature structure. During the period of thermal stratification, from summer through fall, the epilimnion has low concentrations of dissolved inorganic nutrients (N, Si) and CH_4 , and low biomass of phytoplankton (chlorophyll a ca. 1 mgm^{-3}). Dissolved oxygen disappears near the compensation depth for algal photosynthesis (ca. 20 m). Surface water is transparent so that light is present in the anoxic hypolimnion, and a dense plate of purple sulfur photosynthetic bacteria (*Ectothiorhodospira vacuolata*) is present just below 20 m (Bchl a ca. 200 mgm^{-3}). Concentrations of NH_4^+ , Si, and CH_4 are higher in the hypolimnion than in the epilimnion. As the mixolimnion becomes isothermal in winter, oxygen is mixed down to 28 m. Nutrients (NH_4^+ , Si) and CH_4 are released from the hypolimnion and mix to the surface, and a diatom bloom develops in the upper 20 m (chlorophyll a $> 40 \text{ mgm}^{-3}$). The deeper mixing of oxygen and enhanced light attenuation by phytoplankton uncouple the anoxic zone and photic zone, and the plate of photosynthetic bacteria disappears (Bchl a ca. 10 mgm^{-3}). Hence, seasonal changes in temperature distribution and mixing create conditions such that the primary producer community is alternately dominated by phytoplankton and photosynthetic bacteria: the phytoplankton may be nutrient-limited during periods of stratification and the photosynthetic bacteria are light-limited during periods of mixing.

Introduction

Meromictic lakes are interesting aquatic systems because they comprise two distinct water masses that mix slowly. The interface (chemocline) between the lower layer (monimolimnion) and upper layer (mixolimnion) is often the site of intense microbial activity (e.g., Culver & Brunskill 1969; Takahashi *et al.* 1970; Sorokin & Donato 1975; Lawrence *et al.* 1978) and particulate organic matter produced in the surface layer can be permanently lost from the mixolimnion after sinking. Because of these two unique features, meromictic lakes are useful sites to study microbial processes associated with the biogeochemical cycling of nutrients and the anaerobic decomposition of organics. Moreo-

ver, organics that enter the permanently anaerobic water of meromictic lakes might be precursors towards the formation of petroleum (Didyk *et al.* 1978; Demaison & Moore 1980). Indeed, the highly laminated oil shales of the Green River Formation are theorized to have been the bottom sediments of alkaline, saline meromictic lakes (Bradley 1931; Smith & Robb 1973).

In the fall of 1980, initial studies on the chemistry of Big Soda Lake revealed that the monimolimnion of this alkaline, saline environment was highly reduced and contained abundant ammonia, reduced sulfur compounds (Kharaka *et al.* 1981), and methane (Oremland *et al.* 1981); monimolimnion sediments harbored an active methanogenic flora (Oremland *et al.* 1982). Dissolved inorganic carbon

in the monimolimnion was isotopically "light" ($\delta^{13}\text{C} = -2.8$ per mil compared to 0.7 to -1.2 per mil in the mixolimnion), perhaps reflecting inputs of organic matter from the surface (Robinson & Kharaka 1981). Cores (upper ca. 2 m) of the soft sediments had visibly striking laminations. Interspersed upon a dark green background composed of pennate diatoms was a series of thin (ca. 1–5 mm) multicolored (red, brown, white, yellow, black) layers; no pennate diatoms were observed upon microscopic examination of some of the colored layers. These observations suggested that there may be an important seasonal aspect associated with the type of phytoplankton or bacterioplankton sinking out of the lake's water column and entering the sediments. However, the only detailed studies of microplankton in Big Soda Lake were conducted during the spring season when Axler *et al.* (1978) and Priscu *et al.* (1982) observed low phytoplankton biomass (chlorophyll a $< 1 \text{ mg m}^{-3}$), a population of purple sulfur photosynthetic bacteria (Bchl a ca. 9 mg m^{-3}), and low concentrations of dissolved inorganic nitrogen in the epilimnion (NO_3^- ca. $1\text{--}5 \text{ }\mu\text{M}$; $\text{NH}_4^+ < 1 \text{ }\mu\text{M}$) relative to the hypolimnion ($\text{NH}_4^+ > 50 \text{ }\mu\text{M}$). Our study was designed to provide information about seasonal changes in nutrients and the pelagic primary producer community, and processes that regulate the seasonality. In conjunction with this work, research was conducted upon the seasonal changes in primary productivity (Cloern & Cole 1982).

The study site

Big Soda Lake occupies a crater basin and is a remnant of the Pleistocene Lake Lahontan. The surface area is 1.6 km^2 , mean depth is 26 m, and maximum depth is 65 m (Kimmel *et al.* 1978). There is a narrow littoral zone along which submerged macrophytes (*Ruppia* sp.) proliferate from July to November. Prior to 1900 the lake was hypersaline (TDS ca. 125 g l^{-1} ; Breese 1968) and isohaline with depth. Since then, the importation of irrigation water has raised the local groundwater table and the lake level. Between 1905 and 1925, groundwater inflows raised the lake level 18 m and established a new, lower density surface layer. Dissolved solids have been diluted to about 26 g l^{-1} in the mixolimnion and 88 g l^{-1} in the monimolimnion (Y. K. Kharaka, pers. commun.). In 1933 the chemocline

was diffuse and centered around 20 m: wind-mixing has caused the chemocline to descend (Kimmel *et al.* 1978), and a sharp density gradient at 34.5 m now separates the mixolimnion and monimolimnion (Fig. 1). Kimmel *et al.* (1978) estimated that the rate of chemocline descent was 71 cm year^{-1} between 1970 and 1977, and they projected that the lake will become well-mixed over a time span of decades. The mixolimnion is thermally stratified in summer (Fig. 1). The predominant cation is sodium, and anions are chloride, sulfate, and bicarbonate (Table I); pH is 9.7 throughout the water column.

Methods

The lake was sampled once during each of the four seasons: July 1981, November 1981, February 1982, and May 1982. All water column sampling was done at one site near the center of the lake where depth is 65 m; most sampling was confined to the mixolimnion. Temperature was measured in

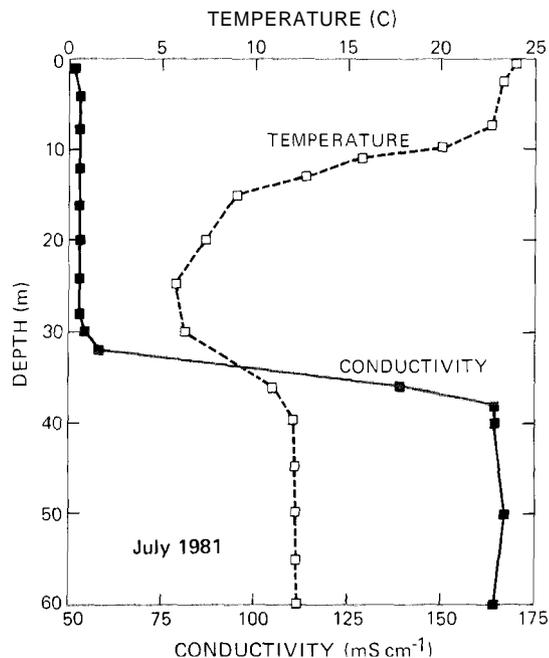


Fig. 1. Vertical profiles of conductivity and temperature in the center of Big Soda Lake. July 1981 (conductivity data from L. M. Law).

Table I. Chemical properties of Big Soda Lake; units are mg l⁻¹ unless otherwise noted. Data from Kharaka *et al.* (1981).

	Mixolimnion	Monimolimnion
Na ⁺	8 000	28 000
K ⁻	310	1 100
Mg ²⁻	145	6
Ca ²⁺	5	0.8
NH ₃	<0.1	45
H ₂ S	<0.2	410
Alkalinity (as HCO ₃)	4 000	24 000
Cl	6 500	27 000
SO ₄ ²⁻	5 600	6 700
Dissolved organic carbon	20	60
TDS	26 000	88 000
Redox ^a	+300 mv	-200 mv
pH	9.7	9.7

^a Priscu *et al.* (1982)

situ with thermistors, usually down to 36 m. Conductivity and salinity were measured in the mixolimnion with an electrodeless induction salinometer (Industrial Instruments, Inc. Model RS5-3). Attenuation of photosynthetically active radiation (400–700 nm) was measured at 1-m intervals over the photic depth with a LiCor 192S quantum sensor. The compensation depth Z_c was assumed to be that depth where irradiance is 0.5% of surface irradiance I_s . Turbidity at discrete depths was measured with a beam transmissometer having a path length of 0.5 m. The instrument was calibrated to 100% transmittance in water at the depth of maximum light transmittance, and values reported here are relative to that transparency.

Samples for measurement of dissolved oxygen (DO) were collected with a 5-L Niskin bottle, and triplicate subsamples were analyzed from each sampling depth using Carpenter's (1965) modification of the Winkler titration. In February and May, DO was also measured *in situ* with an Orbisphere Laboratories DO meter (model 2714) having a polarographic sensor that is insensitive to sulfides. Dissolved methane was extracted from lake water using the syringe shaking method of Rudd *et al.* (1974) and was quantified by flame-ionization gas chromatography (Oremland 1981). Samples for nutrient analyses were collected with a Niskin bottle or were pumped from depth, then filtered through 0.4 μ m Nuclepore filters and frozen. Analyses for dissolved silicate, phosphate, nitrate, nitrite and

ammonia were done in the laboratory with a Technicon AutoAnalyzer using analytical modifications of Hager *et al.* (in prep). Nutrient standards were prepared in artificial lake water (40 meq l⁻¹ NaHCO₃); analysis of spiked samples (100 μ M NO₃⁻ or NO₂⁻) showed a recovery efficiency of 98.5% for NO₃⁻ and 100% for NO₂⁻ (S. W. Hager, pers. commun.).

Biomass of phytoplankton and photosynthetic bacteria was measured by extraction of pigments collected onto Gelman A/E glass fiber filters. The filters were frozen after collection, then ground and extracted in 90% acetone in the laboratory. Chlorophyll *a* and bacteriochlorophyll (Bchl *a*) were measured spectrophotometrically using the phaeopigment-corrected equation of Lorenzen (1967) and the equation of Takahashi & Ichimura (1970). Phytoplankton samples were preserved in Lugol's solution and later enumerated with an inverted microscope. Zooplankton samples were collected with vertical tows from 20 m using an 80 μ m mesh net having a 12.5 cm diameter opening.

Nitrogen fixation experiments were done by the acetylene-reduction technique (Stewart *et al.* 1967). Assays were run during September 1981 using shoreline macrophytes observed to be epiphytized by heterocystous cyanophytes (*Anabaena* sp.). Plant materials (approx. 20–40 cm³ flask⁻¹ or 0.4–0.8 g dry wt flask⁻¹) were placed in 125 ml Erlenmeyer flasks which contained 50 ml of littoral zone lake water. The flasks were sealed with sleeved rubber septa, injected with C₂H₂ (15 Kpa) and subsampled after 0, 1.5 and 3 h incubation. Flasks were incubated in triplicate under experimental conditions of ambient light, darkness, and ambient light plus NH₄Cl (20 mM). Headspace subsamples (2 cm³) were stored in Vacutainers (2 cm³) which were then inverted and injected with 0.25 ml of a 15% NaCl solution. This was done to prevent diffusion of enclosed hydrocarbons through the stopper. Hydrocarbon gases were analyzed by flame ionization gas chromatography (Oremland 1981).

Results

Seasonal changes in the mixolimnion of Big Soda Lake are summarized in Table 2. Surface salinity ranged from 18.9 gl⁻¹ (November) to 17.4 gl⁻¹ (May). Seasonal changes in groundwater inflow and the rate of wind mixing had no effect on the

depth of the chemocline, which remained fixed at 34.5 m. Temperature of the monimolimnion also held constant at about 12 °C. However, temperature structure of the mixolimnion varied seasonally (Fig. 2). The mixolimnion was thermally stratified in July when the thermocline was located at about 11 m. The thermocline dropped to 19 m as the epilimnion cooled in fall, and the mixolimnion was nearly isothermal (ca. 4 °C) to 29 m in February. By May the surface waters had started warming and a thermocline was present at 6 m.

Transparency of the upper 20 m was high during summer and fall (extinction coefficient ca. 0.2 m⁻¹),

however in February the extinction coefficient increased to 0.51 m⁻¹ (Table 2) because of a surface bloom of diatoms. In February, the estimated maximum depth of net photosynthetic oxygen production (Z_c) was 10 m compared to about 20 m during the other seasons. Seasonal changes in dissolved oxygen distribution reflected the changes in transparency and thermal stratification. During those times of the year when the mixolimnion was stratified, the depth of oxygen disappearance coincided with the compensation depth Z_c (Fig. 2). However, after the mixolimnion became isothermal in winter dissolved oxygen was present down to the bottom

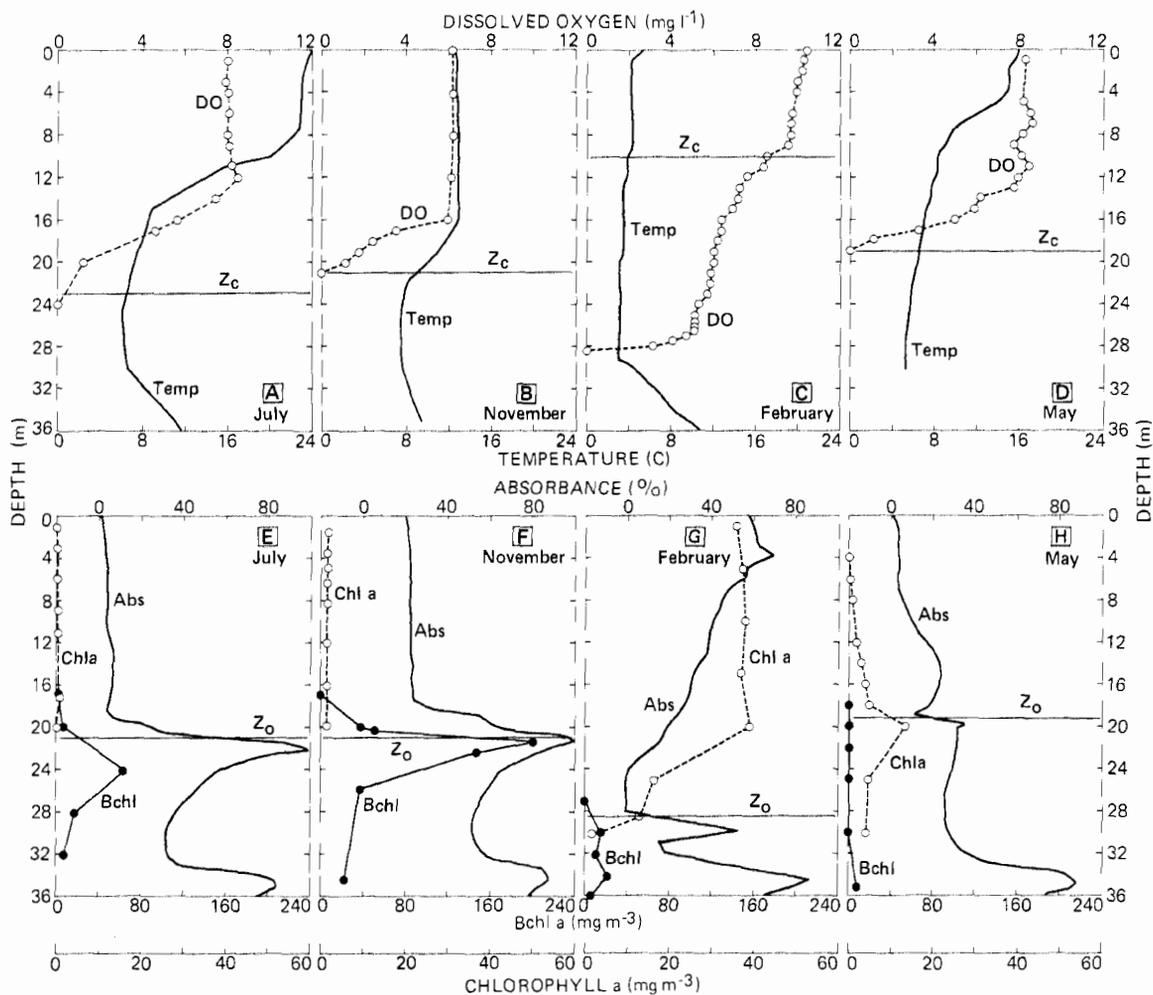


Fig. 2. Vertical profiles of temperature and dissolved oxygen (DO) in Big Soda Lake during July 1981 (A), November 1981 (B), February 1982 (C), and May 1982 (D); horizontal line shows compensation depth Z_c . Vertical profiles of turbidity (percent relative absorbance), chlorophyll a, and Bchl a (E, F, G, H) during the same periods; horizontal line shows depth of oxygen disappearance Z_o .

of the epilimnion, well below Z_c (Fig. 2C). Saturation values of dissolved oxygen were estimated (Brown *et al.* 1970) from barometric pressure, surface water temperature, and chloride concentration. During July and May, DO in the surface water was at or above calculated saturation values; during fall and winter, DO was below saturation (Table 2).

Water column turbidity exhibited three distinct vertical patterns over the year. In July and November, the upper 18 m had very low turbidity; however, sharp turbidity peaks were observed at 20–24 m, and at the chemocline (34.5 m; Figs. 2E, 2F). A different pattern occurred in February when maximum turbidity was observed in the upper 4 m (Fig. 2G); turbidity then decreased to a minimum at about 24 m to 28 m, and showed a small narrow peak at 30 m. In May, turbidity was again low in the epilimnion but increased over a broad peak from 10 m to 18 m, and showed a small sharp peak at 19.5

m (Fig. 2H). Although vertical profiles of turbidity varied over the year, a peak was always seen just below the depth of oxygen disappearance and a second peak was consistently seen at the chemocline. The magnitude and thickness of the first peak varied seasonally.

Chlorophyll profiles mimicked the vertical profiles of turbidity (Fig. 2). In July and November, when turbidity of the upper 18 m was low, phytoplankton biomass was low (Chlorophyll a $< 1.5 \text{ mg m}^{-3}$). However, the turbidity peak observed below 20 m coincided with a dense plate of purple sulfur photosynthetic bacteria (maximum Bchl a $> 200 \text{ mg m}^{-3}$); H. G. Truper identified the organism as *Ectothiorhodospira vacuolata*. By contrast, in February when the mixolimnion was isothermal down to 29 m, phytoplankton biomass was very high (Chlorophyll a $> 40 \text{ mg m}^{-3}$) and roughly paralleled the turbidity profile (Fig. 2G). The plate of photo-

Table 2. Seasonal changes in Big Soda Lake.

	July 1981	Nov. 1981	Feb. 1982	May 1982
Surface salinity (ppt)	..	18.9	18.2	17.4
Surface temperature ($^{\circ}\text{C}$)	23.5	12.4	4.4	15.0
Thermocline depth (m)	11	19	33	6
Surface DO (mg l^{-1})	8.0	6.2	9.2	8.3
Saturation DO (mg l^{-1})	7.1	8.8	11.0	8.5
Extinction coefficient (m^{-1})	0.23	0.17	0.51	0.28
Secchi depth (m)		11	2.8	8
Z_c (m) = depth of 0.5% I	23	21	10	19
Z_0 (m) = depth where DO = 0	21	21	28	19.5
Depth of photosynthetic bacterial plate (m)	22	21.5	30–34	Absent
% of surface irradiance at depth Z_0	0.8%	2.8%	0%	0.4%
$\Sigma\text{chl a}$ (mg m^{-2})	10.9	26.4	945	100
$\Sigma\text{Bchl a}$ (mg m^{-2})	>406	1 037	112	23
Surface DIN = $\text{SO}_4 + \text{NO}_2 + \text{NH}_4^+$ (μM)			14.5	0.10
Surface silicate (μM)	-	-	48	9.9
Surface methane (μM)	0.1	0.1	0.6	0.1
Phytoplankton density at 1 m (cells ml^{-1})				
<i>Oocystis</i> sp.	1 300			
<i>Ankistrodesmus</i> sp. green flagellate	30	370		
<i>Nitzschia palea</i>		340		
<i>Chaetoceros</i> sp. coccoid chlorophyte ($15 \times 11 \mu\text{m}$)			18 500	920
Zooplankton density (l^{-1})			9 700	220
<i>Moina hutchinsoni</i> adult	24	17	0	0.3
<i>Diaptomus sicilis</i> adult	2	0.4	0.3	0.8
copepodite				2.9
nauplius				8.2

synthetic bacteria was greatly diminished. In May, vertical profiles of chlorophyll *a* and turbidity were again parallel in the upper 20 m; however, their respective magnitudes had diminished markedly since February (Fig. 2H). In addition, both chlorophyll *a* and turbidity increased with depth in the mixolimnion reaching maximum values at about 20 m. Phytoplankton samples from 20 m comprised

mostly *Nitzschia palea*, so the subsurface chlorophyll *a* peak could indicate sinking of the winter diatoms (see below) out of the mixolimnion. No photosynthetic bacteria were observed at 20 m in May, although a small amount of bacteriochlorophyll *a* was observed at the chemocline (Fig. 2H).

The total water column abundances and relative proportions of chlorophyll *a* and Bchl *a* were highly

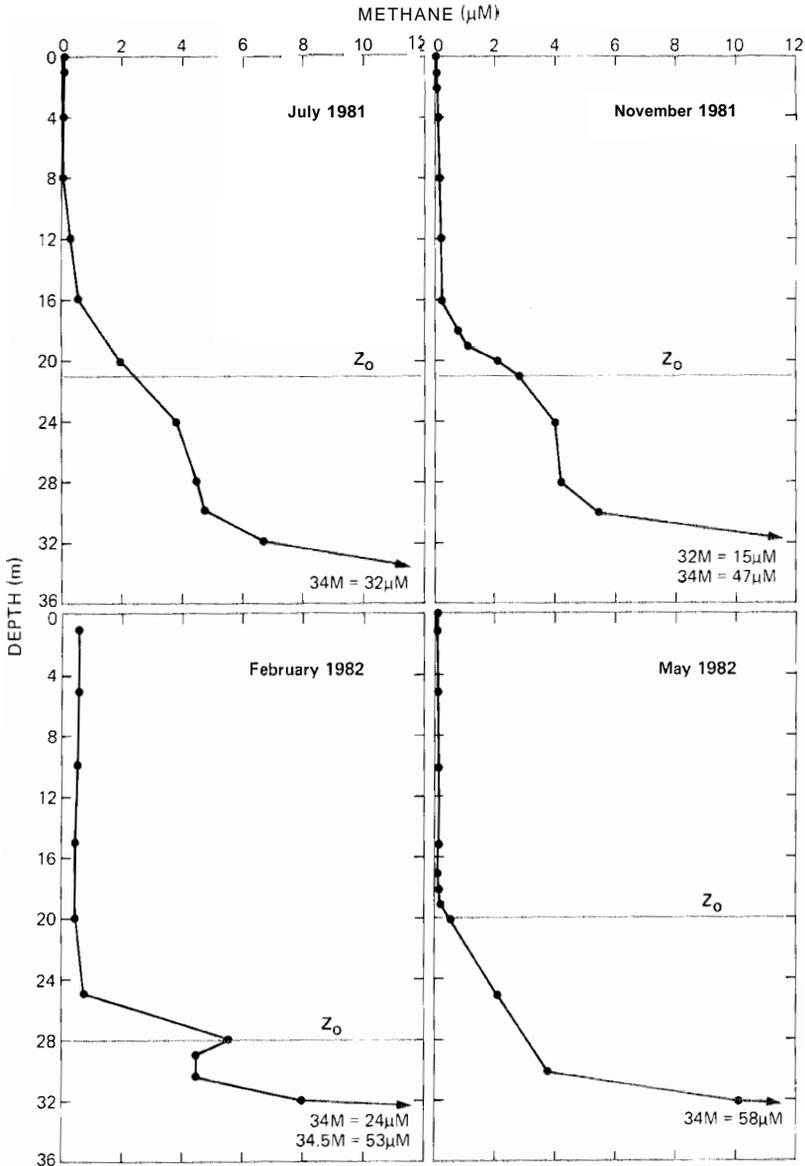


Fig. 3. Vertical profiles of methane concentration in Big Soda Lake during the four sampling periods; horizontal line shows depth of oxygen disappearance Z_0 .

variable seasonally. Total chlorophyll a (Σchl) was estimated by integrating (trapezoidal quadrature) measured values from the surface to the depth of oxygen disappearance Z_o , and total Bchl a (ΣBchl) was estimated by integrating values from Z_o to the chemocline. In July and November, total Bchl a was two or three orders of magnitude higher than total chlorophyll a (Table 2). In February, however, total chlorophyll a greatly exceeded total bacteriochlorophyll a . Total Bchl a reached a seasonal minimum in May, and total chlorophyll a dropped from $> 900 \text{ mg m}^{-2}$ in February to 100 mg m^{-2} in May.

Surface (upper 12 m) methane concentrations were low (ca. $0.1 \mu\text{M}$) for most of the year with the exception of February when elevated concentrations (ca. $0.6 \mu\text{M}$) were noted (Fig. 3). The cold (4°C) isothermal conditions and extension of dissolved oxygen down to 28 m during February (Fig. 2C) indicate that deeper mixing had occurred. Thus, methane previously entrapped in the anoxic waters between 20–28 m was released during February and was mixed upward. A consistent gradient of increasing methane concentrations with depth was always associated with the oxycline (Fig. 3). Methane concentrations were typically $2\text{--}5 \mu\text{M}$ just beneath the oxycline and increased to very high levels (ca. $50 \mu\text{M}$) at the chemocline. Below the

chemocline, methane remained generally invariant (ca. $50 \mu\text{M}$) with depth and season.

Temporal changes in the distributions of dissolved inorganic nitrogen and silica were similar to those of methane. When the upper 28 m were isothermal in February, DIN ($14 \mu\text{M}$) and Si ($49 \mu\text{M}$) concentrations were relatively high and increased across the oxycline (Fig. 4A). As the mixolimnion became stratified in May, DIN fell to $0.1 \mu\text{M}$ and dissolved Si fell to $9 \mu\text{M}$ in the surface water. A gradient of increasing DIN and Si was associated with the oxycline (Fig. 4B). Most available DIN was ammonia: in February NO_3^- concentration was less than $1.2 \mu\text{M}$, and in May NO_3^- was undetectable. Dissolved phosphate concentrations were high ($>100 \mu\text{M}$) throughout the mixolimnion in February and May.

The phytoplankton community was dominated numerically by only two or three species on a given date. A seasonal succession was observed (Table 2): the chlorophyte *Oocystis* sp. dominated in July, the chlorophyte *Ankistrodesmus* sp. and a small green flagellate dominated in November, the February bloom was dominated by the diatom *Nitzschia palea* and a less abundant *Chaeroceros* sp.; the composition observed in May was similar to February. Cyanophytes were rare during the entire year. The zooplankton community included only two species

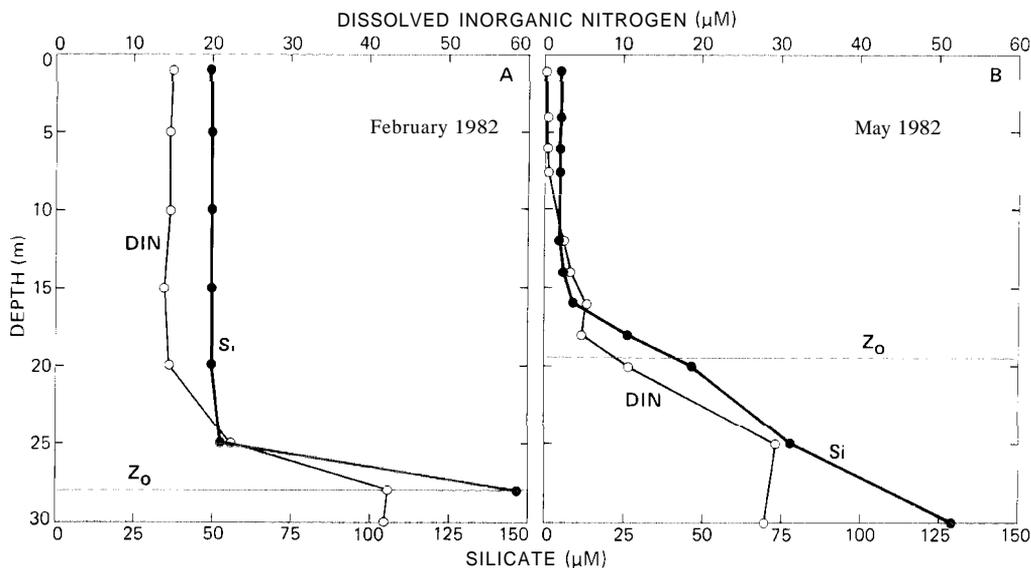


Fig. 4. Vertical profiles of dissolved silica and dissolved inorganic nitrogen (DIN) in Big Soda Lake during February (A) and May (B) 1982; horizontal line shows depth of oxygen disappearance Z_o .

of crustaceans. The cladoceran *Moina hutchinsoni* was most abundant in summer and fall and the calanoid copepod *Diaptomus sicilis* was most abundant in spring (Table 2). Both species were present at low abundances in winter. Microzooplankton included several species of naked ciliates, a tintinnid ciliate, and the rotifers *Brachionus* sp. and *Hexarthra* sp.

The shoreline macrophytes supported a highly active population of nitrogen-fixing cyanophytes (Fig. 5). No activity was observed in the dark and addition of NH_4^+ to light-incubated flasks totally inhibited nitrogenase. Assuming a 3 to 1 ethylene to nitrogen conversion factor (Hardy et al. 1968), the rates observed during September were equivalent to $555 \text{ nM N}_2 \text{ gh}^{-1}$ or $6.7 \mu\text{mol g day}^{-1}$ (assuming 12 h of light). These rates are nearly twice as high as those reported for tropical marine macrophytes (*Thalassia testudinum*) colonized by the cyanophyte *Calo-*

thrix sp. (Capone & Taylor, 1977). No macrophytes were present during the winter. In May, the macrophytes were small (1–2 cm) and harbored no obvious epiphytes. By July, however, the macrophytes were fully developed and were colonized by *Anabaena* sp. (colony size ca. 1–2 mm). In the fall, the *Anabaena* sp. patches had grown considerably (1–2 cm) and entirely covered the *Ruppia* sp. By winter, when the macrophytes were dying off, large clumps (ca. 10 cm diameter) of cyanophyte mats were evident in the littoral zone and were observed floating in the pelagic regions of the lake.

Discussion

The mixolimnion of Big Soda Lake exhibits seasonal changes similar to those expected in a temperate monomictic lake, and we observed three distinct limnological states: (1) the summer-fall period of thermal stratification, (2) the winter circulation of the mixolimnion, and (3) the initiation of stratification during spring. During summer-fall, the most abundant phototrophic producers (in terms of total chlorophyll) are purple sulfur bacteria, and in winter the most abundant primary producers are phytoplankton (pennate diatoms). The spring (May 1982) is a period of transition when the total biomass of phototrophic producers is small (a similar transition period may occur in early winter). Big Soda Lake thus undergoes a seasonal alternation in the dominance of phototrophic bacteria and algae; this alternation appears to be a consequence of seasonal changes in vertical mixing which also influence the distribution of light, dissolved gases (DO , CH_4), and dissolved nutrients (NH_4^+ , Si).

During stratification, the availability of DIN is low and may limit phytoplankton population growth in the epilimnion. This is consistent with high rates of N_2 -fixation observed in the shoreline macrophyte communities during late September (Fig. 5). The absence of cyanophytes from the water column during stratification, however, implies that if water column N_2 -fixation occurs it is probably associated with particulate material (e.g., patches of shoreline bluegreens) and is not available to the phytoplankton community. Bioassays done by Axler et al. (1978) and Priscu et al. (1982) also suggest the limitation of algal growth by nitrogen, and indicate further that trace metals (Fe) may also

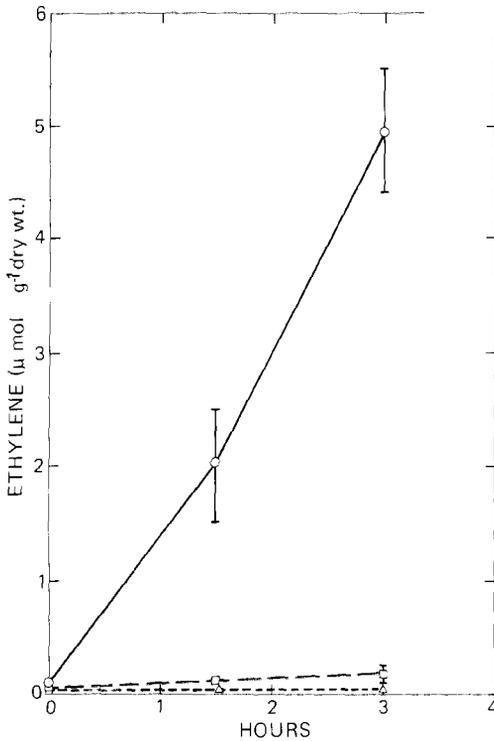


Fig. 5. N_2 -fixation (acetylene reduction) by Big Soda Lake macrophytes (*Ruppia* sp.) epiphytized by heterocystous *Anabaena* sp. Points represent means of three flasks and error bars indicate ± 1 standard deviation. Flasks were incubated in the light (○), dark (□) or in the light with 20 mM NH_4Cl (△).

be limiting. Because algal biomass is low, surface water is transparent and photosynthetic oxygen production occurs down to about 20 m, the depth of about 0.5–3% surface irradiance (Table 2). Dissolved oxygen is not present below this depth, indicating that vertical mixing is slow relative to microbial or chemical processes that utilize oxygen (respiration, sulfide or thiosulfate oxidation, nitrification, methane oxidation). Hence, the depth of oxygen disappearance Z_o appears to be controlled primarily by the depth of light penetration. Anoxic water below Z_o have high concentrations of CH_4 (Fig. 3), NH_4^+ (Fig. 4), and other reduced substances such as H_2S (ca. 0.1–1 mM; R. L. Smith, pers. commun.). The upper layer of the anoxic hypolimnion is within the photic zone and can sustain phototrophic sulfur bacteria.

When the mixolimnion becomes isothermal in winter, dissolved oxygen is mixed well below the compensation depth. This is a consequence of (1) an enhanced rate of vertical mixing, and/or (2) a reduction in the rate of oxygen utilization by chemoautotrophs and heterotrophs. Measures of dark $^{14}CO_2$ fixation were substantially reduced in February relative to November or May (Cloern & Cole, 1982), which suggests that the deeper penetration of oxygen in winter is due, in part, to reduced rates of chemoautotrophy. A second consequence of vertical mixing in winter is the phytoplankton bloom which is sustained by nutrients (NH_4^+ , Si; Fig. 4A) that are brought to the surface from the lower mixolimnion. The enhanced light attenuation by chlorophyll *a* and the increased depth of oxygen penetration separate the photic zone from the anoxic zone, and the population of photosynthetic bacteria declines and apparently sinks.

As the surface layer warms in spring, a thermocline forms and vertical mixing slows. Assimilation by phytoplankton depletes nutrients (DIN, Si; Fig. 4B) in the epilimnion, and chlorophyll *a* concentration declines. During this transition period, residual DIN exists below the thermocline and a chlorophyll *a* peak is seen in the upper hypolimnion (Fig. 2H) where nutrient concentrations are still relatively high. The coexistence of DIN ($>5 \mu M$) and a subsurface chlorophyll *a* peak is consistent with the hypothesis that decline of the winter diatom bloom is a consequence of nutrient limitation. However, we cannot discount the potential significance of grazing because zooplankton abundance increases (Table 2)

simultaneous to the initiation of thermal stratification and decreasing surface DIN. After the winter diatom bloom declines, light reaches the anoxic zone and the population of photosynthetic bacteria can begin to grow.

Photosynthetic bacteria are present in other lakes where light and H_2S coexist (Czeczuga 1968; Triiper & Genovese 1968; I'akahashi & Ichimura 1968, 1970; Culver & Brunskill 1969; Northcote & Halsey 1969; Sorokin 1970; Pfennig 1975; Wetzel 1975; Cohen *et al.* 1977; Lawrence *et al.* 1978). They occur in Big Soda Lake when the mixolimnion is stratified, surface DIN concentrations are low, phytoplankton biomass is low, and the photic zone is deep. When the mixolimnion circulates and nutrient concentrations and phytoplankton biomass increase, the photic zone becomes shallow and the population of the photosynthetic bacteria becomes light limited and it declines and presumably sinks. The alternation between phototrophic bacteria and phytoplankton observed in Big Soda Lake may be a common occurrence in those stratified waters where light seasonally penetrates to the anoxic zone. However, only a few studies of phytoplankton and photosynthetic bacteria have been conducted over an annual cycle, and little is known about the relative utilization of light energy by these two photosynthetic communities. Seasonal changes in phytoplankton and photosynthetic bacterial populations have been observed in several stratified lakes including Fayetteville Green Lake (Culver & Brunskill 1969), Lake Haruna (Takahashi & Ichimura 1968), Soap Lake (Walker 1975), Waldsea Lake (Lawrence *et al.* 1978), and Solar Lake (Cohen *et al.* 1977). Although these lakes and Big Soda Lake are chemically or physically very different, each has a population of photosynthetic bacteria during the period of stratification. Moreover, for those lakes where information is available, the period of stratification is a time of low phytoplankton biomass and, hence, deep light penetration. Low phytoplankton biomass, which may result from nutrient limitation (Big Soda Lake, Soap Lake), light inhibition (Solar Lake), or unfavorable ionic composition of the water (Fayetteville Green Lake), appears to be prerequisite for the development of a population of photosynthetic bacteria.

The relative contribution of photosynthetic bacteria to total phototrophic primary productivity has been measured in numerous lakes, and it ranges

from extremes of 0.3% (Parkin & Brock 1980) to 91% (Cohen *et al.* 1977) of daily rates. Less is known about the contribution of photosynthetic bacteria to annual productivity, although Culver & Brunskill (1969) estimated the contribution to be 83% in Fayetteville Green Lake, Lawrence *et al.* (1978) estimated 46% in Waldsea Lake, and Parker & Hammer (in press) estimated 17% in Deadmoose Lake. Parkin & Brock (1980) used published measures of daily productivity along with their own measures in six Wisconsin lakes, and found that the relative contribution of photosynthetic bacteria to primary productivity is a linear function of light availability (the fraction of surface insolation reaching the bacterial plate). They further postulated that lakes can be divided into three categories, depending upon the amount of light reaching the O_2 - H_2S interface. In lakes where no light reaches sulfide-containing waters, photosynthetic bacteria are absent. When low light intensity reaches the anoxic zone, photosynthetic bacteria are present but contribute a small fraction to total productivity. The third case is lakes in which high light intensity ($>5\% I_s$) penetrates to sulfide waters; in this case the photosynthetic bacteria contribute a substantial fraction to total productivity. Yearlong studies might show that individual lakes, such as Big Soda Lake, fall within different categories at different seasons depending upon changes in transparency and mixing.

Although chemical and biological features of Big Soda Lake change in a predictable manner with seasonal changes in vertical mixing, a number of specific processes require elucidation. For example, the phytoplankton bloom in winter is apparently a response to increased availability of nutrients, yet we do not know the ultimate source of NH_4^+ and Si that supports the winter diatom bloom. Vertical distributions of NH_4^+ and Si (Fig. 4) indicate that mineralization below the oxycline is the process that generates these nutrients. High values of DIN, Si, and CH, in the surface water during circulation of the mixolimnion indicate further that nutrients derived from the hypolimnion are mixed to the surface layer. But we do not know how much (if any) NH_4^+ is derived from the monimolimnion after 'leaking' across the chemocline, and how much NH_4^+ results from recycling within the mixolimnion or from sinking of cyanobacterial aggre-

gates transported from the littoral zone. Axler *et al.* (1978) found a very high concentration (>2 mM) of NH_4^+ at the chemocline, and we found consistently high CH, just above the chemocline (Fig. 3). These observations indicate that the important source of nutrients may be anaerobic decomposition of particulate organic matter associated with the chemocline. In fact, methane concentrations in the anoxic waters trapped beneath the oxycline yet above the chemocline may be reflective of water column methanogenesis (Winfrey & Zeikus 1979). Methanogenic bacteria have been recovered from 33 m in Big Soda Lake and profiles of methane and ethane suggest water column methanogenesis occurs above the chemocline (R. S. Oremland, unpubl. data). These observations imply that decomposition in the water column and nutrient regeneration above the chemocline may be of significance to the fertility of the mixolimnion. The consistently high turbidity at the chemocline is probably a consequence of particulates that originate in the mixolimnion and are retained at the chemocline by increased density of the monimolimnion. Culver & Brunskill (1969) also observed a turbidity peak at the chemocline of Fayetteville Green Lake, and they speculated that organic matter which accumulates and is mineralized at the chemocline retains nutrients within the mixolimnion that otherwise would be lost to the sediments. Parkin & Brock (1981) found that about 85% of phytoplankton productivity of Knaack Lake is mineralized or consumed in the mixolimnion before reaching the sediments. Certainly some particles do sink through the chemocline of Big Soda Lake because sediment cores from the lake center have discrete bands of red and green pigments which reflect surface blooms of photosynthetic bacteria and diatoms (Rau *et al.* 1982).

In this paper we have described seasonal changes in the biomass of two phototrophic communities and presented hypotheses about the causes of seasonality. Subsequent research in Big Soda Lake will quantify primary production by phototrophs, and microbial processes at the chemocline and in the sediments that utilize organic matter originating in the mixolimnion.

Acknowledgements

We greatly appreciate the field assistance of Peter Alexander, Mike Betlach, Charles Culbertson, John Duff, Richard Smith, and Larry Smith. And sincere thanks go to Steven Hager and Dana Harmon for nutrient analyses, Andrea Alpine and Sally Wienke for chlorophyll determinations, Raymond Wong for phytoplankton taxonomy, Jack Hargis for identification of zooplankton, and to Pete Law for conductivity data. We are grateful to Hans Trüper for his identification of *E. vacuolata*.

References

- Axler, R. P., Gersberg, R. M. & Paulson, L. J., 1978. Primary productivity in meromictic Big Soda Lake, Nevada. *Great Basin Nat.* 38: 187-192.
- Bradley, W. H., 1931. Origin and microfossils of the Green River formation of Colorado and Utah. U.S.G.S. prof. Pap. 168, 58 pp.
- Breese, C. R., Jr., 1968. A general limnological study of Big Soda Lake. M.S. Thesis, Univ. Nevada, Reno, 83 pp.
- Brown, E., Skougstad, M. W. & Fishman, M. J., 1970. Methods for collection and analysis of water samples for dissolved minerals and gases. U.S. Geol. Surv. Tech. Wat. Resour. Inv. 5 A1, V pp.
- Capone, D. & Taylor, B. F., 1977. Nitrogen fixation (acetylene reduction) in the phyllosphere of *Thalassia testudinum*. *Mar. Biol.* 40: 19-28.
- Carpenter, J. H., 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. *Limnol. Oceanogr.* 10: 141-143.
- Chern, J. E. & Cole, B. E., 1982. Autotrophic processes in meromictic Big Soda Lake, Nevada. *EOS Trans. Am. Geophys. Un.* 63: 965 (abstract).
- Cohen, Y., Krumbein, W. E. & Shilo, M., 1977. Solar Lake (Sinai). 2. Distribution of photosynthetic microorganisms and primary production. *Limnol. Oceanogr.* 22: 609-620.
- Culver, D. A. & Brunskill, G. J., 1969. Fayetteville Green Lake, New York. 5. Studies of primary production and zooplankton in a meromictic lake. *Limnol. Oceanogr.* 14: 862-873.
- Czczuga, B., 1968. An attempt to determine the primary production of the green sulfur bacteria, *Chlorobium limnicola* Nads. (Chlorobacteriaceae). *Hydrobiologia* 31: 317-333.
- Demaison, G. J. & Moore, G. T., 1980. Anoxic environments and oil source bed genesis. *Am. Ass. Petrol. Geol. Bull.* 64: 1179-1209.
- Didyk, B. M., Simoneit, B. R. T., Brassell, S. C. & Eglinton, G., 1978. Organic geochemical indicators of paleoenvironmental conditions of sedimentation. *Nature* 272: 212-216.
- Hardy, R. W. F., Holsten, R. D., Jackson, E. K. & Burns, R. C., 1968. The acetylene-ethylene assay for N_2 fixation: laboratory and field evaluation. *Pl. Physiol., Lancaster* 43: 1158-1207.
- Kharaka, Y. K., Law, L. M., Carothers, W. W. & Robinson, S. W., 1981. Soda Lake, Nevada, I: Hydrogeochemistry of an alkaline meromictic desert lake. *EOS Trans. Am. Geophys. Un.* 62: 922 (abstr.).
- Kimmel, B. L., Gersberg, R. M., Paulson, L. J., Axler, R. P. & Goldman, C. R., 1978. Recent changes in the meromictic status of Big Soda Lake, Nevada. *Limnol. Oceanogr.* 23: 1021-1025.
- Lawrence, J. R., C. Haynes & U. T. Hammer, 1978. Contribution of photosynthetic green sulfur bacteria to total primary production in a meromictic saline lake. *Verh. int. Ver. Limnol.* 20: 201-207.
- Lorenzen, C. J., 1967. Determination of chlorophyll and phaeopigments: Spectrophotometric equations. *Limnol. Oceanogr.* 12: 343-346.
- Northcote, T. G. & T. G. Halsey, 1969. Seasonal changes in the limnology of some meromictic lakes in southern British Columbia. *J. Fish. Res. Bd. Can.* 26: 1763-1787.
- Oremland, R. S., 1981. Microbial formation of ethane in anoxic estuarine sediments. *Appl. envir. Microbiol.* 42: 122-129.
- Oremland, R. S., Marsh, L. & Culbertson, C., 1981. Soda Lake 3: Dissolved gases and methanogenesis. *EOS Trans. Am. Geophys. Un.* 62: 922 (abstr.).
- Oremland, R. S., Marsh, L. & DesMarais, D. J., 1982. Methanogenesis in Big Soda Lake, Nevada: an alkaline, moderately hypersaline desert lake. *Appl. envir. Microbiol.* 43: 462-468.
- Parker, R. D. & Hammer, U. T., in press. A study of Chromatiaceae in a saline meromictic lake in Saskatchewan. *Canada. Int. Revue ges. Hydrobiol.*
- Parkin, T. B. & Brock, T. D., 1980. Photosynthetic bacterial production in lakes: The effects of light intensity. *Limnol. Oceanogr.* 25: 711-718.
- Parkin, T. B. & Brock, T. D., 1981. Photosynthetic bacterial production and carbon mineralization in a meromictic lake. *Arch. Hydrobiol.* 91: 366-382.
- Pfennig, N., 1975. The phototrophic bacteria and their role in the sulfur cycle. *Pl. Soil* 43: 1-16.
- Priscu, J. C., Axler, R. P., Carlton, R. G., Reuter, J. E., Arneson, P. A. & Goldman, C. R., 1982. Vertical profiles of primary productivity, biomass and physico-chemical properties in meromictic Big Soda Lake, Nevada-U.S.A. *Hydrobiologia* 96: 113-120.
- Rau, G. H., DesMarais, D. J. & Oremland, R. S., 1982. Stable isotope abundance in sedimentary inorganic, organic, and pigment carbon: applications to the paleoecology of Big Soda Lake, Nevada. *EOS Trans. Am. Geophys. Un.* 63: 957 (abstr.).
- Robinson, S. W. & Kharaka, Y. K., 1981. Big Soda Lake, Nevada, 2: Carbon isotopes. *EOS Trans. Am. Geophys. Un.* 62: 922 (abstr.).
- Rudd, J. W. H., Hamilton, R. D. & Campbell, N. E. R., 1974. Measurements of microbial oxidation of methane in lake water. *Limnol. Oceanogr.* 19: 519-524.
- Smith, J. W. & Robb, W. A., 1973. Aragonite and the genesis of carbonates in Mahogany zone oil shales of Colorado's Green River Formation. *U.S. Bur. Mines Rep.* 7727, 21 pp.
- Sorokin, J. I., 1970. Interrelations between sulfur and carbon turnover in meromictic lakes. *Arch. Hydrobiol.* 66: 391-446.
- Sorokin, J. I. & Donato, N., 1975. On the carbon and sulfur metabolism in the meromictic Lake Faro (Sicily). *Hydrobiologia* 47: 241-252.

- Stewart, W. D. P., Fitzgerald, G. P. & Burris, R. H., 1967. In situ studies on N₂ fixation using the acetylene reduction technique. *Proc. Natn. Acad. Sci. U.S.A.* 58: 2071-2078.
- Takahashi, M. & Ichimura, S., 1968. Vertical distribution and organic matter production of photosynthetic sulfur bacteria in Japanese lakes. *Limnol. Oceanogr.* 13: 644-655.
- Takahashi, M. & Ichimura, S., 1970. Photosynthetic properties and growth of photosynthetic sulfur bacteria in lakes. *Limnol. Oceanogr.* 15: 929-944.
- Takahaahi, M., Yamaguchi, Y. & Ichimura, S., 1970. Dark fixation of CO₂ in the lake with special reference to organic matter production. *Bot. Mag., Tokyo* 83: 397-410.
- Truper, H. G. & Genovese, S., 1968. Characterization of photosynthetic sulfur bacteria causing red water in Lake Faro (Messina, Sicily). *Limnol. Oceanogr.* 13: 225-232.
- Walker, K. F., 1975. The seasonal phytoplankton cycles of two saline lakes in central Washington. *Limnol. Oceanogr.* 20: 40-53.
- Wetzel, R. G., 1975. *Limnology*. W. B. Saunders Co., Philad., 733 pp.
- Winfrey, M. R. & Zeikus, J. G., 1979. Microbial methanogenesis and acetate metabolism in a meromictic lake. *Appl. envir. Microbiol.* 37: 213-221.