

## 6. Microbiology of the Great Salt Lake north arm

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### The site

The Great Salt Lake, Utah, Fig. 6.1, is a fairly shallow (10 m) terminal lake consisting of two arms of greatly different salinity separated by a rock fill railroad causeway. Although the causeway was constructed of loose fill with two culverts (Gwynn 1980) to permit exchange of water between the two arms, at present there is very little real water return southward, most of it moves to the north. Salt has migrated to the north arm along with the water reducing the south arm salinity to about one third that of the north arm. Some north arm water has returned to the south forming a dense brine layer about 7 m below the surface. The difference in densities between the two layers (1.076 and 1.164) prevents circulation which excludes oxygen resulting in an anoxic dense brine layer similar to one in the Dead Sea (Nissenbaum 1975) containing hydrogen sulfide (Gwynn 1980). Little is known about the microbiology of this layer. Most of the work reported in this paper has been done in the hypersaline north arm.

In contrast to the majority of saline lakes, including the Dead Sea (Greer 1977; Nissenbaum 1979), the Great Salt Lake is at high elevation, 1 280 m, and is subject to extreme annual air temperature variations,  $-30^{\circ}$  to  $40^{\circ}$  C, although the water temperature rarely exceeds extremes of  $-5^{\circ}$  C to  $30^{\circ}$  C except along the shallow margin with a slope of a few cm km<sup>-1</sup> where temperatures may reach  $50^{\circ}$  C. Chemically the lake is classified as a sodium chloride lake (Eugster & Hardie 1978) with a composition similar to that of seawater (Table 6.1) but ten times as concentrated (Hem

1970). Both the water and the sediment of the lake contain unusually high concentrations of other elements such as Li, B, Cu, Zn, Pb, Cd and As (Gwynn 1980) which may influence the biology of the lake.

The relative humidity of the region is often 8% or lower during the summer and evaporation results in a loss of about 1.5 m of water from the north arm. Since 90–95% of the freshwater inflow is into the south end (Fig. 6.1) water replacement in the north arm is almost entirely by flow from the south through two culverts. During the summer, evaporation on the north arm is sufficient to result in the precipitation of sodium chloride. On calm days,

*Table 6.1 Ions in the north, and south arms of the Great Salt Lake, 1975–1977.*

	North Arm <sup>a</sup>		South Arm <sup>b</sup>	
	g l <sup>-1</sup>	eq. l <sup>-1</sup>	g l <sup>-1</sup>	eq. l <sup>-1</sup>
Ca	0.3	.02	0.2	.01
K	6.7	.17	2.5	.06
Mg	11.1	.91	4.0	.03
Na	105.4	4.58	36.5	1.59
Cl	181.0	5.10	61.0	1.72
SO <sub>4</sub>	27.0	.56	8.4	.17
HCO <sub>3</sub>	0.5	.01	0.5	.01
CO <sub>3</sub>	0.3	.01	0.4	.13
Total	332.5		113.5	
Cation equiv.		5.68+		2.00+
Anion equiv.		5.68-		2.03-
pH	7.7		8.4	

<sup>a</sup> Post (1977a), Utah State Division of Health (1977).

<sup>b</sup> Utah State Division of Health (1977).

Table 6.2 Chemicals of biological interest in the north arm of the Great Salt Lake 1973-1977.

	Wt. per Liter	Low value	High value	Average	s.d.	No. of observations
Nitrate	μg	absent	-	-	-	95
Nitrite	μg	absent	-	-	-	95
O-PO <sub>4</sub> as P	μg	40	1 600	440	174	90
Total P	μg	350	4 000	1 032	489	93
NH <sub>3</sub>	μg	0	1 120	-	-	95
Particulate <sup>a</sup> N	mg	1.0	4.0	1.4	0.5	30
Soluble <sup>a</sup> N	mg	3.0	17.3	6.7	3.0	33
Total <sup>a</sup> N	mg	4.0	18.9	8.0	3.1	33
Soluble <sup>a</sup> C	mg	-	-	43.0	-	1
Total <sup>a</sup> C	mg	-	-	44.1	-	1
Oxygen	mg	0	1.8	0.6	0.4	107

<sup>a</sup> Organic forms.

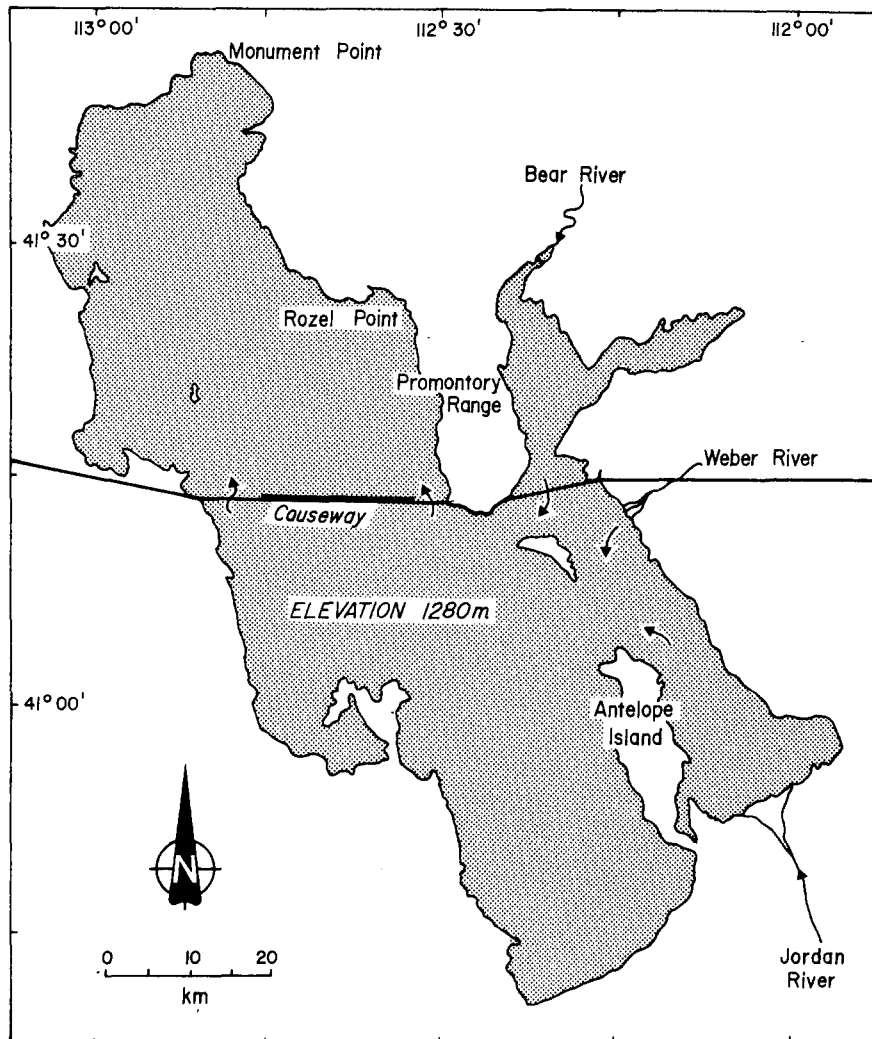


Fig. 6.1 Map of the Great Salt Lake, Utah.

Table 6.3 Carbon/nitrogen ratios in the Great Salt Lake north arm and certain other sites and substances.

	C/N	per liter mg C/mg N
Soluble N	6.4/1	43/6.7
Total N	5.5/1	44.1/8.0
Settled sewage	10/1	219/22
Lakes, ocean (total)	10–30/1	1–25/0.1–1.2
Protein	3.2/1	–
Night soil	6/1	–

sodium chloride crystals grow on the water-air interface forming a thin crust of salt crystals floating on the surface of the lake. Light breezes and currents push these to the margin of the lake in a north to north-easterly direction where they accumulate on the shore line as a salt bank or settle to the bottom forming a loose slush. Sodium chloride precipitation also occurs in the water column over the entire lake and settles to the bottom. With time this loose salt slush compacts to form a concrete-like layer 10–20 cm or more thick. Only vigorous hammering with a solid tool will penetrate this salt layer once compacted. At the lowest historical lake level (1 277.6 m in 1965) up to 1.5 m of sodium chloride occurred on the bottom of the deepest part of the lake. The settling and compaction of salt along the margin of the lake has a profound effect on the microorganisms as will be discussed later. When rains begin in the fall, the salt

Table 6.4 Numbers and biomass of organisms in the North arm of the Great Salt Lake 1973–1977 (Post 1977a; Stube *et al.* 1976).

Organisms	Number ml <sup>-1</sup>	Estimated biomass g · m <sup>-3</sup>
Bacteria-Direct count Av.	7 × 10 <sup>7</sup>	300
-Viable count Max.	5 × 10 <sup>6</sup>	22
Algae- <i>Dunaliella salina</i> Max.	1 × 10 <sup>4</sup>	24
- <i>D. viridis</i> Max.	2 × 10 <sup>3</sup>	1.4
Brineshrimp	obs. <sup>a</sup>	0.1
Brinefly	obs. <sup>b</sup>	–
Fungus ( <i>Cladosporium</i> )	obs. <sup>c</sup>	–
Ciliate	obs. <sup>c</sup>	–
Halophages (virus)	obs. <sup>b</sup>	–

<sup>a</sup> Estimated at 1 animal m<sup>-3</sup>.

<sup>b</sup> Observed in large numbers but not quantified.

<sup>c</sup> One observation.

Table 6.5 Bacterial counts, Great Salt Lake north arm station LVG-3 at 3 meters on basal medium<sup>a</sup> plus various salt concentrations. Surface plates, incubation 6 weeks.

Medium % salt <sup>b</sup>	20 °C	37 °C
0	0 <sup>c</sup>	0
2	0	0
6	0	0
10	160	570
14	5 800	3 800 000
18	110 000	7 600 000
22	150 000	2 200 000

<sup>a</sup> Basal medium: caesin hydrolysate, 5 g; yeast extract, 1 g; KNO<sub>3</sub>, 1 g; Na<sub>2</sub> citrate, 3 g; agar, 10 g; distilled water, 1 l; pH 7.2–7.4.

<sup>b</sup> Salt solution: NaCl, 220 g; MgSO<sub>4</sub> · 7 H<sub>2</sub>O, 10 g; CaCl<sub>2</sub> · 2 H<sub>2</sub>O, 0.2 g; distilled water, per 1 l of basal medium. The % salt is based on the NaCl concentration. Appropriate dilutions of this solution were made for the lower percentages of salt.

<sup>c</sup> No colonies on the 10<sup>-1</sup> dilution plates.

precipitated along the margin in water up to 2 m deep goes back into solution. In deeper areas of the lake, re-resolution may take years.

During the winter when the lake temperature reaches 3–4 °C or below, jellylike hydrated sodium sulfate (Na<sub>2</sub> SO<sub>4</sub> · 10 H<sub>2</sub>O) precipitates on the lake bottom. Winds and waves push the gel shoreward and out of the water to dehydrate and form white banks of crystalline sodium sulfate. Rising lake temperatures and spring rains return this to solution. Crystals of gypsum are often found in the surface sediments on the margin.

The high concentration of dissolved solids combined with the high elevation reduces the solubility of gases in the lake water, most importantly oxygen. Solubility curves calculated from lake water data indicate that saturation is 1.8 mg l<sup>-1</sup> at 0 °C and 0.9 at 30 °C. Several years of sampling has rarely shown oxygen levels above 1.0 mg l<sup>-1</sup> and then only

Table 6.6 Number of days to produce a 90% reduction of *Escherichia coli* in Great Salt Lake water.

Temp. (°C)	North arm	South arm
19	0.76	0.85
9	5.88	–
2	5.88	4.35

Table 6.7 Concentration of major (%) and minor ( $\text{mg l}^{-1}$ ) gas phase components from light and dark microcosms (Stube *et al.* 1976). Both columns fed  $\text{NO}_3^-$  as nitrogen source.

	Light (days)			Dark (days)		
	196	273	316	196	273	316
$\text{O}_2\%$	78.8	67.6	53.9	17.4	16.5	18.8
$\text{N}_2\%$	20.1	31.1	45.0	81.2	79.9	72.8
$\text{CO}_2\%$	0.7	0.9	0.4	1.4	3.6	8.4
$\text{CH}_4\%$	0.4	0.4	0.7	T	T	T
$\text{CH}_3 - \text{CH}_3$ ( $\text{mg l}^{-1}$ )	0.1	0.2	1.0	0.07	0.01	0.2
$\text{CH}_2 = \text{CH}_2$ ( $\text{mg l}^{-1}$ )	0.5	0.5	2.0	0.05	0.01	1.0
$\text{CH}_3 - \text{CH}_2 - \text{CH}_3$ ( $\text{mg l}^{-1}$ )	-	-	2.0	-	-	1.0

T = Trace.

- = Not Done.

when algae were blooming (Stube, Post and Porcella 1976). A four year oxygen average was  $0.6 \text{ mg l}^{-1}$  (Table 6.2). Other metabolically important gases show correspondingly low solubilities. Carbon dioxide solubility is reduced but is still relatively very soluble. Evaporation also causes calcium carbonate to precipitate around a nucleus, usually clay, or the eggs and feces of brine flies or brine shrimp forming the oolitic sand so common around the lake margin. Algal utilization of bicarbonate may also influence this precipitation.

Biochemically the lake is rich in the nutrients necessary for life (Table 6.2). Over the study period phosphate was plentiful especially at the sediment

surface and ortho-phosphate remained fairly constant, declining slightly when algal blooms occurred. Inorganic nitrogen was present only sporadically as ammonia which varied considerably being undetectable about half the time. Nitrates and nitrites were not detected. Organic nitrogen was plentiful averaging about  $8 \text{ mg l}^{-1}$  over several years and was fairly constant. Organic carbon was determined only once and yielded a C/N ratio of 5.5:1 (Table 6.3). Settled sewage contains four times more carbon with a ratio of 10:1 while lakes and oceans are about 0.1 the amount of organic matter present in the Great Salt Lake. The Great Salt Lake is fairly nutrient rich being limited in inorganic nitrogen (Stube *et al.* 1976).

The multiple stresses of high salt, low oxygen, and temperature has resulted in a community of organisms adapted in one way or another to these stresses. One of the obvious consequences of the stresses is a marked reduction in diversity of the species encountered. Table 6.4 shows the organisms present in greatest abundance in the plankton of the north arm. Each of these organisms has adapted in its own way to the extreme environment.

### The bacteria

The bacteria, primarily *Halobacterium* and *Halococcus*, represent the dominant biota in terms of biomass most likely as a result of the high organic

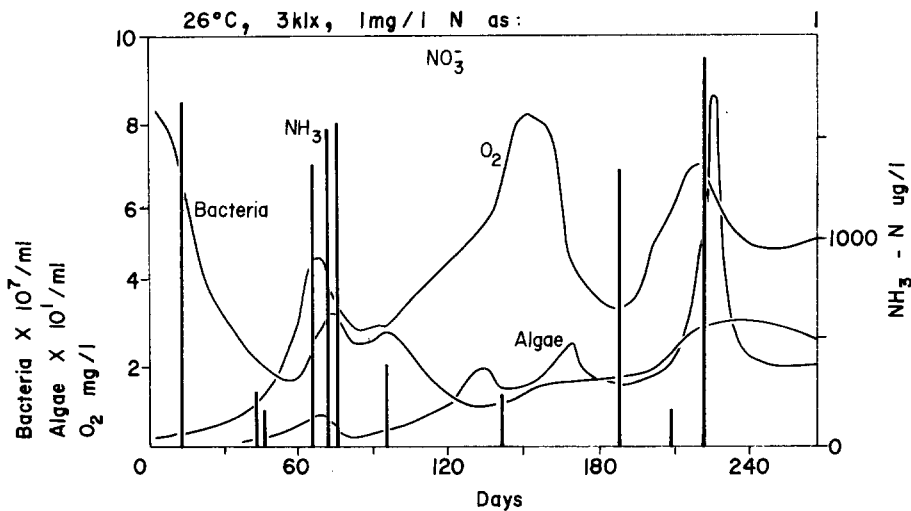


Fig. 6.2 Bacteria, algae, ammonia and oxygen cycles for 316 days in lighted microcosm fed only nitrate.

matter content of the lake. This biomass is so great that the north arm is a light red wine color (Post 1975). The bacterial adaptation to the stresses of the lake is perhaps the most complete of all the organisms. The lake bacteria have made a number of cellular changes and evolved some unique properties presumably in response to the environmental stress (Bayley & Morton 1978; Dundas 1977; Kushner 1978). They are sufficiently different from all other prokaryotes that a separate group, the archaeobacteria, has been proposed for them (Woese, Margrum & Fox 1978). Several of these alterations are of interest in the Great Salt Lake environment. The osmotic stress posed by the high salt has resulted in membrane and protein changes which allow salt to enter the cell but are very selective in which ions enter (Brown 1976; Ginzburg 1978). Potassium is increased in the cytoplasm 10–100 times over the water concentration by an active 'pumping' mechanism while sodium concentration is reduced. One result of these evolutionary changes is an absolute requirement for high salt including sodium, potassium, and magnesium. In fact, reduction of salt content to below about 12%, i.e. 120 g l<sup>-1</sup> will not support growth. Table 6.5 presents the results of an experiment, repeated several times, showing the absolute bacterial dependence on high salt content. The fact that no non-halophiles or moderate halophiles were found in the plankton is interesting. Many of the halophiles isolated from the lake digest the cells of *Escherichia coli* (Crane 1974) and when placed in unmodified lake water, *E. coli* dies very rapidly (Table 6.6) (Burdyl and Post 1979). The mechanism of *E. coli* death is not clear but the unusually large number of bacteria in a ml of lake water (Table 6.4) could excrete sufficient enzymes to digest non-halophiles which have a different cell wall and membrane than the halophiles. It should be noted that the sediments have not yet been examined for non-halophiles. Preliminary studies on methane producers suggests that moderate halophiles may be found extensively in the sediments.

Another cellular adaptation to high salinity in these bacteria is a modified cell membrane lipid. Instead of the usual fatty acids found in the normal cell membrane bilayer, these bacteria have a many branched di-phytanyl di-glycerol (a diether) (Kushner 1978) making up 2 to 4% of the cell dry weight. This lipid bilayer is fluid (a necessity for

function) at the high temperature (Degani *et al.* 1978) encountered in many salt pools throughout the world and in the Great Salt Lake margin during the summer. Table 6.5 also illustrates the dependency of elevated temperatures for growth. Many of these bacteria have optimum growth temperatures of 45–50 °C (Crane 1974) although some cannot grow above 38° or 39 °C. In the lake the most dense growth of bacteria occurs in a heavy red slime on dark, radiation absorbing wood or tar along the margin of the lake where the temperature may reach 50 °C during the summer. Reduction of the temperature of incubation from 37 °C to 20 °C reduces the count 10–100 fold (Table 6.5). Incubation at 10 °C reduces the count to virtually zero in 6 weeks at all salt concentrations. During the winter months the viable bacterial count drops to about 10% of the summer counts although the direct counts remain fairly constant (Stube *et al.* 1976). Growth of the bacteria in the plankton is apparently a summer phenomenon when temperatures are about 20 °C. Utilization of the lake organic matter seems to be limited by low temperatures normally encountered. Ward (Ward & Brock 1978) has clearly indicated a salinity relationship with glutamate utilization. This slow-down may be combined salinity-temperature-oxygen interaction.

The lipid also has some other interesting properties which are potentially exploitable. As an ether-glycerol rather than a fatty acid-glycerol (fat) it has some properties of a fat, yet may be non-metabolised by animals. It has been studied by one of our group as an emulsifying agent in foods and found to be non-toxic (short term) to mice with emulsification characteristics much like Tween 80 (Collins 1977).

One of the most fascinating adaptations of these bacteria is the utilization of sunlight to manufacture ATP. This is photophosphorylation, i.e., photosynthesis but without chlorophyll (Kushner 1978). Instead, a purple membrane rhodopsin-protein complex absorbs light and pumps protons across the cell membrane ultimately creating ATP. The primary requirement for this, in addition to sunlight is the absence of oxygen. The north arm of the Great Salt Lake averages 0.6 mg l<sup>-1</sup> oxygen normally and a thermocline is observed in the lake during the summer which becomes anaerobic below about 5 meters (Post 1977a). The conditions for this type of photosynthesis thus occur on a regular basis. What use is made of the ATP is still an open

question (Ginzburg 1978). Its primary use is probably to maintain the intracellular  $K^+/Na^+$  ratios until oxygen returns. Carbon dioxide has been reported to be incorporated into cellular carbon compounds (Danon & Caplan 1977). If so, this would be true photosynthesis without chlorophyll.

The sediments of the north arm have been little studied except in a general way. Direct microscopic observations of water immediately above the sediments show a massive accumulation of organic debris and bacterial cells, the latter so great in number that direct counts are meaningless, estimated in some instances to be greater than  $10^9$  cells per ml, usually in large clumps. Tests using the ethylene method indicate that nitrogen fixation does not occur although more work should be done. Hydrogen sulfide is plentiful in the sediments precipitating with iron to form black FeS wherever organic matter is high. The anaerobic summer hypolimnion contains sufficient  $H_2S$  to cause an odor when collected.

Bacteria appear to be involved in  $H_2S$  production but are extremely slow growing on the medium used (Post 1979) supplemented with 22% salt solution (Table 6.5, Footnote b). They form colonies in dilution tubes after 4–5 weeks incubation but have not yet been isolated.

Methane and a few other hydrocarbons are produced in the lake. Ward (Montana State University, personal communication) has detected methane directly from lake sediments. Our evidence using microcosms supports this (Stube *et al.* 1976). (Table 6.7 presents the results of one pair of several parallel experiments in which gas was trapped from closed microcosms. Figure 6.2 shows the corresponding organism cycles. Several things are of interest here. Nitrate at  $1 \text{ mg l}^{-1}$  was used as the nitrogen source over the study period (Stube *et al.* 1976). Methane was produced in largest amounts in the lighted columns where biological activity was greatest. Dissolved oxygen exceeded saturation as determined for the lake itself and generally was highest when algal peaks occurred. Bacterial populations declined from the initial lake concentration but stabilized at about  $2 \times 10^7 \text{ ml}^{-1}$ . In the dark column, no algae were present, oxygen was at or below observed lake levels, bacterial numbers declined to less than  $1 \times 10^6 \text{ ml}^{-1}$  and methane was reduced to a trace. In all columns, several other hydrocarbon gases were produced in small amounts.

Two other unknown hydrocarbon peaks were observed accounting for 20–60% of the hydrocarbon gas phase making this fraction nearly equal to that of methane. Other than being a short chain hydrocarbon, they have not as yet been identified. Isopentene or isopentane, derivatives of phytane synthesis or degradation could be the gases in question.

Attempts are now underway to isolate the methane producers using some rather general techniques (Post 1979). Other than demonstrating gas production from formate and a mixture of formate and acetate with an optimum near  $45^\circ \text{C}$  little progress has been made to date. As with the  $H_2S$  producers, these bacteria grow extremely slow in 22% salt which complicates isolation. Growth is very rapid with much gas production when salt is reduced to 5–10%, however. This suggests that these are moderate rather than extreme halophiles. In addition to the methane and  $H_2S$  producers, many organic degrading bacteria are found in the sediments but very little is known about them. So far work has focused on the most prevalent plankton forms. Other bacteria do occur in the lake. For example a spirillum has been observed both microscopically and with scanning electron microscopy.

Biochemically the bacteria are fairly demanding under aerobic conditions requiring complex nutrients for growth (Kushner 1978). Some utilize carbohydrates (Tomlinson & Hochstein 1976), some reduce nitrates to nitrite and a few to nitrogen gas. Some produce hydrogen sulfide and some release ammonia from protein and amino acids (Crane 1974; Post, unpublished). It should be noted (Table 6.2) that no nitrate or nitrite has been observed in north arm water during a 2-year period. If ammonia oxidizing bacteria occur in the lake, the nitrate or nitrite could be used up too quickly to be detected. This will be discussed later.

Also present in the lake are virus parasites of the bacteria. These bacteriophages are host specific and the ease of isolation together with the large number of host bacteria suggests that a great many viruses are present in the north arm. Fifteen strains of *Halobacterium halobium* obtained from the National Research Council of Canada together with fourteen lake isolates and five from other sources were used as hosts. Nine viruses were isolated in one attempt (Post 1977b) seven on *H. halobium* strains and two on lake strains. One *H.*

*halobium* virus crossreacted with nine other *H. halobium* strains and one lake strain. The patterns of cross reaction indicate these viruses may be useful in classification of the *Halobacterium* genus. It also indicates 1) *Halobacterium halobium* is a common member of the lake bacteria, and, 2) there are many varieties of lake bacteria which did not react with the viruses and may or may not be *H. halobium*, but are extreme halophiles on other grounds (Crane 1974; Post, unpublished).

### The algae

No concerted effort has been made to study the algae of the north arm, reported to be *Dunaliella salina* (Brock 1975) and *D. viridis*, aside from the studies on their role in the community. One study (May 1978) with an axenic culture of the numerically dominant but extremely fragile red pigmented alga *D. salina* from the north arm (Table 6.4) showed that its optimum salinity was 10–15% sodium chloride with an optimum temperature about 28 °C. Furthermore, in the reduced light levels of the laboratory, 10–12 klx, the red pigmentation was reduced at high salinities and lost completely at salinities near optimum. Under laboratory conditions of nutrition, the cell size became smaller. The second alga, green pigmented (Table 6.4) was smaller (about 1/20 the volume of the red pigmented alga) and was similar to the dominant alga in the south arm. Extensive studies on an algal strain (Van Auken & McNulty 1973) originally isolated from the south arm indicate a salinity optimum of 10–15% and a temperature optimum near 32 °C. This smaller alga is much less

fragile and divides more rapidly at optimum conditions than the red alga, 23.8 hrs (Van Auken & McNulty 1973) vs 40 hrs (May 1978).

The algae have adapted to this high salinity by another mechanism, the production of equal osmolar intracellular glycerol (Ben-Amotz 1978; Brown 1976) to keep salt out of the cell allowing only water to enter or leave. The red form undergoes periodic blooms in the lake where cell concentrations may approach 10 000 ml<sup>-1</sup>. At this time, red-orange swirls appear on the lake giving some contrast to the purple-red bacterial background color. These algae averaged about 170 ml<sup>-1</sup> over a two year period. Contrasted to this, the green pigmented alga in the same samples averaged 48 ml<sup>-1</sup> and was often absent, with a high of 280 ml<sup>-1</sup>. In August a one day series of depth profiles at 8 sampling station (Post 1977b; Stube *et al.* 1976) showed that maximum algal concentrations occurred at about the 4 m depth being considerably fewer above and fewer below (Table 6.8). This was also the approximate point of the thermal density gradient and below this it was anaerobic. At those stations less than 4 meters in depth without a thermocline, maximum algal numbers occurred at the bottom. By October of the same year, turnover had occurred and algal numbers were more or less uniform top to bottom. The green pigmented alga tended to follow the same pattern although less than 0.1 the number. In winter, the red form was highest on the bottom, mostly rounded, non-motile forms. No green forms were observed except in a surface layer of low density water from the south arm floating on the north arm surface. This phenomenon occurred rather commonly during periods of calm (see Table 6.8, 'surface' for a summer example).

During summer evaporation, along the shallow margin the red alga float to the surface and are gently blown shoreward to accumulate in red-orange windrows along the edge. One observed windrow was crudely sampled and found to have 200 000 ml<sup>-1</sup> of sluggishly motile cells. The green alga was absent. As the water recedes, the salt is colored red-orange, gradually becoming a purple band. Green bands have been observed but not studied.

By far the most interesting habitats in the north arm involve both bacteria and algae. Mention has already been made of the growth of the bacteria in a

Table 6.8 Depth profile for 11 Aug 1975 of Station LVG-3 showing temperature, specific gravity, oxygen and *Dunaliella salina* counts.

Depth (m)	Temp. (°C)	Specific gravity	Dissolved oxygen (mg l <sup>-1</sup> )	<i>D. salina</i> (ml <sup>-1</sup> )
Surface	25.6	1.198	0.80	400
1.5	26.1	1.212	0.45	540
3.0	25.0	1.214	0.70	1 700
4.5	24.4	1.214	0.60	4 000
6.0	21.7	1.218	0.00	2 100
8.2 (bottom)	17.8	1.224	0.00	140

thick red slime on dark wood, rocks, and tar submerged on the lake margin. When removed from the water, a deep green layer of algae was observed on the underside of the edge of the object protected from direct sunlight. The alga is larger than the planktonic green form and much smaller than the planktonic red form and is non-motile. It greatly resembles the axenic laboratory culture of the red form described above. Red pigmented algal cells are observed mingled with the bacteria on top of the object, but there are relatively few of them generally embedded in a bacterial matrix.

In the early summer, the bacterial mass appears to be growing on the shallow sand surface mixed with some *D. salina* cells. As the NaCl begins to precipitate later in July, and floating salt is driven shoreward to settle out, the growing mass on the sand, especially noticeable in small sand pockets, is buried under the sedimenting salt. At first a slush, it gradually hardens, and still under a few centimeters of water, absorbs much radiation. The temperature under the 3–4 cm thick submerged salt with 7 cm of water above was in one case 34 °C. If the salt is above the water line the temperature exceeds 40 °C under the salt crust. The algae continue to photosynthesize under the salt crust (3 cm of salt reduces the light from 119 Klx to 34 Klx) and produce oxygen. Since oxygen is not very soluble in the lake water at the temperatures observed, it escapes as a gas but is trapped under the salt crust. Gas collecting under the crust produces sufficient pressure to lift it several cm above the sand forming a characteristic dome structure. The crust is under sufficient stress to cause it to crack, whereupon the gas is emitted as a series of bubbles. Stepping on the edge of these domes causes the sudden release of several liters of gas. Analysis of the gas on several occasions shows it to be 82–86% O<sub>2</sub> and 14–18% N<sub>2</sub>. Methane was absent or <0.2%, but Ward (personal communication) indicated its presence in small amounts from similar domes elsewhere on the lake. The gas composition resembles that of the microcosms (Table 6.7) in their early stage. The crust of a dome appears bright red in the lower cm or so where the salt slush first settled on the sand. When dissolved in 22% NaCl the bacterial count in this red layer was enormous (Table 6.9). The algae count of both types were also very high in the between-crystal liquid phase of the crust. Water in the space between the gas and the sand was not studied.

Table 6.9 Bacterial and algal cell counts in Great Salt Lake Water and salt crust red zone, Monument Point.

	Water (ml <sup>-1</sup> )	Salt (g m <sup>-1</sup> )
Bacteria	4.9 × 10 <sup>7</sup>	3.4 × 10 <sup>8</sup>
<i>D. viridis</i>	–	2 × 10 <sup>3</sup>
<i>D. salina</i>	73	3.5 × 10 <sup>4</sup>
Total algae	73	3.7 × 10 <sup>4</sup>

<sup>a</sup> Clump count; each clump had 2–100 cells averaging about 50.

### The grazers

Not much work has been done with the grazer trophic level. Only two potential grazers occur in the north arm: *Artemia salina*, the brine shrimp and several species of brine fly, *Ephydra*. There is some question as to whether eggs of either organism can actually hatch in north arm water. Numerous attempts in our laboratory to hatch eggs of brine shrimp and brine flies in north arm water have failed although reducing the salinity by half produces a hatch of both animals. Brine pools of 8–15% salt around the margin of the north arm produce immense hatches of both organisms. None the less, shrimp, fly larvae and fly pupae are found in the north arm during the summer season. Most of the shrimp and fly larvae would appear to flow into the north arm from the south arm where both the shrimp and the fly are found in incredible numbers. The death rate upon exposure to north arm water is apparently high since relatively few of the observed animals are alive. Live shrimp die rapidly upon return to the laboratory even in aerated jars. Fly larvae when present do progress to pupae, then to adulthood. Presumably both animals feed on the algae or other organic debris, although preference studies have not been done. Shrimp nauplii have been fed halobacteria alone but are smaller than normal and short-lived. Both organisms develop pigmentation, the fly larvae becoming a bright orange, and the shrimp a wine red possibly due to increased hemoglobin production at the low oxygen levels of the lake. In addition, the shrimp surviving in the lake all appear to have intracellular symbionts in cells lining the gut, while shrimp at lower salinities in pools nearby do not (Post & Youssef 1977). The role of these symbionts is unknown.



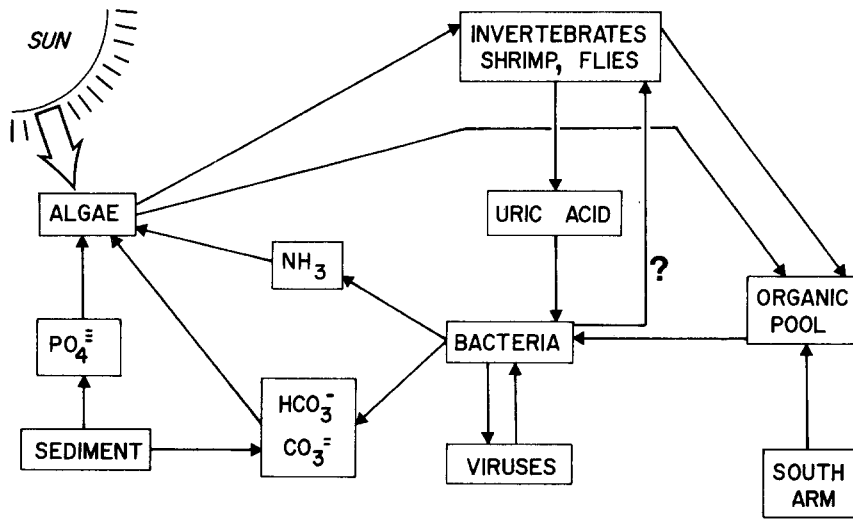


Fig. 6.3 Model for the community ecology of the Great Salt Lake.

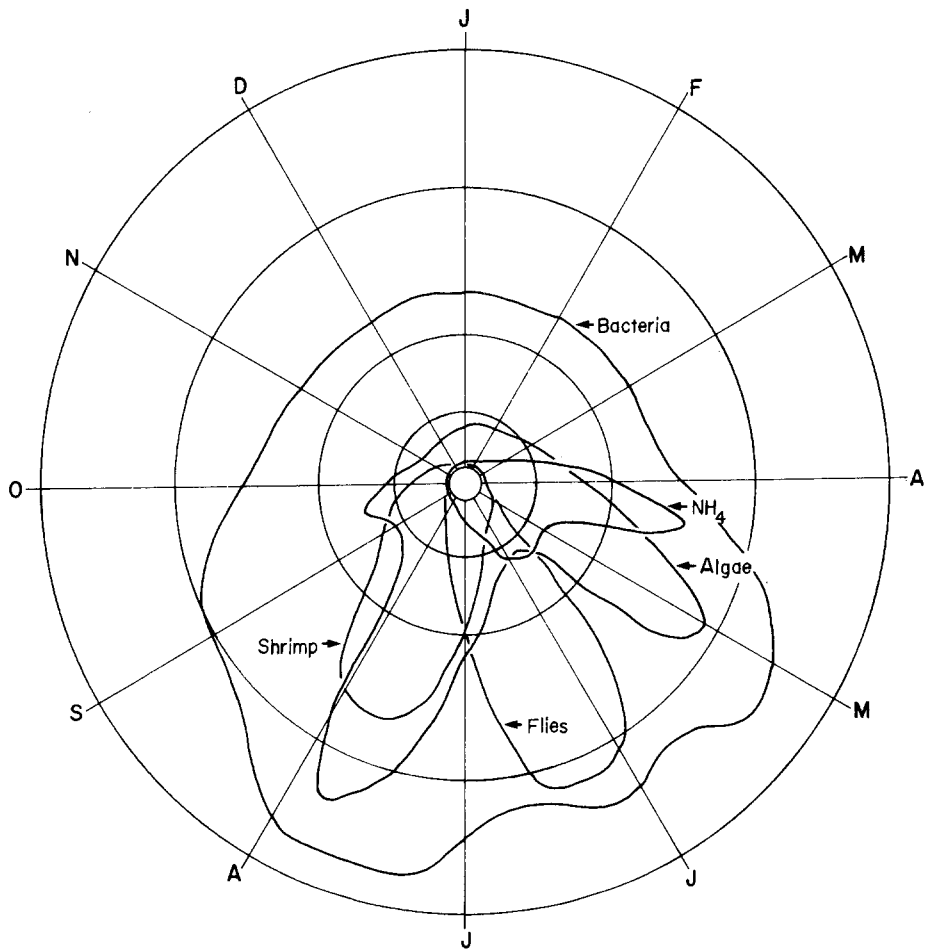


Fig. 6.4 Polar projection of a year lake cycle for four organisms and the limiting nutrient.

## Other organisms

Other organisms are occasionally observed in north arm water including a fungus (Cronin & Post 1977) and a ciliate resembling *Uronema* (Stube *et al.* 1976) at least once. When a low density south arm surface layer is floating on the top of the north arm (Table 6.8), this layer contains a number of south arm type algae and Protozoa which are not observed once the layer breaks up. Undoubtedly other organisms occur since an aquarium of lake water established in 1974 contains a variety of flagellates and amoeba (Post 1977a). Further work needs to be done on the Protozoa.

Blue-green algae have been reported from the lake especially associated with reef-life bioherms or biostromes (Collins 1977) and Brock (1976) reports the isolation of *Aphanothece halophytica* from the Great Salt Lake. Unfortunately these interesting reef-like structures are several meters below the lake surface and unavailable. To date, we have not observed blue-green bacteria in the lake proper or in the margin communities.

## Community metabolism

Since community metabolism has been discussed at length elsewhere (Post 1977a, b, 1980; Stube *et al.* 1976) only a brief summary is presented here. Based on direct lake measurements or microcosm studies (Stube *et al.* 1976), the following cycle is proposed (Fig. 6.3). Organic and inorganic nutrients enter the north arm from the south. Bacteria decompose the organics to form ammonia and CO<sub>2</sub>. The algae, utilizing ammonia and CO<sub>2</sub>, produce organic matter of unknown nature on which the bacteria grow. Ammonia oxidation does not appear to occur in the north arm at least at a detectable rate and thus nitrates and nitrites are absent. Nitrogen fixation has not been detected yet. The organic pool is large in the lake and appears to persist despite the presence of bacteria. This may reflect either the unavailability of the nitrogen to the bacteria, that is, in some unusable organic form, or the very limited period of the year when temperatures are high enough for bacterial growth and metabolism. Thus the north arm appears to be a closed nutrient system limited by the availability of a form of nitrogen usable by the algae on one hand

and the bacteria on the other. Superimposed on this are the brine shrimp and brine fly larvae feeding on debris and algae and possibly the bacteria. Excretory nitrogen forms for these organisms include ammonia from the brine shrimp and uric acid from the fly larvae. The only nutrients which are believed to escape from the lake, and then only in small quantities, are methane, oxygen, and adult brine flies. The yearly cycle as actually observed in the lake is presented in Fig. 6.4.

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