Hydrobiologia **297**: 173–185, 1995.

A bloom of *Dunaliella parva* in the Dead Sea in 1992: biological and biogeochemical aspects

Aharon Oren[1,2], Peter Gurevich[1], David A. Anati[3], Eugene Barkan[3] & Boaz Luz[2,3]
[1] *Division of Microbial and Molecular Ecology, The Alexander Silberman Institute of Life Sciences,*
[2] *The Moshe Shilo Center for Marine Biogeochemistry, and*
[3] *The Institute of Earth Sciences, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel*

Received 16 September 1993; in revised form 23 November 1993; accepted 26 January 1994

Key words: Dead Sea, *Dunaliella*, hypersaline, stratification, carbon isotopes

Abstract

A bloom of the unicellular green alga *Dunaliella parva* (up to 15 000 cells ml^{-1}) developed in the upper 5 m of the water column of the Dead Sea in May–June 1992. This was the first mass development of *Dunaliella* observed in the lake since 1980, when another bloom was reported (up to 8800 cells ml^{-1}). For a bloom of *Dunaliella* to develop in the Dead Sea, two conditions must be fulfilled: the salinity of the upper water layers must become sufficiently low as a result of dilution with rain floods, and phosphate must be available. During the period 1983–1991 the lake was holomictic, hardly any dilution with rainwater occurred, and no *Dunaliella* cells were observed. Heavy rain floods in the winter of 1991–1992 caused a new stratification, in which the upper 5 m of the water column became diluted to about 70% of their former salinity. Measurements of the isotopic composition of inorganic carbon in the upper water layer during the bloom ($\delta^{13}C = 5.1‰$) indicate a strong fractionation when compared with the estimated −3.4‰ prior to the bloom. The particulate organic carbon formed was highly enriched in light carbon isotopes ($\delta^{13}C = -13.5‰$). The algal bloom rapidly declined during the months June–July, probably as a result of the formation of resting stages, which sank to the bottom. A smaller secondary bloom (up to 1850 cells ml^{-1}) developed between 6 and 10 m depth at the end of the summer. Salinity values at this deep chlorophyll maximum were much beyond those conductive for the growth of *Dunaliella*, and the factors responsible for the development of this bloom are still unclear.

Introduction

The Dead Sea is an extremely hypersaline terminal desert lake, with an average concentration of about 340 g l^{-1} total dissolved salts. The ionic composition is dominated by divalent cations (Mg^{2+}, about 1.86 M, Ca^{2+}, about 0.44 M) rather than monovalent cations (Na^+, about 1.60 M, K^+, about 0.20 M) (Oren, 1988, 1992a). Chloride is the main anion. The lack of balance between water input (runoff from the catchment area during winter, the river Jordan) and evaporation causes strong fluctuations in water level and changes in the physical structure of the water column. A long period of 'permanent' stratification that ended with an overturn event in 1979 was followed by a new period of stratification that lasted till the end of 1982, and a holomictic period from 1983 till 1991 (Anati & Shasha, 1989; Anati & Stiller, 1991; Anati, unpublished results).

The Dead Sea as an ecosystem is extremely simplified, comprising only one primary producer, the unicellular green alga *Dunaliella parva*, and a few types of red halophilic archaeobacteria are the main consumers (Oren, 1988, 1992b). Predators such as protozoa are absent or play at best a very minor role. Higher forms of life are absent altogether. *Dunaliella* has been found in the Dead Sea since the pioneering studies of Volcani (1944). Hardly any quantitative data exist on the biota of the Dead Sea prior to 1980, with the exception of a few measurements performed during 1963–1964; in 1964 *Dunaliella* counts as high as 4×10^4 cells ml^{-1} of surface water were observed (Kaplan & Friedmann,

1970). From 1980 onwards the quantitative aspects of life in the Dead Sea have been studied systematically (Oren, 1988). In the summer of 1980 a bloom of *Dunaliella* was observed in the upper 5–15 m of the water column, reaching a peak density of 8800 cells ml^{-1} (Oren & Shilo, 1982). This bloom developed following an extremely rainy winter, in which rain floods caused a significant dilution of the upper water layers. Laboratory simulation experiments showed that in order for *Dunaliella* to multiply in Dead Sea water two conditions must be fulfilled. Firstly, the salinity must be reduced. Undiluted Dead Sea water with a specific gravity of about 1.235 g cm^{-3} does not support growth of *Dunaliella*. Significant growth rates can be obtained at a specific gravity of 1.21 g cm^{-3} or below. Secondly, phosphate must be present, as lack of phosphate limits the amount of algal biomass that can be formed (Oren & Shilo, 1985). Rain floods are expected to supply large amounts of phosphate; quantitative estimates, though, are lacking.

The temporary stratification of the lake, initiated in 1979–1980, was abolished in the end of 1982, and was followed by nine years of holomixis (Anati & Shasha, 1989). The high salinity, and the concomitant increase in the relative proportion of divalent cations (Oren, 1992a) were not conducive for a renewed development of *Dunaliella*. We did not observe any *Dunaliella* cells in the lake during this period.

The winter 1991–1992 was again an extremely rainy one, and large amounts of rainwater once more caused a dilution of the upper water layers of the Dead Sea, even more extensive than in 1979–1980 (Beyth *et al.*, 1993). The specific gravity decreased to values as low as 1.17–1.18, and as a result, a new event of *Dunaliella* development could be expected to occur. In this study we describe the dynamics of the rise and decline of a bloom of *Dunaliella parva* in the Dead Sea in 1992, and some of its biogeochemical effects.

Materials and methods

Water samples were collected at four stations in the Dead Sea (Fig. 1). Most deep samples were taken about 8 km east of Ein Gedi (Station A) in the deepest part of the lake (maximum depth about 325 m). On two occasions samples were taken at other stations (Station C on June 15, 1992, station D on May 4, 1992). Samples were collected from different depths by means of Niskin bottles or pumped though a hose. The relative accuracy in depth determinations was estimated to be between 2% (Niskin bottle samples) and 15% (pumped samples), depending on sea conditions. Additional surface samples were collected at the shore near Ein Gedi (Station B). *Dunaliella* counts in surface water samples collected on the same day at this station and at the center of the lake did not differ significantly. Samples were kept in 1 l opaque polyethylene bottles, and biological parameters were determined within 4 h of sampling.

Salinity was determined through density at a fixed temperature, either by hydrometry with an accuracy of $\pm$ 0.2 σ u, or by pycnometry with an accuracy of $\pm$ 0.02 σ u. The sigma unit (σ u) denotes density in the MKS system (kg m^{-3}) excess to the standard reference density of 1000 kg m^{-3}. Salinity (density at 25 °C) is denoted as σ_{25}. Temperature was determined either by means of Yellow Springs Instrument thermistors of accuracy $\pm$ 0.04 °C (whenever the vertical detailed structure was important), or by means of reversing thermometers of accuracy of $\pm$ 0.02 °C attached to the Niskin bottles.

For the enumeration of *Dunaliella* cells, 50-ml portions of samples were supplemented with 0.1 ml of 0.1 *N* iodine to stain intracellular starch. Portions (2–50 ml) were then filtered through Millipore filters (25 mm diameter, 3 μm mean pore size). Filters were placed on microscope slides, covered with cover slips, and cells were counted under a 40× objective. 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. Photomicrographs were taken using a Zeiss photomicroscope, using phase optics. Bacteria were enumerated microscopically, using a Petroff-Hauser counting chamber, when necessary after prior concentration by centrifugation (Oren, 1983).

Chlorophyll was determined by filtering portions (10–400 ml) through glass fiber filters (Whatman GF/C), extracting the filters overnight in 3–5 ml methanol/acetone (1:1, by volume), and measuring the absorption of the extract at 665 nm. Chlorophyll concentrations were calculated, assuming a specific absorption of 13.61 mg $^{-1}$ cm^{-1}. Absorption spectra of extracts were recorded in a Hewlett-Packard model 8452A diode array spectrophotometer. In selected samples pigments were separated by means of high-performance liquid chromatography, using a Merck-Hitachi HPLC setup, including pump L6200A and UV-visible detector L-4200. Pigments were injected through a 20 μl sample loop into a Lichrospher RP 18 column (Merck), and were eluted at a rate of 1 ml

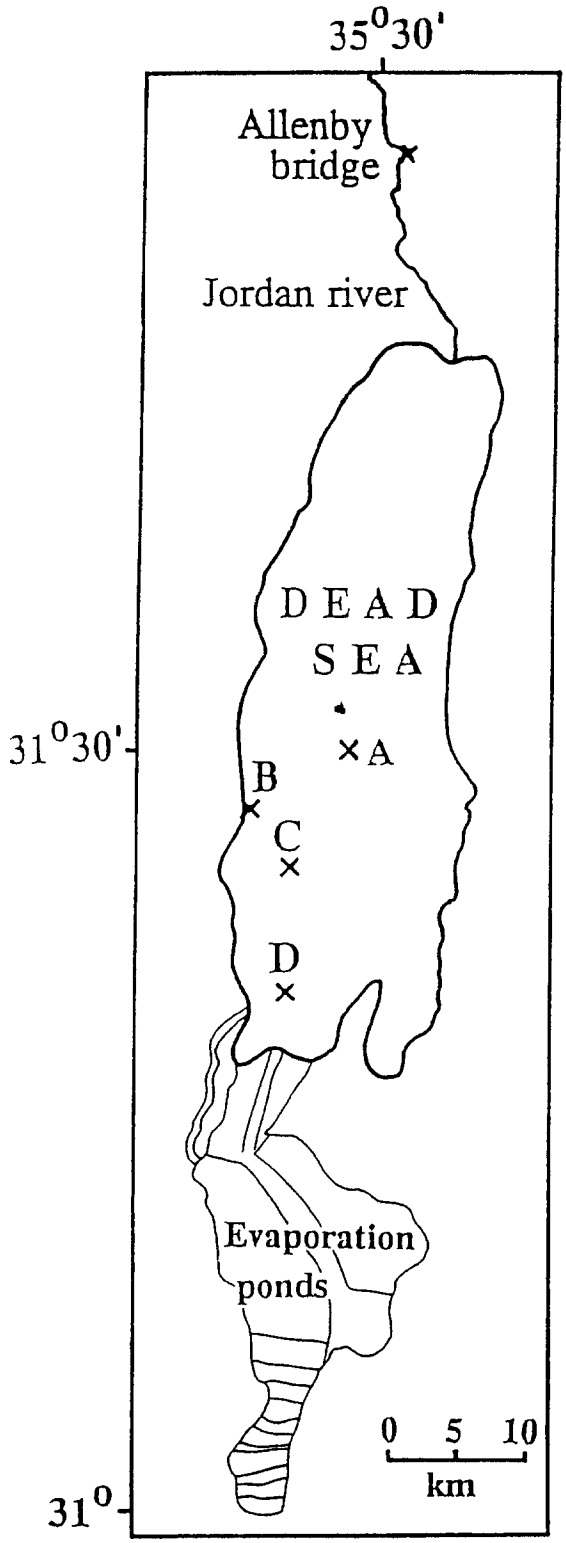

Fig. 1. Location map of the sampling stations. Most deep samples were taken at station A (at the deepest part of the Dead Sea, maximum depth about 310 m). One set of samples (4 May, 1992) was collected at station C, one set (15 June, 1992) at station D, and a number of additional surface samples were collected at the shore (station B).

min^{-1} by a gradient of acetone and water (from 70–30% to 15–85% in 10 min, from 85 to 100% acetone in the next 5 min, followed by 6 min 100% acetone). The elution of pigments was monitored at 450 nm, and the eluted peaks were characterized using a Chrom-A-Scope and Chrom-A-Set 500 (Bar-Spec, Rehovot, Israel) spectrum analyzer (Oren *et al.*, 1992). CO_2 photoassimilation was determined in the laboratory by incubating water samples in completely filled 110-ml glass bottles with 100 μl of a solution of 74 MBq ml^{-1} $NaH^{14}CO_3$ (Amersham, 2 GBq $mmol^{-1}$) in 50 mM Tris.HCl buffer, pH 9.0. After incubation at 25 °C in the light (white fluorescent tubes, incident irradiance 14 W m^{-2}) and in the dark for periods between 4 and 20 h, 75 ml portions were filtered through glass fiber filters (Whatman GF/C). Filters were washed with 20 ml cold 10% trichloroacetic acid, dried, 5 ml Instagel (Packard) scintillation cocktail was added, and radioactivity retained on the filters was counted in a Beckman model LS 1801 scintillation counter. Counts were corrected for quenching by using the channel ratio method. CO_2 photoassimilation rates were calculated, assuming a total inorganic carbon concentration of 1210 μM in the upper 5 m of the Dead Sea water column (see below).

The total dissolved inorganic carbon was measured by a method similar to that of Graber and Aharon (1991). Extraction yield was better than 99.9%, while the precision of measurements of total CO_2 was better than 0.2%. Carbon isotope ratios (δ^{13} C) were measured with a precision better than 0.1%, using a Micromass model 602 mass spectrometer. The isotopic composition of particulate organic carbon (collected by centrifugation) was determined after removal of any inorganic carbon by acidification with HCl (Sofer, 1980).

Results

As a result of winter rain floods (November 1991–March 1992) the water column of the Dead Sea became stratified, with a sharp pycnocline at a depth between 4 and 6 m (Fig. 2). The water above the pycnocline was greatly lowered in salinity (σ_{25} around 180 in June, compared with above 230 in the lower water mass). The degree of dilution was much greater than in 1980, when σ_{25} in June was about 215 in the upper 10 m (Oren & Shilo, 1982). During the summer months a thermocline developed between 5 and 9 m depth, and maximum temperatures in the surface water layer

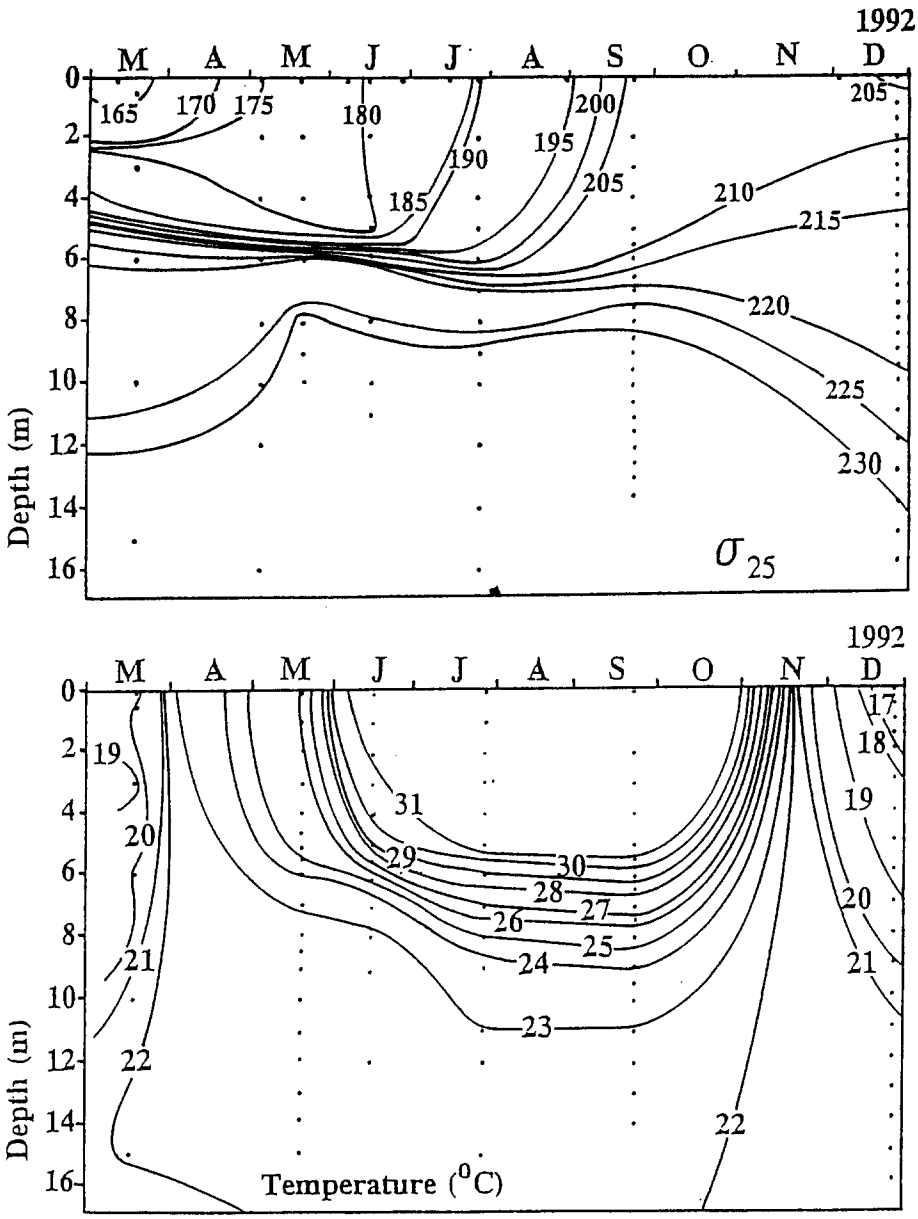

Fig. 2. Seasonal and vertical distribution of salinity (expressed as σ_{25}, upper panel), and temperature (lower panel), March–December 1992.

reached a value of 31.8 °C (compared with 33.6 °C – early morning – and 36.0 °C – afternoon – in the summer of 1980).

A dense bloom of *Dunaliella parva* was observed in the spring of 1992. The bloom developed extremely rapidly: while in March no *Dunaliella* cells were observed at all, peak densities of up to 15000 cells ml^{-1} were found in the middle of May (Fig. 3). The bloom was restricted to the upper 4–5 m above the pycnocline, and no cells were observed below a depth of 8 m during this period. The high cell counts were parallelled by a high chlorophyll content of the water: up to 29 μ g l^{-1} (Fig. 3, lower panel). The bloom declined rapidly at the end of June–beginning of July, and during the remainder of the year cell numbers in surface water remained low (30–370 cells ml^{-1}). Comparison with the bloom in 1980 shows that the 1992 bloom both appeared much earlier in the season than in 1980

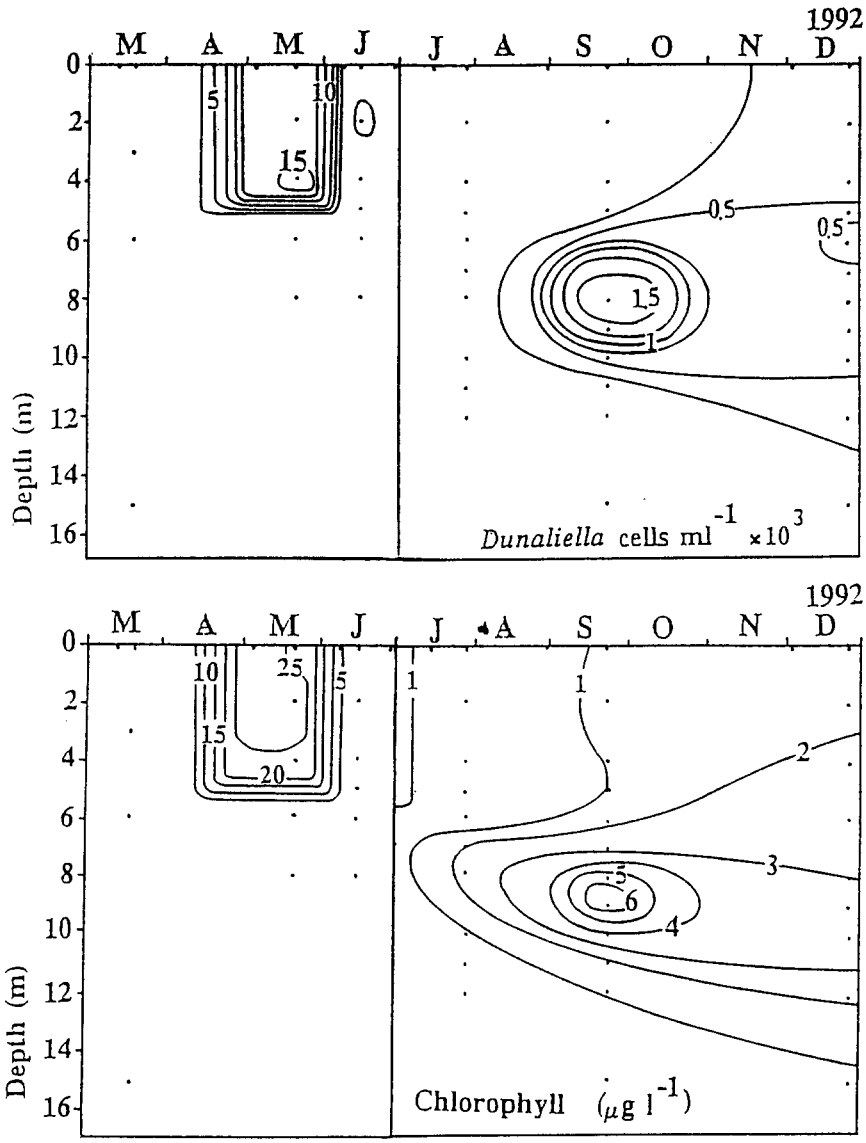

Fig. 3. Seasonal and vertical distribution of *Dunaliella* cells (upper panel) and chlorophyll (lower panel) in the Dead Sea, March–December 1992.

(when the dilution of the upper water layers was less extensive), and reached higher peak densities (Fig. 4, upper panel). The same is true for bacterial densities (Fig. 4, lower panel); more comprehensive data on the bacterial community that developed in the Dead Sea in 1992 concomitantly with the algae will be published elsewhere.

An extract of Dead Sea biomass collected at the height of the bloom (May 20) in methanol/acetone showed an absorption spectrum characteristic of *Dunaliella*, with peaks due to chlorophyll and carotenoid pigments (Fig. 5, upper panel). The minor peak at 530 nm is due to archaeobacterial pigments (α-bacterioruberin and derivatives). These bacterial carotenoids contribute also a minor part of the broad absorption maximum between 400 and 500 nm (see e.g. Oren *et al.*, 1992). Separation of pigments by HPLC (Fig. 5, lower panel) shows a dominance of pigments derived from *Dunaliella*: chlorophyll *a*, chlorophyll *b*, β-carotene, and another carotenoid which was identified as zeaxanthin or lutein on the basis of its retention time and absorption spectrum. Additional peaks can be attributed to α-bacterioruberin and related compounds, derived from the bacteria (Oren *et al.*, 1992).

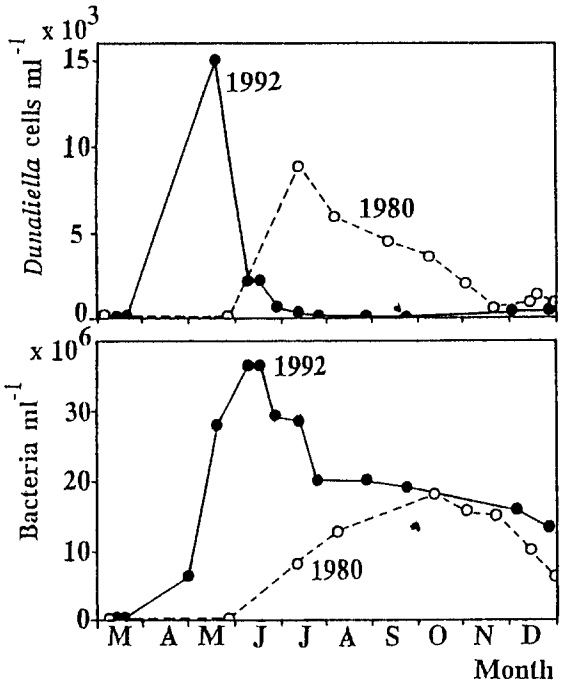

Fig. 4. Average numbers of *Dunaliella* cells (upper panel) and bacteria (lower panel) in the upper 4–5 m of the Dead Sea water column in 1992 (•), as compared with 1980 (o). Data for 1980 were derived from Oren (1983, 1988), and Oren & Shilo (1982).

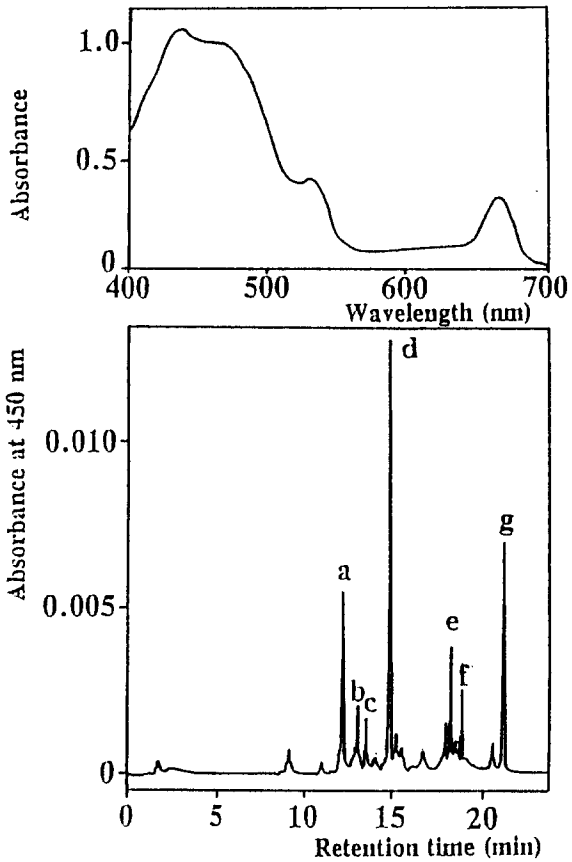

Fig. 5. Absorption spectrum of an extract of Dead Sea biomass (upper panel). Cells from 600 ml water collected from the surface of the lake on 20 May, 1992 were collected by means of filtration, and extracted in 2.5 ml methanol/acetone (1:1, by volume). Separation of pigments by HPLC (lower panel) shows a dominance of pigments derived from *Dunaliella*: chlorophyll *a* (f), chlorophyll *b* (e), zeaxanthin or lutein (d), and β-carotene (g), with additional components that can be identified as α-bacterioruberin (a) and related compounds (b, c), derived from halophilic archaeobacteria (Oren *et al.*, 1992).

At the end of July a small secondary *Dunaliella* maximum started to develop at a depth of 7–9 m, and the maximum cell density observed in this secondary bloom was about 1850 cells ml^{-1} at the end of September (Fig. 3). It may be noted here that few sampling cruises were performed during the second half of the year, and that therefore the exact time of the occurrence of the peak of this second bloom cannot be determined.

In an attempt to estimate primary productivity in the Dead Sea we incubated water samples with $NaH^{14}CO_3$ in the light and in the dark. For logistic reasons *in situ* incubations were not feasible, and samples were incubated in the laboratory at 25 °C, with illumination by white fluorescent tubes (incident irradiance 14 W m^{-2}, *i.e.* about 2% of full sunlight). Thus, the values obtained represent a potential CO_2 assimilation activity under standardized light conditions. CO_2 photoassimilation measurements were performed from the middle of May (at the height of the bloom) onwards. For the calculations we used a measured value of 1025 μmol kg^{-1} total inorganic carbon in the upper water layers (= 1210 μmol l^{-1} at σ_{25} = 180) (Table 1). Peak values of CO_2 photoassimilation of 980 nmol l^{-1} h^{-1} were observed during that period (Fig. 6), and values decreased with the decline of the bloom. The secondary deep *Dunaliella* maximum in the late summer was accompanied by a maximum in potential CO_2 photoassimilation (up to 40 nmol l^{-1} h^{-1}).

To supplement the biological observations, a study of the carbonate system and carbon isotope composition was made (Table 1). In May, the bulk of the water body contained about 860 μmol kg^{-1} total inorganic carbon with a δ^{13} C of about 1.6‰. (using the PDB standard as reference). Total inorganic carbon values above the pycnocline were higher as a result of dilution

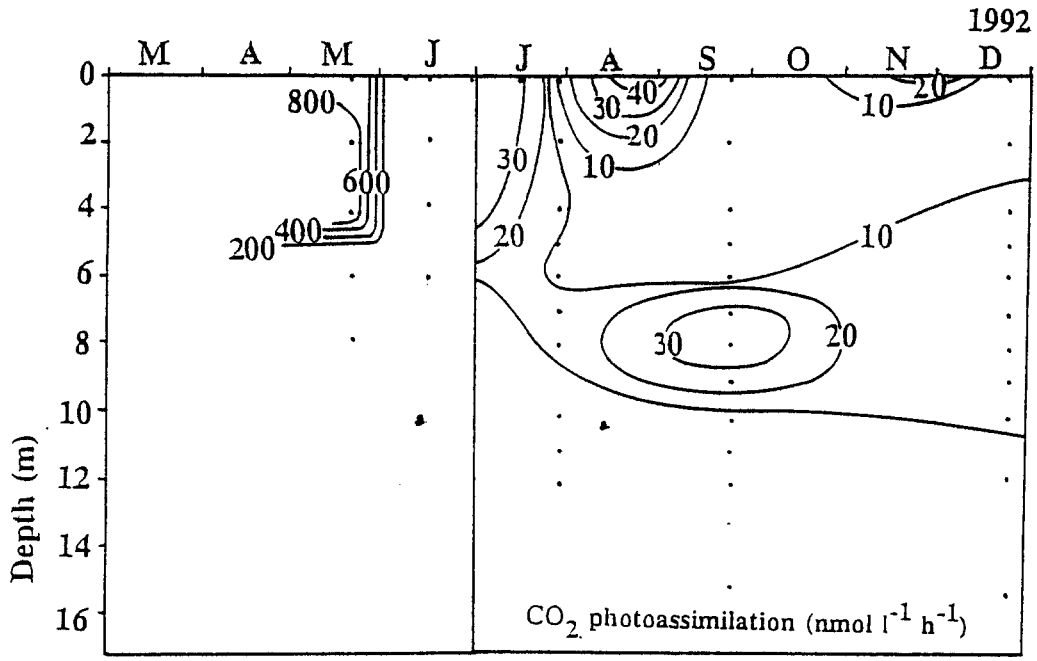

Fig. 6. Seasonal and vertical distribution of CO_2 photoassimilation potential (nmol l^{-1} h^{-1}), May–December 1993. Photoassimilation rates were estimated in the laboratory at 25 °C at an incident irradiance of 14 W m^{-2}. Values were corrected for dark CO_2 assimilation.

Table 1. Total inorganic carbon and $\delta^{13}C$ in the Dead Sea and in R. Jordan water (Allenby bridge).

Date	Depth (m)	Total inorganic carbon (μmol kg^{-1})	$\delta^{13}C$ (‰ vs PDB)	Replicates
18/3/92	300	846	1.65	3
20/5/92	0		5.06	2
	100		1.61	2
	310		1.64	1
27/7/92	0		2.51	2
	200		1.58	2
22/9/92	2	1030	2.39	1
	4	1025	2.48	1
	8.5	862	1.40	2
	14	862	1.40	2
	100	861	1.35	2
	200	859	1.38	2
	300	859	1.43	2
14/1/93	R. Jordan	3537	−7.2	2

with fresh water with a higher inorganic carbon content: the upper layer contained about 1,025 μmol kg^{-1} total inorganic carbon with δ^{13} C ranging from about 5‰ in May to 2.5‰ after July (Table 1). The isotopic variations can be explained as the result of an interplay between influx of inorganic carbon with the Jordan river and rain floods, atmospheric exchange, and biological effects. We may assume that the measurements of the deep water represent a state of the Dead Sea close to equilibrium with the atmosphere of the decade before the winter of 1991/92. Table 2 shows a crude mass balance of carbon and its isotopes in the upper layer, showing a deficit of carbon in the upper layer. The amount of missing carbon corresponds rather well with the accumulation of organic carbon fixed as algal and bacterial biomass (a measured particulate protein content of 2.7 mg kg^{-1} in May approximately corresponds with 135 μ mol carbon kg^{-1}, a number that should be doubled in view of the estimate that half the organic carbon may be found in the protein fraction). The particulate fraction was highly enriched in ^{13}(δ^{13} C = −13.5‰). The high ^{13} C enrichment in inorganic carbon in May was probably the result of a fast removal of inorganic carbon by photosynthesis (with an isotopic fractionation effect of about 25‰) (Peng

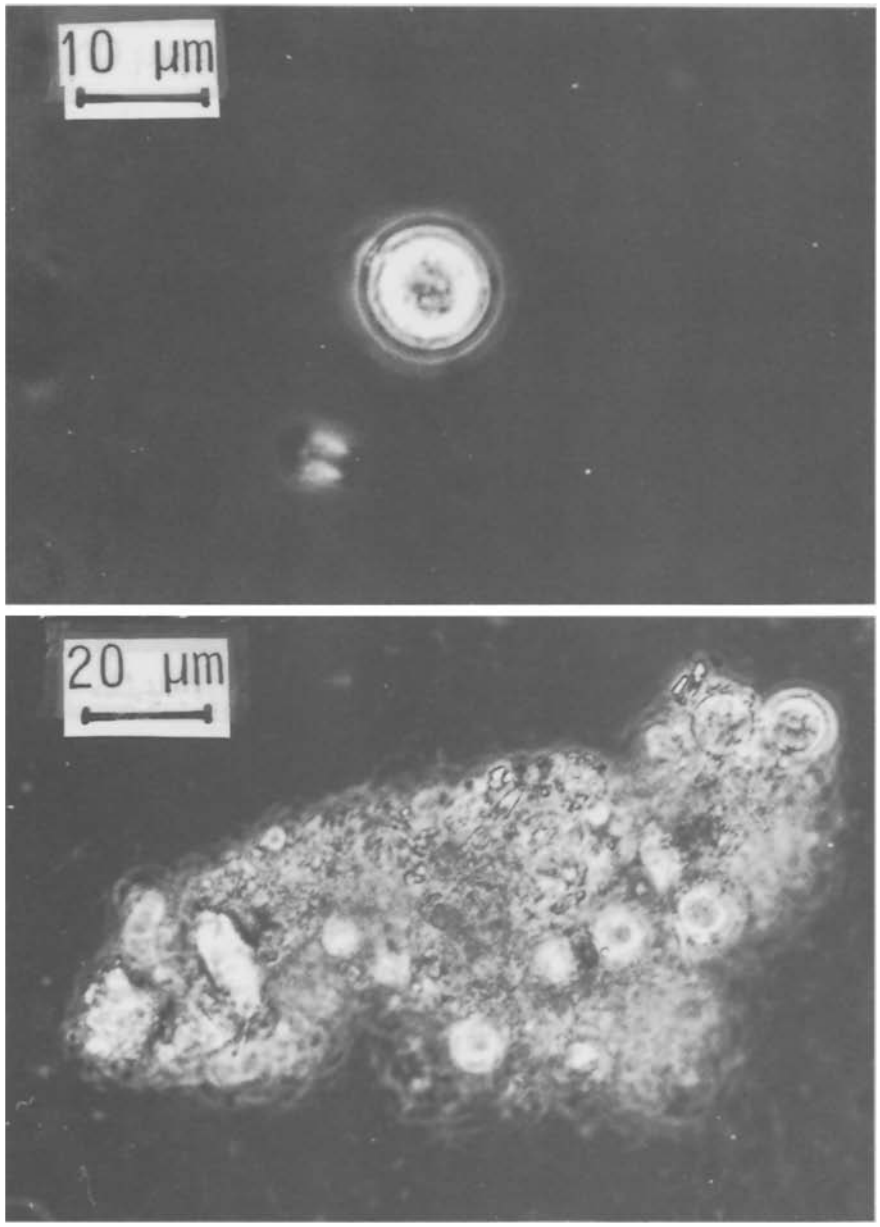

Fig. 7. Photomicrograph of structures probably representing cysts or zygotes of *Dunaliella*, observed in surface water during the decline of the *Dunaliella* bloom (8 June, 1992).

et al., 1983). Following the decrease in algal activity in May, and the decline in algal biomass, δ^{13} C values of the inorganic carbon decreased (Table 1), and probably approached equilibrium with the atmosphere.

During the period of rapid decline of the bloom (June), we observed in the upper water layer high numbers of structures that can probably be identified as cysts or zygotes of *Dunaliella* (Fig. 7). Though zygotes have to our knowledge never been identified in the species *D. parva*, morphologically similar structures were described as zygotes in other *Dunaliella* species (Hamel, 1931; Lerche, 1937). Often these structures were found in clusters, embedded in amorphous material, which can be expected to sink to the bottom at relatively high rates. It may be noted here that chlorophyll was detected in large amounts in the bottom sedi-

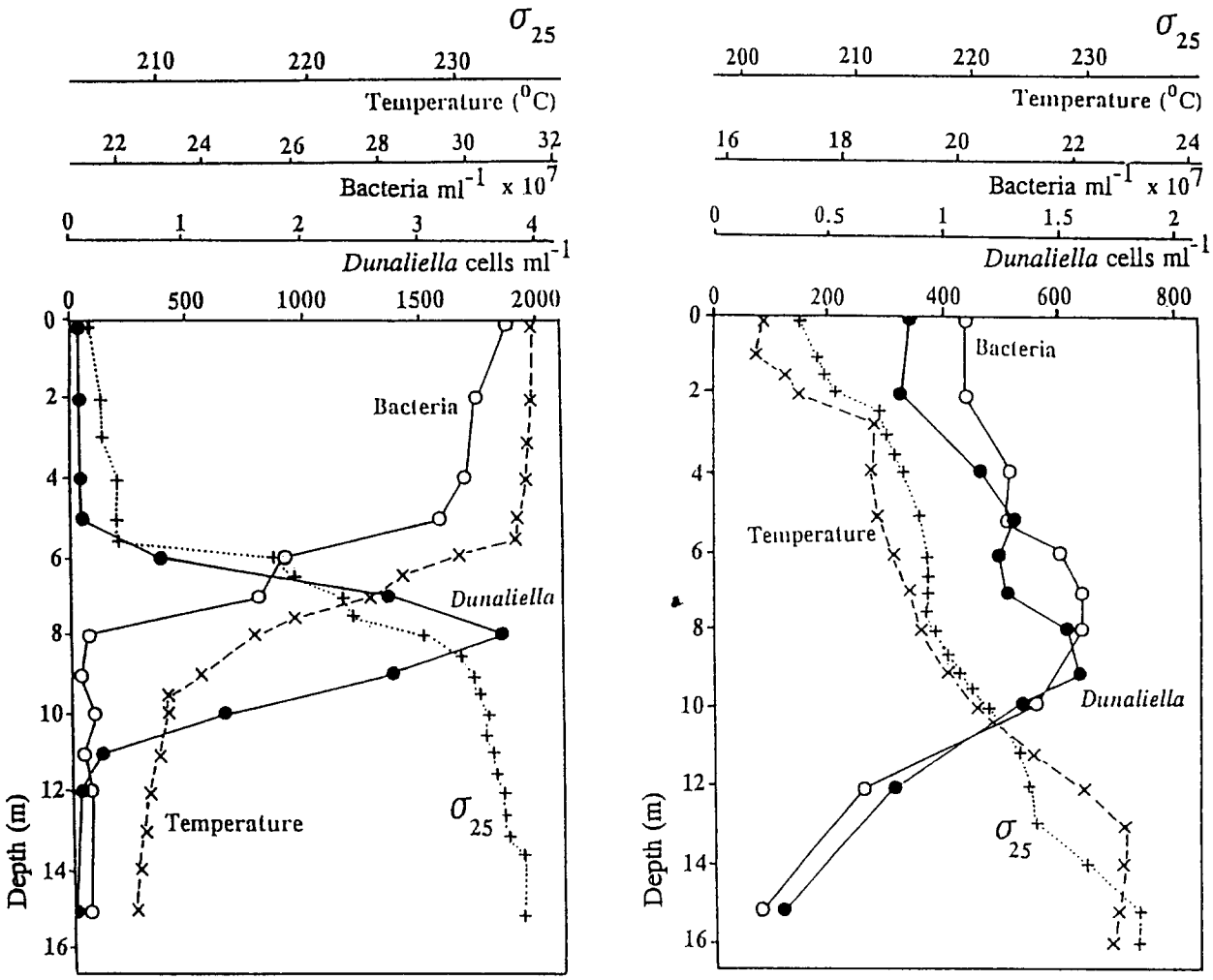

Fig. 8. Vertical distribution of *Dunaliella* cells (•) and bacteria (o) on 22 September, 1992 (left panel) and 27 December, 1992 (right panel). To provide information on the physical structure of the water column, data on temperature (×) and salinity (expressed as σ_{25}) (+) are also shown.

ments of the Dead Sea (Nissenbaum *et al.*, 1972). From July–August onwards these structures were only rarely seen.

As stated above, after the decline of the major surface bloom of *Dunaliella* a minor bloom developed at a depth of 7–9 m during the second half of the year. This bloom was found at the lower end of the pycnocline (Fig. 8, left panel), at very high salinities (σ_{25} above 220, exceeding by much the maximum values in which *Dunaliella* is known to develop in Dead Sea water (Oren, 1988; Oren & Shilo, 1985). During the same period the majority of the bacterial community was still found in the upper water layer above the pycnocline, and did not show a similar deep maximum. It is worth noting, that during this period there were indications of a three-layer structure, in which two pycnoclines were present. The depth range of the secondary algal bloom coincided with the intermediary layer. *Dunaliella* cells present at depths of 7–9 m in September 1992 looked healthy, were motile, and contained large amounts of starch, as shown by microscopic examination after staining with iodine. The remainder of the secondary bloom was still visibile at the end of the year (December 27, Fig. 8, right panel), though peak numbers were much lower. The physical structure of the water column during this cruise was already influenced by the first rain floods of the new winter, and a new pycnocline was formed at a depth of about 2 m. Above this pycnocline *Dunaliella* numbers were lower by as much as 32% as compared with the

Table 2. Mass balance of inorganic carbon, organic carbon, and carbon isotopes, in the upper 7 m of the Dead Sea, calculated per m^2 of lake surface. Calculations were based on the formation of an upper layer of 7 m as the result of mixing of 5 m of Dead Sea brine with 2 m of fresh water (in accordance with a 2-m rise in water level and a σ_{25} value of 168 at the end of the winter).

Component	Weight (kg)	Total inorganic carbon (μmol kg^{-1})	Total inorganic carbon (mol)	$\delta^{13}C$ (‰ *vs* PDB)
Inorganic carbon				
5 m^3 Dead Sea brine	6175	860	5.311	1.6
2 m^3 Jordan water	2000	3537	7.074	−7.2
7 m^3 (calculated)	8175	1515	12.385	−3.4
7 m^3 (measured)	8175	1025	8.379	5.1
Difference	0	490	4.006	8.5
Particulate organic carbon		270[a]		−13.5±0.3[b]

[a] Estimated on the basis of particulate protein, for details on the calculation see text.

[b] Average value for 5 biomass samples collected during the period 6 June–22 September, 1992.

water layer immediately below, though the difference in salinity indicates a dilution of 4% only (compare also a decrease of 15% in bacterial numbers at 0–2 m depth, as compared with 4–5 m).

Discussion

The present study documents the reappearance of *Dunaliella parva* in the Dead Sea, after a period of about ten years in which no primary producers were found in the lake. After the *Dunaliella* bloom of 1980 (Oren & Shilo, 1982) no similar blooms developed in the years 1981–1991. The reason of this can be understood from the results of simulation experiments in the laboratory and in outdoor tanks (Oren & Shilo, 1985). It was found that two conditions are required for the development of *Dunaliella* in the Dead Sea water: phosphate has to be available, and the salinity of the brine should drop to σ_{25} values below 210–220 (compared with a value of about 235 in undiluted Dead Sea water) (Beyth *et al.*, 1993). Salinity values in the Dead Sea are supraoptimal for the development of *Dunaliella*. A similar phenomenon has been described for *Dunaliella* in the Great Salt Lake, Utah (Brock, 1975). During 1981–1991 the salinity of the upper water layers of the Dead Sea never reached σ_{25} values below 220 g cm^{-3}, and *Dunaliella* did not grow.

Unprecedently heavy rain floods during the winter of 1991–1992 caused a rise in the water level of the Dead Sea by almost 2 m (Oren, 1993). The lake became stratified again, with a pycnocline at a depth of 4–5 m, isolating an upper layer of water with a specific gravity of 1.17–1.18 g cm^{-3} during the months April–June. As expected, *Dunaliella* developed again in the Dead Sea, with peak population densities even higher than those in 1980 (Fig. 4). As in previous years, it was demonstrated that addition of phosphate, in combination with a lowered salinity, are the factors determining the rate and extent of the multiplication of *Dunaliella* (not shown). Simultaneously with the algal bloom, a mass development of bacteria was observed; data on the nature and activities of this heterotrophic community will be published elsewhere.

Reliable estimates of primary productivity in the Dead Sea are still lacking. This is both due to logistic reasons, but also to more fundamental questions with respect to the methodology to be used. The commonly used methods to measure primary production are based on incorporation of $^{14}CO_2$, followed by filtration and determination of the amount of label retained in the particulate fraction. These methods may lead to

a significant underestimation of the primary production. *Dunaliella* cells are very fragile, and burst upon filtration and drying of the filters (Goldman & Dennett, 1985), thereby releasing the intracellular glycerol which may represent a substantial fraction of the newly produced organic carbon. The few attempts that have been reported in the literature to measure primary production in other hypersaline lakes dominated by *Dunaliella*, such as the Great Salt Lake, Utah (Stephens & Gillespie, 1976) do not take this problem into account. We attempted in part of the experiments (at the end of the year only) to overcome this problem by collecting particulate matter from 20-ml portions of water after incubation with $NaH^{14}CO_3$ by centrifugation, followed by removing of most of the supernatant, acidification to remove non-incorporated $^{14}CO_2$, and counting the remaining radioactivity. This method (results not shown) gave results in the same order of magnitude as those obtained with the filtration method (Fig. 6).

Our estimates of primary productivity are based on laboratory simulations, rather than on *in situ* incubations. Experiments were performed at 25 °C. For a number of samples similar experiments were also performed at 35 °C; CO_2 photoassimilation rates at 35 °C were 80±30% of those at 25 °C. The light conditions chosen for the experiments were a constant illumination, at an irradiance comparable with that during mid-day at a depth of about 4 m, as based on light penetration curves measured in the Dead Sea in 1980 (Oren & Shilo, 1982), when algal and bacterial community densities were comparable (Oren, 1983; Oren & Shilo, 1982). Due to technical reasons similar light measurements were not performed in 1992. Thus, effects due to differences in temperature and irradiance (including possible photoinhibition effects in the upper meters) were not taken into account.

For the calculation of CO_2 photoassimilation rates we used measured values of 1025 μmol kg^{-1} total inorganic carbon in the upper water layers (= 1210 μmol l^{-1} at σ_{25} = 180), and 860 μmol kg^{-1} in the deeper layers. The last value is close to that reported by Stiller *et al.* (1985) (750 μmol kg^{-1} at a depth of 0.5 m at a non-specified site in the Dead Sea in July 1984). Total inorganic carbon values above the pycnocline are higher as a result of dilution with fresh water with a higher inorganic carbon content (Table 2). The value of 2.5 mM inorganic carbon in the Dead Sea calculated by Sass & Ben-Yaakov (1977) on the basis of total alkalinity titrations, and used by Oren (1981) for the calculation of primary productivity values, is much too high, probably due to the high borate concentration in Dead Sea water (E. Sass, personal communication). A similar phenomenon was reported in a study on primary productivity in the Great Salt Lake, Utah (Stephens & Gillespie, 1976).

Our estimate of primary productivity in the Dead Sea (Fig. 6) during 1992 shows a maximum of 980 nmol C l^{-1} h^{-1} (11.8 mg C l^{-1} h^{-1}, or 142 mg C l^{-1} d^{-1}, based on 12 h light per day), and an integrated value of 0.66 g C m^{-2} d^{-1}. These values may be compared with primary productivity data on other water bodies: characteristic values (in g C m^{-2} d^{-1}) are for oligotrophic lakes 0.05–0.3, eutrophic lakes 0.6–8, open ocean around 1, and coastal zones 0.5 to 3 (Morris, 1982). In the Great Salt Lake, Utah during blooms of *Dunaliella* values of about 2.13 g C m^{-2} d^{-1} were reported (Stephens & Gillespie, 1976). Comparison with data for Lake Kinneret (Berman, 1978) during a bloom of the dinoflagellate alga *Peridinium* values of 2.5–4 mg C m^{-2} d^{-1}, and up to 0.9 g C m^{-3} d^{-1} were reported (during the remainder of the year values were between 0.8–1.2 g C m^{-2} d^{-1}). Assimilation numbers in lake Kinneret varied between 0.4 and 5 mg C mg chlorophyll^{-1} h^{-1}, the lower values being measured at the height of the bloom. For the Dead Sea we calculated values of around 0.41 mg C mg chlorophyll^{-1} h^{-1} (May, during the *Dunaliella* bloom), and 0.05–0.13 mg C mg chlorophyll^{-1} h^{-1} for the secondary *Dunaliella* maximum in September.

The 1992 *Dunaliella* bloom developed much earlier in the season than the 1980 bloom, reached higher peak values, but also declined much faster: at the end of June 1992 less than 40 cells ml^{-1} were left in the upper water mass. The causes of the decline are yet unclear, and among the possibilities we can name autolysis, sedimentation to the bottom of the lake, and predation by protozoa. The last option is unlikely, as protozoa have rarely, if at all, been seen in Dead Sea water samples (Oren, 1988), and were not observed in 1992. The finding of cyst-like structures during the decline period suggests that *Dunaliella* may survive as resting stages on the bottom of the lake, and this may also explain the extremely rapid appearance of the alga as soon as conditions for growth became favorable, in spite of the fact that no living *Dunaliella* cells were observed in the lake during the previous ten years. The importance of resting stages of *Dunaliella* has been suggested in other hypersaline ecosystems as well (Borowitzka, 1981). In addition, *Dunaliella* has been observed in saline springs on the shore of the lake, and these also may serve as an inoculum.

Of special interest is the additional decline in *Dunaliella* numbers in the upper 2 m after the first rain floods at the end of the year (Fig. 8, right panel). As stated above, there is a greater decrease than expected on the basis of dilution alone. One possible explanation is the occurrence of damage to the cells as a result of dilution. It has been reported that dilution of *Dunaliella* suspensions in Dead Sea water with more than 20% fresh water caused a sharp decrease in the number of cells remaining in suspension, and an increase in the amounts of cells sinking (Dor & Doron, 1989). Whether the extent (4%) and the rate of the dilution in our case was sufficient to elicit a similar effect remains to be ascertained.

An unusual phenomenon, never reported before in the Dead Sea, was observed at the end of the summer of 1992: after the decline of the *Dunaliella* population in the surface layer above the pycnocline, a renewed development of *Dunaliella* occurred, but this time at a depth of 6–10 m, at the lower end of the pycnocline. The nature of this deep maximum is far from understood: at these depths the irradiance is very low, due to the turbidity caused by the dense bacterial community present in the upper layers; measurements in 1980 showed a tenfold decrease in irradiance for every two meters depth (Oren & Shilo, 1982). Moreover, simulation studies have shown that at the salinities present growth of *Dunaliella* is negligible (Oren & Shilo, 1985). One hypothesis is that the development of the algae in the deeper layers may be related to the availability of nutrients – possibly phosphate. The possibility can also not be excluded that the motile *Dunaliella* cells maintain a diel migration, and may at times be found closer to the surface, where the salinity is lower and more light is available for photosynthesis. However, for logistic reasons sampling was performed only around noon.

The extent of biological activity in the Dead Sea in its present state depends primarily on 'catastrophic' unusual events of abundant rainfall in its catchment area. Though it may be expected that a simplified ecosystem like the Dead Sea, with only one primary producer, and a few heterotrophic bacteria, should be relatively easy to understand, comparison of the two bloom events of 1980 and of 1992 shows that our understanding of the factors underlying the development of the algal and bacterial communities is still limited, in spite of the wealth of field and laboratory data collected in the more than fifty years since indigenous life was first discovered in the Dead Sea.

Acknowledgments

We thank skipper Motti Gonen and his crew for assistance during Dead Sea cruises. This study was performed in the framework of the Moshe Shilo Center for Marine Biogeochemistry, BMFT-Minerva Gesellschaft für Forschung, München, Germany, and was further supported by grants from the Israel Science Foundation administered by the Israel Academy of Sciences and Humanities (to A.O.) and the Israeli Ministry of Energy and Infrastructure (to D.A.).

References

Anati, D. A. & S. Shasha, 1989. The stability of the Dead Sea stratification. Israel J. Earth Sci. 38: 33–35.

Anati, D. A. & M. Stiller, 1991. The post-1979 thermohaline structure of the Dead Sea and the role of double-diffusive mixing. Limnol. Oceanogr. 36: 342–354.

Berman, T., 1978. Primary productivity and photosynthetic efficiency of light utilization by phytoplankton. In C. Serruya (ed.), Lake Kinneret, Dr W. Junk Publishers, The Hague: 253–258.

Beyth, M., I. Gavrieli, D. Anati & O. Katz, 1993. Effects of the December 1991–May 1992 floods on the southern Dead Sea vertical structure. Earth Sci., in press.

Borowitzka, L. J., 1981. The microflora. Adaptations to life in extremely saline lakes. Hydrobiologia 81: 33–46.

Brock, T. D., 1975. Salinity and the ecology of *Dunaliella* from Great Salt Lake. J. gen. Microbiol. 89: 285–292.

Dor, I. & B. Doron, 1989. Energy from solar ponds: control of the green flagellate *Dunaliella* using osmotic shock of dilution. Envir. Sci. Technol. 23: 227–231.

Goldman, J. C. & M. R. Dennett, 1985. Susceptibility of some marine phytoplankton species to cell breakage during filtration and post-filtration rinsing. J. exp. Mar. Biol. Ecol. 86: 47–58.

Graber, E. R. & P. Aharon, 1991. An improved microextraction technique for measuring dissolved inorganic carbon (DIC), $\delta^{13}C_{DIC}$ and $\delta^{18}O_{H_2O}$ from milliliter-size water samples. Chem. Geol. 94: 137–144.

Hamel, G., 1931. Chlorophycees des côtes françaises. Extr. Rev. algol. t. I–V.

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

Lerche, W., 1937. Untersuchungen über Entwicklung und Fortpflanzung in der Gattung *Dunaliella*. Arch. Protistenk. 88: 236–268.

Morris, I., 1982. Primary production of the oceans. In R. G. Burns & J. H. Slater (eds), Experimental microbial ecology, Blackwell Scientific Publications, Oxford: 239–252.

Nissenbaum, A., M. J. Baedecker & I. R. Kaplan, 1972. Organic geochemistry of Dead Sea sediments. Geochim. cosmochim. Acta 36: 709–727.

Oren, A., 1981. Approaches to the microbial ecology of the Dead Sea. Kieler Meeresforsch. Sonderh. 5: 416–424.

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

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

Oren, A., 1992a. Bacterial activities in the Dead Sea, 1980–1991: survival at the upper limit of salinity. Int. J. Salt Lake Res 1: 7–20.

Oren, A., 1992b. Ecology of extremely halophilic microorganisms. In R. H. Vreeland & L. I. Hochstein (eds), The biology of halophilic bacteria, CRC Press, Boca Raton: 25–53.

Oren, A., 1993. The Dead Sea – alive again. Experientia 49: 518–522.

Oren, A. & M. Shilo, 1982. Population dynamics of *Dunaliella parva* in the Dead Sea. Limnol. Oceanogr. 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 Microbiol. Ecol. 31: 229–237.

Oren, A., N. Stambler & Z. Dubinsky, 1992. On the red coloration of saltern crystallizer ponds. Int. J. Salt Lake Res. 1 (no. 2): 77–89.

Peng, T.-H., W. S. Broecker, H. D. Freyer & S. Trumbore. 1983. A deconvolution of the tree ring based δ^{13}C record. J. geophys. Res. 88: 3609–3620.

Sass, E. & S. Ben-Yaakov, 1977. The carbonate system in hypersaline solutions: Dead Sea brines. Mar. Chem. 5: 183–199.

Sofer, Z., 1980. Preparation of carbon dioxide for stable carbon isotope analysis of petroleum fractions. Anal. Chem. 52: 1389–1391.

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

Stiller, M., J. S. Rounick & S. Shasha, 1985. Extreme carbon-isotope enrichments in evaporating brines. Nature 316: 434–435.

Volcani, B. E., 1944. The microorganisms of the Dead Sea. In Papers Collected to commemorate the 70th anniversary of Dr Chaim Weizmann, Collective volume, Daniel Sieff Research Institute, Rehovoth: 71–85.