Natural Resources and Environmental Issues

Volume 15 *Saline Lakes Around the World: Unique Systems with Unique Values*

Article 27

1-1-2009

Long-term mesocosm simulation of algal and archaeal blooms in the Dead Sea following dilution with Red Sea water

Aharon Oren
Department of Plant and Environmental Sciences, Hebrew University of Jerusalem, Israel

Jonha Gavrieli
IMI (TAMI) Institute for Research and Development, Haifa Bay, Israel

Marco Kohen
Dead Sea Works Ltd., Beer-Sheva, Israel

Joseph Lati
Dead Sea Works Ltd., Beer-Sheva, Israel

Mordehay Aharoni
Dead Sea Works Ltd., Beer-Sheva, Israel

See next page for additional authors

Authors
Aharon Oren, Jonha Gavrieli, Marco Kohen, Joseph Lati, Mordehay Aharoni, and Ittai Gavrieli

Long-term Mesocosm Simulation of Algal and Archaeal Blooms in the Dead Sea Following Dilution with Red Sea Water

Aharon Oren[1], Jonah Gavrieli[2], Marco Kohen[3], Joseph Lati[3], Mordehay Aharoni[3] & Ittai Gavrieli[4]

[1]Department of Plant and Environmental Sciences, The Institute of Life Sciences, and the Moshe Shilo Minerva Center for Marine Biogeochemistry, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel; [2]IMI (TAMI) Institute for Research and Development, PO Box 10140, 26111 Haifa Bay, Israel; [3]Dead Sea Works Ltd., P.O.B. 75, 84100 Beer-Sheva, Israel; [4]Geological Survey of Israel, 30 Malkhei Yisrael St., 95501 Jerusalem, Israel

Corresponding author:
Aharon Oren, Department of Plant and Environmental Sciences, The Institute of Life Sciences, and the Moshe Shilo Minerva Center for Marine Biogeochemistry, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel
E-mail: orena@shum.cc.huji.ac.il

ABSTRACT

To understand the factors that determine the extent of blooms of the unicellular green alga *Dunaliella* and halophilic Archaea in the Dead Sea, and to predict the possible effects of the planned conveyance of Red Sea water to the Dead Sea, we performed simulation experiments in 0.9 m^3 outdoor mesocosms on the grounds of the Dead Sea Works Ltd. at Sedom, as well as in the laboratory. The laboratory simulations showed that development of *Dunaliella* was possible only when Dead Sea water (340 g l^{-1} total dissolved salts) was diluted with minimally 10% (by volume) of Red Sea water (40 g l^{-1} total dissolved salts). Addition of phosphate was essential for the algae to grow, and growth rates and yields increased with increasing phosphate concentration and decreasing salinity. Field simulations in the mesocosms showed that development of algae was rapidly followed by development of dense blooms of red halophilic Archaea, which imparted an intensely red color to the ponds. While algal numbers declined after the peak of the bloom had been reached, number of halophilic Archaea and levels of archaeal pigments remained high for over two years. Although it should be realized that the closed system formed by the shallow ponds differs from the conditions in the lake, the results suggest that a microbial bloom, once formed, can remain present in the Dead Sea for months to years. These observations are important when attempting to predict how the biological properties of the lake may change in the future, and they have important implications for the planning of the Red Sea–Dead Sea conduit.

INTRODUCTION

The Dead Sea is located on the border between Israel and Jordan, has an area of about 630 km^2 and a maximum depth of 310 m. The lake presents fascinating challenges to the biologist who attempts to understand the biological processes and the limits of life in one of the most extreme environments on Earth. Its waters contain around 340 g l^{-1} of salts, and have a highly unusual ionic composition: divalent cations (1.98 M Mg^{2+}, 0.47 M Ca^{2+}) dominate over monovalent cations (1.54 M Na^+, 0.21 M K^+). The anions are 99% Cl^- (6.48 M) and 1% Br^- (0.08 M) (values for 2007). Sulfate concentrations are low (0.004 M), and the brine has a pH of about 6. The main water source to the Dead Sea was the Jordan River. However, diversion of water from its catchment area has decreased the Jordan River discharge to the Dead Sea to only about 10% of its natural flow (Lensky et al. 2005).

Only few microorganisms can live in such an environment. Quantitatively the most important inhabitants of the water column are the unicellular green alga *Dunaliella*–the sole primary producer in the lake, and extremely halophilic Archaea of the family *Halobacteriaceae*. Archaea first reported from the Dead Sea include *Haloferax volcanii*, *Haloarcula marismortui*, *Halorubrum sodomense*, and *Halobaculum gomorrense*. Other organisms have been isolated from the Dead Sea as well, including colorless members of the domain Bacteria, protozoa, and fungi (Oren 1988, 2003). Their quantitative importance in governing the biological properties of the lake has never been ascertained.

Systematic monitoring of the algal and prokaryotic communities in the water column of the Dead Sea since 1980 has yielded the following general picture: undiluted Dead Sea water is a too harsh environment even for the best salt-adapted microorganisms. However, exceptionally rainy winters can turn the holomictic regime into a meromictic one with the formation of a pycnocline at depths varying between 5 and about 15 m (Gavrieli & Oren 2004). When the surface waters become sufficiently diluted, dense blooms of algae and red Archaea develop in the upper meters of Dead Sea water column. Such blooms were recorded in 1980 (lasting until a renewed mixing of the water column in the end of 1982) and in 1992 (lasting until the end of 1995). During these blooms the density of the biota reached very high values: up to 9 x 10^3 and 1.5 x 10^4 *Dunaliella* cells ml^{-1}, and up to 2 x 10^7 and 3.5 x 10^7 archaeal cells ml^{-1} were counted in 1980 and 1992, respectively (Oren 2000; Oren et al. 1995). These archaeal blooms imparted a red color to the entire lake. Field observations combined with laboratory simulations have

shown that two conditions must be fulfilled for a microbial bloom to occur in the Dead Sea: the upper water layers must become diluted to a sufficient extent, and phosphate, the limiting nutrient in the lake, must be available.

A thorough understanding of the biological phenomena in the Dead Sea and the factors that determine the nature and extent of biological blooms in the lake is of great importance when planning human interference in the properties of the lake. From the 1930s the water balance of the lake has generally been negative. Since the 1960s anthropogenic intervention through diversion of freshwater from the catchment area for irrigation and drinking water has greatly increased. As a result, during the 20th century the Dead Sea level has dropped by more than 20 m, and during the past decade it has dropped by approximately one meter per year, on the average (Gavrieli & Oren 2004). This negative water balance is attributed primarily to water pumping from Lake Kinneret to the Israel National Water Carrier and diversion of water from the Yarmouk River by Syria and Jordan. The latter constructed the King Abdullah Canal which runs along the eastern side of the Jordan Rift Valley and supplies Yarmouk water for irrigation in the region. About 40% of the water level decline of the Dead Sea is attributed to evaporation of Dead Sea brine in the evaporation ponds of the Israeli and Jordanian mineral industries located in the southern basin of the Dead Sea. These industries pump together about 500 million cubic meters from the Dead Sea into the evaporation ponds where halite (NaCl) and carnallite ($KMgCl_3 \cdot 6H_2O$) precipitate. At the end of the process less than 250 million cubic meters of concentrated end brines, composed mainly of Mg-Ca-Cl, are returned to the Dead Sea. The drop in water level is causing severe problems in the area for local infrastructure, tourism, and industrial activities.

Since the peace treaty between Israel and Jordan was established in 1994, the construction of the "Peace Conduit", connecting the Dead Sea with the Gulf of Aqaba (Red Sea) is being discussed. This planned water carrier is intended to counteract the drop in Dead Sea water level, mitigating damaging processes that currently occur in the Dead Sea and its surrounding area. The difference in elevation between the Red Sea and the Dead Sea (current surface level: -420 m) may be exploited for the generation of energy which can be used for seawater desalination (Oren et al. 2004; Gavrieli et al. 2005).

The present study, combining laboratory model experiments with simulations in outdoor ponds, was intended to provide answers to two basic questions: (1), what are the boundary conditions with respect to dilution and phosphate concentrations that enable the development of algae in the Dead Sea, and (2), how long may algal and archaeal blooms, once formed, remain in the lake when limnological conditions remain constant.

METHODS

Field-Scale Simulation Experiments in the Experimental Ponds at Sedom

Mixtures of Dead Sea water and Red Sea water were incubated in mesocosms on the grounds of the Dead Sea Works Ltd. at Sedom. The experimental setup consisted of white plastic tanks (1 x 1 x 1 m; Dolav, Kibbutz Dvir, Israel), buried 0.75 m in the ground. These tanks were filled with 900 l of mixtures of Dead Sea water (sampled from the channel that feeds the evaporation ponds of the Dead Sea Works Ltd. with water from the northern basin of the lake) and water from the Gulf of Aqaba, purified through a filter of 60-70 cm sand, eliminating particles larger than 20-30 μm. The first set of experiments performed at the site, initiated in July 2002, as well as further details of the experimental setup, have been documented by Oren et al. (2004). The experiments documented in the present paper started in 2002–2003, and are based on two ponds. One mesocosm ("no. 4") was filled with a mixture of 80% Dead Sea water and 20% Red Sea water, amended with 1 μM KH_2PO_4 and inoculated with 50 ml of brine from a mesocosm that had developed a bloom of *Dunaliella* and halophilic Archaea in the previous set of experiments. The second mesocosm ("no. 9") contained a 1:1 mixture of water from mesocosms no. 9 and 10 from the earlier experiment. Mesocosms 9 and 10 both contained a 70% Dead Sea water –30% Red Sea mixture and 1 and 10 μM KH_2PO_4, respectively, thus the new experiment was based on brine that had received an equivalent concentration of 5.5 μM phosphate, and started at the high algal and archaeal densities that had developed in the first round of experiments as documented (Oren et al. 2004). The mesocosms were mixed daily, and their water level was kept constant by adding deionized water every 1-2 days, followed by thorough mixing. No conspicuous growth of algae or other organisms was ever observed attached to the walls or to the bottom of the containers. In November 2004, an additional portion of 1 μM KH_2PO_4 was added to mesocosm no. 4. The ponds were sampled once every two weeks for the determination of the density of the *Dunaliella* population, the halophilic archaeal community density, and the content of algal chlorophyll and archaeal carotenoids.

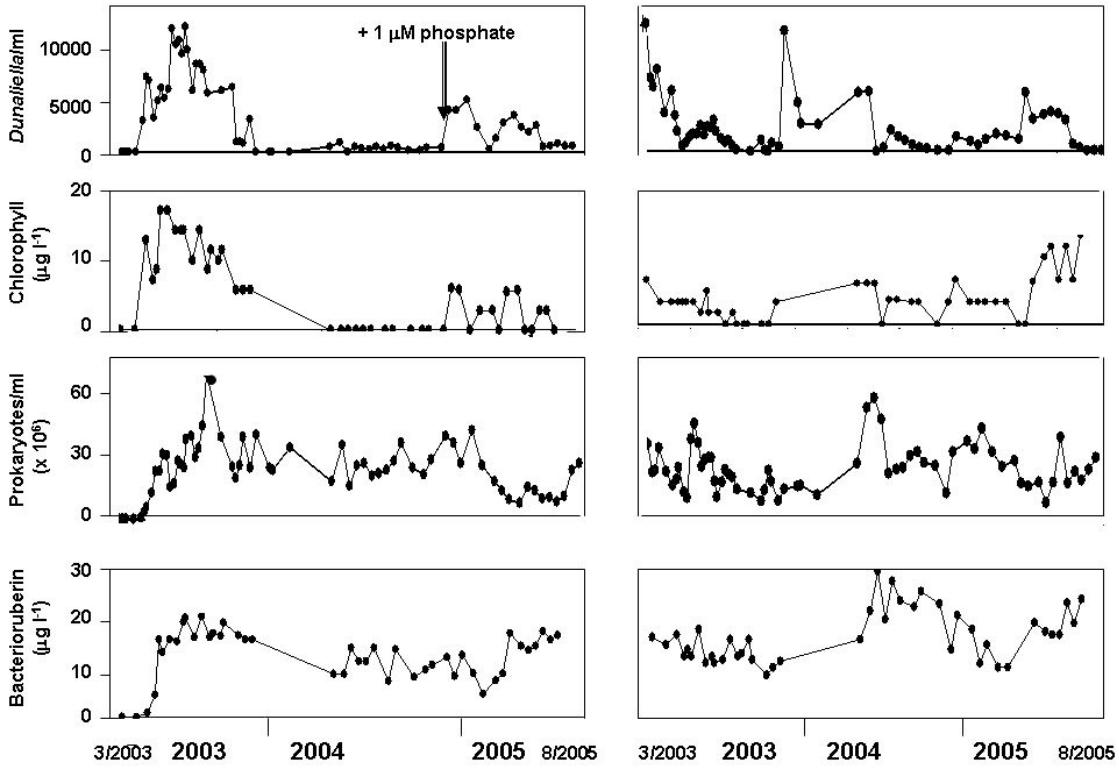

Figure 1–Left panels: numbers of *Dunaliella* cells, concentrations of chlorophyll, numbers of prokaryotic cells, and concentration of bacterioruberin carotenoids in an outdoor pond filled with a mixture of 80% Dead Sea water and 20% Red Sea water, and amended with 1 μM KH_2PO_4 from the start of the experiment in March 2003 until August 2005. An additional portion of 1 μM KH_2PO_4 was added in November 2004 (arrow). Right panels: numbers of *Dunaliella* cells, concentrations of chlorophyll, numbers of prokaryotic cells, and concentration of bacterioruberin carotenoids in an outdoor pond filled with a mixture of 70% Dead Sea water and 30% Red Sea water. In March 2003 the pond was filled with a 1:1 mixture of water from ponds no. 9 and 10 from an earlier experiment, which contained 70% Dead Sea water–30% Red Sea and 1 and 10 μM KH_2PO_4 (Oren et al. 2004), explaining the high initial values of biological parameters.

Laboratory-Scale Simulation Experiments of Micro-bial Development in Dead Sea–Red Sea Water Mixtures

To examine in further depth the effect of salinity and phosphate concentration on the development of *Dunaliella* in Dead Sea–Red Sea waters, we set up laboratory experiments in which 100 ml Erlenmeyer flasks were filled with 75 ml portions of Dead Sea water (sampled in July 2005 from a depth of 10 m at the deepest point of the lake 8 km east of Ein Gedi) and filtered Red Sea water as described above. Different concentrations of KH_2PO_4 were added, and all flasks were inoculated with a unialgal, non-axenic culture of *Dunaliella* from the Dead Sea in 80% Dead Sea water –20% Red Sea water to supply an inoculum of about 500 *Dunaliella* cells ml^{-1}. The flasks were incubated without agitation at 30°C under constant illumination (100 μmol quanta m^{-2} s^{-1}) by white fluorescent tubes. To prevent evaporation and to ensure constant salinity for the duration of the experiment, the flasks were closed with Parafilm. After 25 days samples were withdrawn for microscopic enumeration of *Dunaliella* cells and chlorophyll assay.

Enumeration of Algae and Halophilic Archaea

To count the density of the algal (*Dunaliella*) and halophilic archaeal communities, 50 ml of samples from the experimental ponds were fixed with 1 ml of 37% formaldehyde, previously cleared by filtration through a 0.2 μm pore size membrane filter. Samples were stored at room temperature until counted within 3-4 weeks. For the enumeration of *Dunaliella* cells, 2.5 ml portions of fixed samples were supplemented with 0.1 ml of 0.1 N iodine to stain intracellular starch. The samples were then filtered through Millipore filters (25 mm diameter, 5 μm mean pore size, cat. no. SMWP-25). Filters were placed on microscope slides, and cells were counted at 128x or 320x magnification.

A similar procedure was followed for the enumeration of algal cells in laboratory experiments. However, no prior fixation was used in this case, and variable volumes of water filtered were filtered according to the density of *Dunaliella* in the flasks. Cell numbers were calculated from the average number of cells per field and the field diameter,

calibrated with the aid of the grid of a Petroff-Hauser counting chamber (Oren & Shilo 1982; Oren et al. 1995). Prokaryotic cells (Archaea and Bacteria combined) were enumerated microscopically using a Petroff-Hauser counting chamber after 5-10-fold concentration by centrifugation (20 min, 12000 x g). The relative accuracy of the algal and prokaryotic cell counts was estimated at ± 10 and 20%, respectively.

Pigment Determinations

The content of chlorophyll and carotenoids was determined by filtering 30-50 ml sample portions through glass fiber filters (Whatman GF/C, 25 or 47 mm diameter) within 1 hour after sampling. Filters were kept at -20°C in the dark until further processing within 3-4 weeks. Filters were then extracted overnight in 2.5-5 ml methanol/acetone (1:1, by volume). The extracts were cleared of particles by centrifugation, and their absorption spectra (400-700 nm) were measured in a Cary Varian model E1 scanning spectrophotometer, using the solvent as a blank. Chlorophyll concentrations were calculated, based on a specific absorption of 73.5 l mg^{-1} cm^{-1} for chlorophyll *a* at 665 nm.

Archaeal bacterioruberin pigments were quantified based on a specific absorption of 25.4 l mg^{-1} cm^{-1} at 496 nm for α-bacterioruberin. A correction was made for the contribution of algal pigments to the total absorbance at this wavelength, as outlined in Oren et al. (2004).

RESULTS

Our outdoor simulation experiments in 0.9 m^3 mesocosms show that once a microbial bloom has formed in a Dead Sea–Red Sea water mixture, it can persist for over two years (Figure 1). The left panels of Figure 1 document a bloom of *Dunaliella* and halophilic Archaea in a mixture of 80% Dead Sea water and 20% Red Sea water, supplemented with 1 μM orthophosphate. Algal numbers reached values of up to 1.2 x 10^4 cells ml^{-1} (16 μg chlorophyll l^{-1}) after 4 months, and then declined to low values. Mass development of algae was followed by the growth of halophilic Archaea, which are heterotrophic microorganisms that develop at the expense of organic compounds produced by the autotrophic algae. We counted up to 65 x 10^6 prokaryotic cells ml^{-1}, and their bacterioruberin carotenoids (up to 18 μg l^{-1}) imparted an intensely red color to the brine. This community remained throughout the experiment, without any major decline for more than two years. To prove that further algal development was limited by the availability of phosphate after the initially added phosphate had been taken up by the microbial community and was incorporated in the biomass, we added an additional 1 μM orthophosphate in November 2004. This addition quickly resulted in a renewed development of *Dunaliella.* A similar long-living microbial bloom was obtained in a pond that had received a mixture of 70% Dead Sea water–30% Red Sea and 5.5 μM phosphate (Figure 1, right panels). This experiment was a continuation of an experiment set up in July 2002, documented earlier (Oren et al. 2004). It shows once more that such microbial blooms can be sustained for long periods–in this case for over three years.

The examples shown in Figure 1 are part of a more extensive set of experiments in which we examined the effect of different parameters on the timing and extent of microbial development in Dead Sea–Red Sea mixtures. Some of the early experiments have been described in an earlier paper (Oren et al. 2004). Without added phosphate no significant algal and archaeal blooms were observed. Insoluble finely powdered rock phosphate (apatite) did not trigger blooms (not shown).

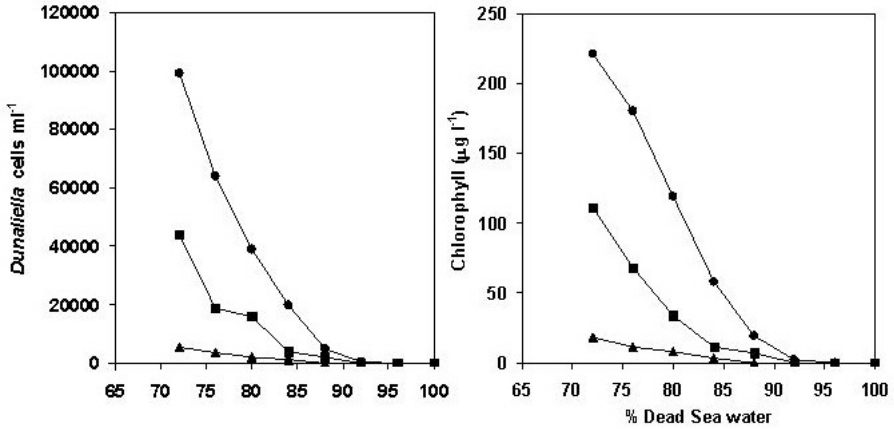

Figure 2–Development of *Dunaliella* cells and chlorophyll in a laboratory simulation experiment in which Dead Sea–Red Sea water mixtures were incubated for 25 days at 30°C in the light in the presence of 1 (▲), 2.5 (■) and 5 mM KH_2PO_4 (●) and an inoculum of 500 *Dunaliella* cells ml^{-1}, whereafter the density of *Dunaliella* cells (left panel) and the chlorophyll content of the water (right panel) were determined.

To further test the boundary conditions that enable the onset of an algal bloom in Dead Sea–Red Sea water mixtures, we set up a laboratory simulation experiment in which different mixtures were supplemented with different concentrations of orthophosphate and an inoculum of *Dunaliella*. After incubation in the light for four weeks, algae developed only when the concentration of Dead Sea water in the mixtures was below 90%, and the rate at which the cells multiplied increased with decreasing salinity of the water mixture. The extent of the algal growth obtained was a function of the concentration of phosphate added (Figure 2). No significant further changes were noted when incubation was continued for three additional weeks. These results confirm and extend laboratory simulation experiments performed in the early 1980s in which Dead Sea water was diluted with freshwater (Oren & Shilo 1985).

DISCUSSION

Compared to all other aquatic environments of lower salinity, the Dead Sea is a very simple ecosystem. Higher animals are absent, and protozoa, if they are present at all, do not appear to play a significant role in regulating community densities of unicellular algae and heterotrophic prokaryotes. The main players are one type of primary producer–the alga *Dunaliella*, and several species of halophilic Archaea (Kaplan & Friedmann 1970; Oren 1988, 1997). Figure 3 presents a general model of the biological processes that occur in the aerobic water column of the Dead Sea, the organisms involved, and some of the interrelationships between the biota. This model is based on observations of the dynamics of algal and archaeal communities in the lake, laboratory simulations, as well as field-scale simulations such as documented in the present study.

Undiluted Dead Sea water is too harsh an environment even for *Dunaliella*, the best salt-adapted alga known. Therefore algal blooms, and subsequent mass development of Archaea that live at the expense of organic material produced by the algae, can only occur after dilution with less saline water. Analysis of the biological events following the rainy winters of 1979–1980 and 1991–1992 have provided ample illustration of this (Oren & Shilo 1982; Oren 1983; Oren & Gurevich 1995; Oren et al. 1995), as have simulation experiments (Oren & Shilo 1985; Figure 2 in the present study). One of the organic compounds produced in massive amounts by *Dunaliella* is glycerol, used by the algae to provide osmotic stabilization (Ben-Amotz & Avron 1973). Evidence has accumulated that this glycerol is probably one of the major nutrients used by the halophilic Archaea.

Phosphate is clearly the limiting nutrient that governs the extent of microbial blooms in the lake. Inorganic nitrogen is plentifully available in the form of ammonium ions (Nissenbaum et al. 1990; Stiller & Nissenbaum 1999) but phosphate concentrations are low. Stiller & Nissenbaum (1999) and Nissenbaum et al. (1990) reported dissolved phosphate levels in the lake of about 1 μM. This value is approximate, due to the difficulty in performing high-precision chemical analyses in the presence of molar concentrations of other interfering salts. Furthermore, little information has been obtained on the spatial and temporal variation in the concentration of dissolved phosphate in the Dead Sea water column. In any case, the dramatic response of the *Dunaliella* community to phosphate addition in laboratory and field-scale simulation experiments shows its importance as a key nutrient controlling ecological processes in the Dead Sea. Following uptake by the algae, the phosphate becomes fixed in the algal and archaeal biomass. Addition of more phosphate provides the opportunity for renewed algal growth (Figure 1).

The simulation studies documented in Figure 1, as well as in an earlier publication (Oren et al. 2004), show that mass development of *Dunaliella* is generally followed by a rapid decline. The causes of this decline are still poorly understood. Following the 1992 spring bloom of the alga in the lake, the cells formed cyst-like structures, possibly zygotes, which sank to the bottom (Oren et al. 1995). Evidence has been obtained that such thick-walled cysts serve as the inoculum that enables rapid development of *Dunaliella* in the Dead Sea as soon as the upper water layers become diluted by freshwater floods (Oren 1999; Oren & Ben-Yosef 1997). However, we never observed formation of such cysts in the experimental outdoor ponds.

While algal blooms, both in the Dead Sea itself and in the pond simulation experiments, were always of limited duration, the Archaea remained present for over three years, both in the lake (Oren 1983; Oren & Gurevich 1995) and in the experimental ponds, and the mesocosms remained as brightly red colored as when the bloom first started (Figure 1). It has been suggested that the halophilic Archaea in the Dead Sea can to some extent use light energy absorbed by the retinal pigment bacteriorhodopsin as an energy source for maintenance (Oren & Shilo 1981; Oren 1983). Little is known about the factors that remove archaeal cells from the Dead Sea water column. Overturn of the water column with mixing of the Archaea-rich upper layer with the lower water masses has been a major factor in the decrease in prokaryote densities following the 1980–1982 and 1992–

1995 blooms (Oren 1985, 1988, 2000, 2003). Bacteriophages may also be involved in regulating archaeal community densities in the lake, as direct electron microscopic examination revealed large numbers of phage-like particles (Oren et al. 1997). However, their true impact on the community dynamics has never been ascertained (Oren 1999).

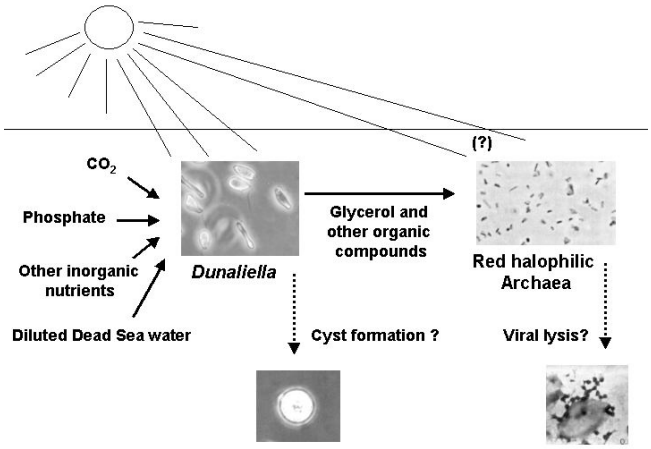

Figure 3–Schematic representation of the processes that govern the development of algal and archaeal blooms in the Dead Sea water column.

Although the microcosms simulate the events observed during natural microbial blooms in the Dead Sea to a large extent, it should be realized that the closed system formed by the shallow ponds differs from the conditions in the lake in certain important aspects. In the lake, particles can sediment to the bottom, and the nutrients bound to them will then no longer be available in the upper water layer. In the mixed microcosm systems, nutrients once added will remain present for indefinite times.

The Dead Sea, while unique in its ionic composition, is not the only hypersaline lake whose biology is dominated by *Dunaliella* and halophilic Archaea. The properties of the Dead Sea as a biotope can be compared to some extent with those of Great Salt Lake, Utah. The water level and the salt concentrations of Great Salt Lake have also been subject to major fluctuations in the past century (Stephens 1990). There has never been a systematic monitoring program of the communities of algae and of prokaryotes, and measurements of community densities and dynamics have been infrequent. Nitrogen rather than phosphorus is the inorganic nutrient that limits algal production (Post 1977; Stephens & Gillespie 1976). After more than two decades in which hardly any microbiological studies were performed in the lake, interest in the archaea and other microorganisms in Great Salt Lake has recently been renewed (Baxter et al. 2005).

Understanding the factors that trigger the development of microbial blooms and determine their longevity is important in the planning of the Red Sea–Dead Sea water carrier (Gavrieli et al. 2005; Oren et al. 2004). A permanent stratification is likely to become established as the upper layers of the lake will become diluted with much less dense Red Sea water. When the upper layers become diluted by more that 10% by the waters from the Red Sea, combined with any flood waters that naturally enter the Dead Sea each winter, conditions are established for the development of blooms. The extent of these blooms will be a direct function of the availability of phosphate. The waters of the Gulf of Aqaba are very low in phosphate (concentrations in surface waters are generally between 0-5 nM, with maximal values up to 50 nM following winter mixing) (Stihl et al. 2001; A.F. Post, personal communication), but other sources (phosphate entering with flood waters from the catchment area, anthropogenic sources) can be quantitatively far more important. The results of simulation experiments documented in this study show that the conditions that lead to the formation of a microbial bloom in the Dead Sea are now quite well understood. They also show that such blooms, once formed, can remain present for long periods and determine to a large extent the properties of the lake for many years.

ACKNOWLEDGEMENTS

We thank the staff of the Dead Sea Works, Sedom, for logistic support and the staff of the analytical laboratory at IMI (TAMI), Haifa, for the pigment analyses. This study was supported by the Israel Science Foundation (grant #902/05 to IG) and by the Israel Ministry for Natural Infrastructures and by the Middle East Regional Cooperation (MERC) program, USAID award No. TA-MOU-03-M23-024.

REFERENCES

Baxter, B.K., C.D. Litchfield, K. Sowers, J.D. Griffith, P.A. DasSarma & S. DasSarma. 2005. Microbial diversity of Great Salt Lake. In: Gunde-Cimerman, N., A. Oren & A. Plemenitaš (eds), Adaptation to Life at High Salt Concentrations in Archaea, Bacteria, and Eukarya. Springer, Dordrecht: 11–25.

Ben-Amotz, A. & M. Avron. 1973. The role of glycerol in the osmotic regulation of the halophilic alga *Dunaliella parva*. Plant Physiology 51: 875–878.

Gavrieli, I. & A. Oren. 2004. The Dead Sea as a dying lake. In: Nihoul, J.C.J., P.O. Zavialov & P.P. Micklin (eds), Dying and Dead Seas. Climatic versus Anthropic Causes. Kluwer Academic Publishers, Dordrecht: 287–305.

Gavrieli, I., A. Bein & A. Oren. 2005. The expected impact of the "Peace Conduit" project (the Red Sea–Dead Sea pipeline) on the Dead Sea. Mitigation and Adaptation Strategies for Global Change 10: 3–22.

Kaplan, I.R. & A. Friedmann. 1970. Biological productivity in the Dead Sea. Part 1. Microorganisms in the water column. Israel Journal of Chemistry 8: 513–528.

Lensky, N.G., Y. Dvorkin, V. Lyakhovsky, I. Gertman & I. Gavrieli. 2005. Mass and energy balance of a hypersaline lake: the Dead Sea. Water Resources Research 41, W12418, doi:10.1029/2005WR004084.

Nissenbaum, A., M. Stiller & A. Nishri. 1990. Nutrients in pore waters from Dead Sea sediments. Hydrobiologia 197: 83–90.

Oren, A. 1983. Population dynamics of halobacteria in the Dead Sea water column. Limnology and Oceanography 28: 1094–1103.

Oren, A. 1985. The rise and decline of a bloom of halobacteria in the Dead Sea. Limnology and Oceanography 30: 911–915.

Oren, A. 1988. The microbial ecology of the Dead Sea. In: Marshall, K.C. (ed), Advances in Microbial Ecology, Vol. 10. Plenum Publishing Company, New York: 193–229.

Oren, A. 1997. Microbiological studies in the Dead Sea: 1892–1992. In: Niemi, T., Z. Ben-Avraham & J.R. Gat (eds), The Dead Sea - The Lake and its Setting. Oxford University Press, New York: 205–213.

Oren, A. 1999. Microbiological studies in the Dead Sea: future challenges toward the understanding of life at the limit of salt concentrations. Hydrobiologia 405: 1–9.

Oren, A. 2000. Biological processes in the Dead Sea as influenced by short-term and long-term salinity changes Archives of Hydrobiology Special Issues Advances in Limnology 55: 531–542.

Oren, A. 2003. Biodiversity and community dynamics in the Dead Sea: archaea, bacteria and eucaryotic algae. In: Nevo, E., A. Oren & S.P. Wasser (eds), Fungal Life in the Dead Sea. A.R.G. Gantner Verlag, Ruggell: 117–140.

Oren, A. & N. Ben-Yosef. 1997. Development and spatial distribution of an algal bloom in the Dead Sea: a remote sensing study. Aquatic Microbial Ecology 13: 219–223.

Oren, A. & P. Gurevich. 1995. Dynamics of a bloom of halophilic archaea in the Dead Sea. Hydrobiologia 315: 149–158.

Oren, A. & M. Shilo. 1981. Bacteriorhodopsin in a bloom of halobacteria in the Dead Sea. Archives of Microbiology 130: 185–187.

Oren, A. & M. Shilo. 1982. Population dynamics of *Dunaliella parva* in the Dead Sea. Limnology and Oceanography 27: 201–211.

Oren, A. & M. Shilo. 1985. Factors determining the development of algal and bacterial blooms in the Dead Sea: a study of simulation experiments in outdoor ponds FEMS Microbiology Ecology 31: 229–237.

Oren, A., P. Gurevich, D.A. Anati, E. Barkan & B. Luz. 1995. A bloom of *Dunaliella parva* in the Dead Sea in 1992: biological and biogeochemical aspects. Hydrobiologia 297: 173–185.

Oren, A., G. Bratbak & M. Heldal. 1997. Occurrence of virus-like particles in the Dead Sea. Extremophiles 1: 143–149.

Oren, A., I. Gavrieli, J. Gavrieli, J. Lati, M. Kohen & M. Aharoni. 2004. Biological effects of dilution of Dead Sea water with seawater: implications for the planning of the Red Sea–Dead Sea "Peace Conduit". Journal of Marine Systems 46: 121–131.

Post, F.J. 1977. The microbial ecology of the Great Salt Lake. Microbial Ecology 3: 143–165.

Stephens, D.W. 1990. Changes in lake levels, salinity and the biological community of Great Salt Lake (Utah, USA), 1847–1987. Hydrobiologia 197: 139–146.

Stephens, D.W. & D.M. Gillespie. 1976. Phytoplankton production in Great Salt Lake, Utah, and a laboratory study of algal response to enrichment. Limnology and Oceanography 21: 74–87.

Stihl, A., U. Sommer & A.F. Post. 2001. Alkaline phosphatase activities among populations of the colony-forming diazotrophic cyanobacterium *Trichodesmium* spp. (Cyanobacteria) in the Red Sea. Journal of Phycology 37: 310–317.

Stiller, M. & A. Nissenbaum. 1999. Geochemical investigation of phosphorus and nitrogen in the hypersaline Dead Sea. Geochimica et Cosmochimica Acta 63: 3467–3475.