

Phytoplankton dynamics in the Salton Sea, California, 1997-1999

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Abstract

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The dynamics of phytoplankton populations in the Salton Sea were studied over the 3-year period 1997-1999. Dinoflagellates were important components, often contributing over 80% of the total biovolume of cells larger than 5 µm. *Gyrodinium uncatenum* along with a similar, but rarer species *Gyrodinium instriatum*, was the most dominant taxon, present year-round, and became especially abundant in spring and summer. Diversity of dinoflagellates was high with three or four species often co-occurring with similar densities. The largest dinoflagellate, *Gonyaulax grindleyi* (= *Protoceratium reticulatum*), increased greatly in abundance during 1997-1999. Diatoms co-dominated year round with the colonial araphid *Thalassionema* sp. also becoming especially abundant in 1999. During the winter mixing period, diatom populations often were dominated by pennate species usually considered benthic, such as *Pleurosigma ambrosianum*, *Ceratoneis closterium* and *Tryblionella punctata*. Cryptomonads, represented by several species, were usually numerous and, although relatively small, constituted as much as 20-30% of total phytoplankton biovolume. A raphidophyte, *Chattonella marina*, reported to be ichthyotoxic in other locales, was abundant in summer, comprising about a third of total phytoplankton biovolume then and reaching mid-lake densities of nearly 1,500 cells ml⁻¹. Two colonial non-motile green algae were usually present; one of these, *Crucigenia rectangularis*, increased greatly in density in 1999. A euglenoid, *Eutreptia lanowii*, was highest in density in summer when it contributed about 5-10% of total biovolume at times after other species were reduced by sulfide events. Filamentous planktonic cyanobacteria were very rare. The increase in large species of phytoplankton over the three-year period coincided with a dramatic decrease in abundance of a planktivorous fish, the Mozambique mouthbrooder (*Oreochromis mossambicus* x *O. urolepis honorum*), which likely was responsible for these changes in phytoplankton composition. Phytoplankton biovolume densities and chlorophyll *a* concentrations each year were highest, 6-16 mm³ l⁻¹ and 30-40 µg l⁻¹ respectively, in the spring. In summer and early fall, occasional windstorms mixed the water column causing sulfide-laden bottom waters to upwell and strip surface waters of oxygen. Sharp drops in abundance of most phytoplankton species occurred during these events presumably due to poisoning by hydrogen sulfide. Satellite images confirm the presence of large patches of high albedo surface waters at these times, lasting days to over a week, produced by backscattering from abundant crystals of gypsum produced following oxidation of hydrogen sulfide to sulfate.

Key words: zooplankton, saline lakes, polymixis, tilapia, remote sensing, sulfide, anoxia, dinoflagellates, diatoms, grazing

Introduction

Salt lakes are understudied in comparison to fresh water lakes although nearly as much inland water is saline as is fresh by volume (Eagleson 1970; Hammer 1986). In particular, multi-year studies of phytoplankton dynamics of salt lakes have been few in number (*e.g.*, Lake Nakuru, East Africa, Vareschi and Jacobs 1985; Mono Lake, California, USA, Jellison and Melack 1988, 1993; Lake Shira in Siberia, Russia, Zotina *et al.* 1999; Ethiopian lakes, Zinabu *et al.* 2002). This is because most are quite distant from universities and research institutes and unimportant as sources of water for human use. The present study documents phytoplankton dynamics over a three-year period in a large, man-made, discontinuous warm polymictic (*sensu* Lewis 1983) salt lake fed mainly by agricultural and municipal wastewaters.

The Salton Sea is the largest lake in California (area 980 km²) and is located in the southeastern part of the state. It has been in existence for 100 years since unusually high flooding in 1905 allowed the entire Colorado River to flow into the Salton Sink for well over a year (Sykes 1914). It is relatively shallow (mean depth 8 m) and, although originally composed of relatively fresh water, has become saline due to a lack of outflows and high evaporation rates. Marine fish were introduced at a time when the salinity was similar to marine waters (*ca.* 35 g l⁻¹) (Walker 1961). At the time of our present study, 1997-1999, the salinity was about 41-45 g l⁻¹ (Watts *et al.* 2001). The temperature of the water varies between about 12 and 40 °C throughout the year with intermittent mixing in summer (Watts *et al.* 2001; Holdren and Montaña 2002). Oxygen at times is supersaturated due to phytoplankton photosynthesis, but also is often severely depleted, occasionally even in surface waters (Watts *et al.* 2001; Holdren and Montaña 2002).

The lake has long had high phytoplankton densities due to the input of nutrient-rich agricultural and municipal wastewaters from the Mexicali, Imperial and Coachella valleys but, until recently, its phytoplankton has been the object of only three serious studies (Carpelan 1961a; Bain *et al.* 1970; González 1997). Phytoplankton provides a food base for other aquatic organisms in the lake, but also can cause problems if toxic blooms occur or when anoxic conditions develop as blooms decompose.

Carpelan (1961a) monitored phytoplankton in surface water at two stations, one 100 m from shore (depth 3 m) and another about five km offshore (depth 12 m) during 18 months in 1955-1956. He did not measure chlorophyll concentrations but mentioned that Secchi disc depth was always < 1 m. Using a light-dark bottle technique he found that average productivity of the Salton Sea at a location approximately 0.4 km offshore was about 0.75 g C m⁻³ day⁻¹. Dominant algal species during his study were diatoms, dinoflagellates and a “non-motile green alga.” Most abundant diatoms were a

chain-forming species of *Cyclotella*, *Nitzschia longissima* (which we now know to be *Ceratoneis closterium*), *Thalassionema nitzschioides* (probably the same undescribed *Thalassionema* species we found in 1997-1999; see Lange and Tiffany 2002), and *Pleurosigma* sp. (probably *P. ambrosianum*: Sterrenburg *et al.* 2000; Lange and Tiffany 2002). (Describers of current Salton Sea taxa are given in Table 1). *Ceratoneis closterium* densities as high as 56,000 cells ml⁻¹ were found. Dominant dinoflagellates were a *Prorocentrum* species (which he identified as *Exuviella compressa*) and *Glenodinium* sp. (now called *Heterocapsa niei*). *Hermesinium adriaticum* Zacharias, an ebrüidian (Hargraves and Miller 1974), was also observed in high abundance, although Carpelan was unsure of its identity and called it a silicoflagellate. Carpelan found that microscopic filamentous cyanobacteria were absent from the plankton but were abundant in benthic mats that occasionally broke loose to form floating masses nearshore. There were no macroalgae detected in the Salton Sea at that time. Carpelan found sulfide levels in anoxic bottom waters, up to 0.085 mg l⁻¹ (16 Jul 1956), with much lower values in surface waters. Surface water at his offshore deep station was low in oxygen on only one occasion (16 Sep 1955) when it dipped to 0.55 mg l⁻¹ and was more usually in the range of 3-8 mg l⁻¹. A thriving sportfishery existed during Carpelan’s study, but none of the fish present then were considered planktivorous in the adult stage.

In July 1968 and 1969 Bain *et al.* (1970) found the phytoplankton of the Salton Sea to be abundant with Secchi disk readings in the range of 0.5 to 2 m and chl-*a* in the range of 35 to 50 µg l⁻¹. Dinoflagellates and diatoms were the dominant forms, as in the 1950s study. Additionally, they observed that two small “motile green algae” had become abundant. The dinoflagellates they reported were *Cachonina niei* (now *Heterocapsa niei*), *Exuviella* spp. (now *Prorocentrum* spp.) and a dinoflagellate that they identified as *Gyrodinium resplendens* Hulburt. This latter species could have been *Gyrodinium uncatenum* or *G. instriatum*, species now common in the lake. A *Peridinium* sp. was common and may have been *Scrippsiella trochoidea*, now also abundant. Diatoms were abundant at times in 1968-1969, mostly the same genera found in 1955-1956 (*Cyclotella*, *Pleurosigma* and *Thalassionema*). Also found was a *Nitzschia* sp. that could have been *Tryblionella punctata* or *Nitzschia frustulum*, both now occasionally found in the winter phytoplankton. From nutrient addition experiments, Bain *et al.* (1970) concluded that self-shading rather than nutrients limited algal production in the Salton Sea. They also noted the odor of hydrogen sulfide at times during fish kills, including an event in May 1969. They suggested adding a planktivorous fish to control algal production, foreshadowing the accidental introduction of the omnivorous *Oreochromis mossambicus* Peters x *O. urolepis honorum* Trewavas, a hybrid tilapia that apparently invaded about the time of their study (Costa-Pierce and Doyle 1997; Riedel and Costa-Pierce 2001; Hurlbert *et al.* 2007).

Table 1.—Estimated biovolumes, mean greatest linear dimension (GLD) for individual phytoplankters, maximum density observed in mid-lake samples, and month each year, 1997-1999, when mean density was maximal.

Taxon	Biovolume (μm^3)	GLD (μm)	maximum density, cells ml^{-1}	month of maximum observed mean density		
				1997	1998	1999
Dinophyceae						
<i>Gonyaulax grindleyi</i> Reinecke	44,700	48	165	Aug	Aug	Jul
<i>Gonyaulax spinifera</i> (Claparede & Lachmann) Bütschli	20,300	34	22	Jul	Jun	Jun
<i>Gyrodinium uncatenum</i> Hulburt/ <i>instriatum</i> Freudenthal & Lee ^a	17,500	39	1,700	Mar	Mar	Jul
<i>Gonyaulax turbynei</i> Murray & Whitting	14,800	33	36	Oct	Jul	Aug
<i>Gymnodinium</i> sp. 2	9,430	30	138	Sep	Aug	Aug
Scrippsielloids ^b	8,350	30	608	Jun	Jul	Jun
<i>Gymnodinium</i> sp. 1	8,250	27	648	Feb	Feb	Feb
<i>Oblea rotundata</i> (Lebour) Balech	6,600	25	25	Feb	Jun	Feb
<i>Protoperdinium brevipes</i> (Paulsen) Balech	4,570	22	12	Jun	Apr	May
<i>Oxyrrhis marina</i> Dujardin	2,550	22	295	Apr	Jun	May
<i>Amphidinium</i> cf. <i>operculatum</i>	1,480	16	160	-	Sep	Aug
<i>Prorocentrum minimum</i> (Pavillard) Schiller	1,120	18	76	Mar	May	Nov
Other dinoflagellates < 20 μm	893	14	135	Mar	Apr	Jul
<i>Heterocapsa niei</i> (Loeblich) Morrill & Loeblich III	656	21	8,390	Feb	Mar	Jan
Bacillariophyceae						
<i>Fallacia</i> spp.	1,350	21	92	May	Feb	Jun
<i>Pleurosigma ambrosianum</i> Sterrenburg, Tiffany & Lange	1,210	73	2,260	Feb	Mar	Mar
<i>Cyclotella</i> > 7.5 μm^c	1,020	13	366	Jul	Jan	Aug
<i>Tryblionella punctata</i> Smith	379	18	499	Jan	-	-
<i>Thalassionema</i> sp.	337	54	22,800	Nov	Aug	Jul
<i>Cyclotella</i> < 7.5 μm^d	216	5	3,930	Feb	Feb	May
<i>Chaetoceros muelleri</i> var <i>subsalsum</i>	158	7	4,900	Jun	Jul	Jun
<i>Ceratoneis closterium</i> (Ehrenberg)	107	17	3,460	Apr	Jun	May
<i>Nitzschia frustulum</i> (Kützing) Grunow	22.7	9	1,280	Nov	Apr	Jan
Chlorophyceae						
<i>Oocystis</i> sp. ^e	1,580	17	143	Jun	Aug	Apr
<i>Crucigenia rectangularis</i> ^e (Braun) Gay	262	14	13,100	Jun	Jul	Mar
Euglenophyceae						
<i>Eutreptia lanowii</i> Steur	2,440	44	324	Sep	Jul	Jun
Rhaphidophyceae						
<i>Chattonella marina</i> (Subrahmanyam) Hara & Chihara	13,100	40	1,480	Jul	Jul	Jul
Prymnesiophyceae						
<i>Pleurochrysis pseudoroscoffensis</i> Gayral & Fresnel	840	11	1,670	May	Apr	Feb
Cryptophyceae						
Large cryptomonads	1,010	19	602	Nov	Jan	Aug
Small cryptomonads	247	10	23,600	Apr	Apr	May

^aprimarily *G. uncatenum*, ^bprimarily *Scrippsiella trochoidea* (Stein) Balech, ^cprimarily *Cyclotella* sp., ^dprimarily *Cyclotella choctawhatcheeana* Prasad, ^eenumerated and measured as colonies.

González (1997) studied the effects of salinity and tilapia grazing on phytoplankton and periphyton in the Salton Sea with a microcosm experiment that employed 380-liter tanks inoculated with invertebrates and algae from the Salton Sea and its environs and adjusted to salinities of 30, 39, 48, 57 and 65 g l⁻¹. Extra tanks with one small tilapia each were added at two salinities, 37 and 57 g l⁻¹, to test for tilapia effects. Phytoplankton was greatly reduced as a result of grazing by *Artemia franciscana* Kellogg, a brine shrimp, at 65 g l⁻¹. Periphyton was most abundant when the density of *Gammarus mucronatus* Say, an amphipod, was reduced by its inability to withstand high salinities. Some phytoplankters found in the microcosms were the same as those found in previous studies (as well as this one), others were novel. In particular, a potentially toxic *Prymnesium* sp. became highly abundant at two salinities (48 and 57 g l⁻¹). A chlorophyte, *Oocystis* sp., was abundant at the lower salinities. Some species not noted in earlier studies were abundant in the microcosms, such as *Scrippsiella trochoidea*, *Chaetoceros muelleri* var. *subsalsum*, *Chroomonas* sp., *Romeria* sp. and *Pleurochrysis pseudoroscoffensis*. Grazing by tilapia reduced chlorophyll and phytoplankton density up to 88% at both 39 and 57 g l⁻¹.

Recent studies on the Salton Sea reveal that it is a dynamic system with great diversity of microbial forms. Reifel *et al.* (2001) reported on blooms of a coccolithophorid, *Pleurochrysis pseudoroscoffensis*, that produced vast scums on the surface of the Sea in 1999. Tiffany *et al.* (2001) discovered a raphidophyte, *Chattonella marina*, to be an important component of the warm season phytoplankton in 1997. Barlow and Kugrens (2002) reported eight genera of cryptomonads. Lange and Tiffany (2002) found 96 diatom species in the Sea. Rogerson and Hauer (2002) found 45 morphospecies of naked amoebae and up to 237 amoebae ml⁻¹. Wood *et al.* (2002) found at least 10 genera of cyanobacteria in the Sea, mostly in mats associated with the sulfur-oxidizing bacterium *Beggiatoa* sp. Two tiny planktonic open-water forms, *Synechococcus* sp. and *Synechocystis* sp., had total densities of ~ 2,000-3,000 cells ml⁻¹ in shoreline water samples. Wood *et al.* also determined heterotrophic bacteria in the same samples were in the range of 4-5 × 10⁶ ml⁻¹. Miller *et al.* (2005) discovered an unusual free-living cyanobacterium within an epilithic assemblage at the Salton Sea, similar to *Acaryochloris marina* Miyashita and Chihara, containing mostly chlorophyll *d* and utilizing light in the far-red portion of the spectrum. Eugene Small reported 145 species of ciliates from various habitats of the Sea (see Tiffany *et al.* 2007b).

Interest has been growing in restoring this salt lake to a condition with lower salinity, less phytoplankton, less anoxia and fewer fish kills and bird die-offs. The present study was carried out to assess the present status of the phytoplankton of the Salton Sea in order to help guide restoration planning. Its specific objective was documentation of seasonal and

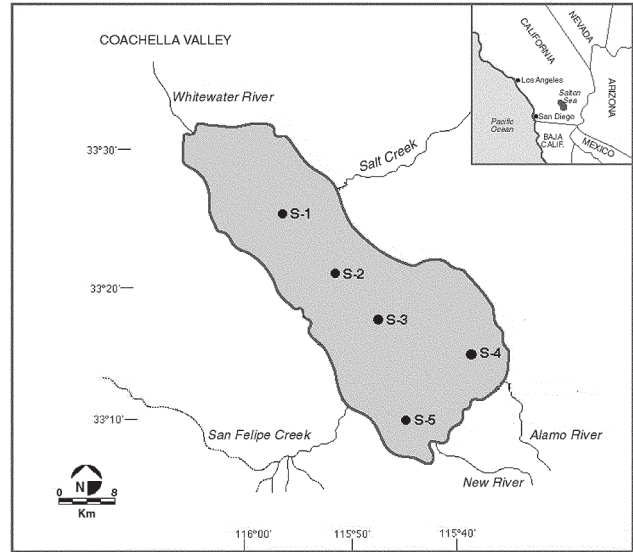


Figure 1.-Sampling stations in the Salton Sea, 1997-1999.

year-to-year variations in the phytoplankton over a three-year period (1997-1999) and interpretation of those variations in relation to physical, chemical and biological factors likely to be driving them. This investigation was carried out in parallel with three-year investigations of the protozooplankton (Tiffany *et al.* 2007b), metazooplankton (Tiffany *et al.* 2002) and temperature, oxygen and mixing regimes (Watts *et al.* 2001), and in the same general time frame (1998-2005) as numerous other shorter term studies at the Salton Sea of its birds, fish, macroinvertebrates, water chemistry, mixing regime, sediments, and pollutants.

Methods

Sampling regime

Samples for chlorophyll *a* and phytoplankton analysis were taken at 2 to 5 week intervals at three mid-lake stations (S-1, S-2 and S-3) throughout 1997 and 1998 and at the same three mid-lake stations plus two shallower southerly stations (S-4 and S-5) during 1999 (Fig. 1; for exact sampling dates, see Watts *et al.* 2001). Water samples were taken with a 3-m long, 4 cm diameter PVC tube for depth strata at 0-3, 3-6 and 6-9 m. These were filtered through 200 µm mesh netting to remove larger zooplankters. From samples thus obtained, subsamples were taken for chlorophyll *a* analysis and phytoplankton enumeration. For chlorophyll *a* analysis duplicate 500 ml samples were taken at each depth interval and placed on ice in a cooler for transport.

Information on temperature, oxygen, nutrients and metazooplankton was gathered at the same stations on the same dates and has been mostly presented in other manuscripts (Watts *et*

al. 2001; Tiffany *et al.* 2002; Swan *et al.* 2007b; S. Hurlbert *et al.* unpubl. data).

Silica analysis

Samples for determining silica concentrations were collected using a 2 L Kemmerer bottle at 2 m intervals from the surface to bottom (to 14 m at S-1 and to 12 m at S-2 and S-3). At each station and depth, duplicate 500 ml water samples were collected and stored at 4 °C until returning to shore. 30 ml aliquots were removed from the 500 ml samples and centrifuged at 5000 rpm for 10 minutes to remove diatoms. Silicate samples were analyzed using a continuous-flow analyzer (AutoAnalyzer II™) and a modified molybdate blue method and concentrations reported as silicate, SiO₂. We report here geometric means for silicate averaged over the collective depths and the three mid-lake stations for each date. Concentrations of nitrogen and phosphorus species were also measured (S. Hurlbert, unpublished data).

Chlorophyll a analysis

Within 12 h samples for chl-*a* were filtered through GF/F filters. When the amount of water that could pass through the filters was less than the entire 500 ml sample owing to high phytoplankton density, this lesser volume was recorded. Filters were stored at -80 °C until extraction in 90% acetone and spectrophotometric analysis was carried out. The trichromatic method of determination for chlorophyll *a* values was used (American Public Health Association 1998).

Phytoplankton counts and biovolume calculations

For cell counts, 30-60 ml subsamples were immediately preserved in 1% Lugol's solution. 25 ml subsamples settled in a counting chamber for 24 hours were enumerated with a Leitz Diavert inverted microscope. Cells were counted on two transects (crossed diameters of the counting chamber) or, in the case of very abundant species, 5-10 fields of view. Identifications were made to the species level whenever possible, with the aid of experts on the taxonomy of algal groups and the taxonomic literature. Some species encountered are new to science and are in the process of being formally described by systematists. Very small cryptomonad species could not be distinguished from each other under the light microscope and have been combined in the enumerations. Other tiny (< 5 µm) eukaryotic algae and cyanobacteria are present (Wood *et al.* 2002) but the methodology employed here did not allow them to be included in the enumerations as they often do not settle out in settling chambers and are difficult to identify.

Some colonial species were enumerated and reported as colonies, some as cells. Only colonies of *Crucigenia rectangularis* with four clusters of tiny spherical cells (*ca.* 2.5 µm diameter) were enumerated and an average number of cells per colony was determined. Abundance of this taxon was probably underestimated because no single cells or clusters occurring by themselves were included as they would not have been identifiable with certainty. *Oocystis* sp. was also enumerated as colonies. The smaller *Cyclotella* (*C. choctawhatcheeana* Prasad) was not seen in colonies but the larger *Cyclotella* sp., although occasionally seen in chains, was enumerated as individual cells. Likewise, *Thalassionema* sp., sometimes observed in stellate colonies of 2-4 cells, was enumerated as cells.

For the 1997-1999 mid-lake data on numerical densities, biovolume densities and chlorophyll *a* concentrations, geometric means and their standard errors were calculated for the three mid-lake stations (S-1, S-2 and S-3) on those dates when all three stations were visited. Values for the depth interval 0-9 m were determined either by averaging values for the three strata (0-3, 3-6, 6-9 m) or by analysis of a composite of samples from the three strata. On dates when, because of boat problems or bad weather, only one or two stations were sampled, the data for those stations were used.

Because of the presence of some zero values, a constant was added to every value to permit logarithmic transform and calculation of geometric means. This constant was 0.99 cells ml⁻¹, the lowest possible non-zero density given our sampling and counting procedures. Values for the three 3-m depth intervals were combined into a density representing 0-9 m in three ways. On some dates in 1997, the casts from each of the three intervals, 0-3, 3-6 and 6-9 m were physically combined in the field and a subsample then taken. On some dates, the density was evaluated for separate samples from each depth interval and then averaged. In 1999, equal volumes of samples from the 0-3 m and 3-6 m depth intervals at the same station and date were composited and then enumerated, and the 6-9 m sample was counted separately. This was done in order to allow comparison, for the 0-6 m stratum, of phytoplankton densities at the two shallower stations (S-4, S-5; depths *ca.* 7 m) with those of the deeper mid-lake stations (S-1, S-2, S-3). Then the average density over the 0-9 m stratum was calculated giving the 0-6 m value twice the weight than that of the 6-9 m value.

Biovolume densities for major taxa and total phytoplankton were analyzed without the addition of a constant as no zero values were present in those data sets. Cell biovolume was estimated by measuring the linear dimensions of a minimum of 25 individuals and calculating biovolume by approximation to simple geometric shapes (Table 1). These cell biovolumes were used to calculate total biovolume for each major taxon and for total phytoplankton on each date.

Satellite imagery

Satellite imagery gives information on spatial and temporal scales impossible to obtain by boat sampling. Anoxia, fish kills and plankton crashes are often partially correlated with bright green water caused by suspended, highly reflective, gypsum crystals that precipitate during sulfide eruptions (Tiffany *et al.* 2007a). These dramatic “green tide” events are detectable by analysis of imagery of specific wavelengths from blue-green to red. We chose to use data from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) as it was launched in late 1997 during our monitoring study. The best resolution of SeaWiFS images is 1.1 km² at nadir (Hooker *et al.* 1992). This was sufficient to obtain useful information on events in this large lake. SeaWiFS data from the Salton Sea region were obtained for four cloud-free dates (on, or within a day, of boat sampling) from the data access system at Goddard Distributed Active Archive Center (DAAC). These dates were chosen to represent periods of either very high (26 Feb 1998 and 28 Feb 1999) or very low (12 Sep 1998 and 24 Sep 1999) mid-lake algal abundance as determined from our chlorophyll and phytoplankton enumerations. In order to compare images on different dates with seasonally varying sun angles and different view angles from the sensor to the study site, this data was then displayed with the SeaWiFS Data Analysis System (SeaDAS) software package after it was mapped with an orthographic projection and processed to SeaWiFS level-2 (Fu *et al.* 1998; Baith *et al.* 2001). This produced atmospherically corrected images of normalized water-leaving radiances for three wavelengths, 510 nm (blue-green), 555 nm (green) and 670 nm (red).

Results

Seasonal variation in total phytoplankton abundance

Total phytoplankton biovolume densities were extremely high during most of the study, generally above 3 mm³ l⁻¹, and maximal in spring and midsummer (Fig. 2A). Sharp decreases were seen in May and again in August-September of each year. The lowest density measured (~0.5 mm³ l⁻¹) was in September 1999 and the highest densities were in late February to late April 1998 (~14-16 mm³ l⁻¹). The late summer-fall crashes in phytoplankton seemed to reflect sudden mortality events as attested to by the presence, especially in 1999, of many empty diatom frustules at these times.

Chlorophyll *a* values followed the same general pattern as did phytoplankton biovolume (Fig. 2B) with concentrations increasing in spring and minima occurring in September. Chlorophyll *a* concentrations derive from both the eukaryotic phytoplankton reported here and tiny autotrophic cyanobacteria, such as *Synechococcus* sp. and *Synechocystis* sp., which are present in the Salton Sea but for which we have

no abundance data other than those reported by Wood *et al.* (2002).

Phytoplankton biovolume density was generally ~10-fold higher than that of the metazooplankton, which consisted of three rotifers, a copepod and the larvae of a barnacle and a polychaete worm (Figs. 2C, 2D in Tiffany *et al.* 2002). The copepod, a cyclopoid mostly present in summer, has been determined to be *Apocyclops dimorphus* Kiefer rather than *A. dengizicus* Lapeschkin (J. Reid *et al.* 2002), as previously identified by us (Dexter 1993; Tiffany *et al.* 2002). Abundance of the rotifer *Brachionus rotundiformis* increased from late winter and into summer, perhaps in response to increased phytoplankton. Then the population density of the copepod increased with a lag period of a month or two, perhaps in response to both increased phytoplankton and rotifer abundance as cyclopoid copepods are known to feed on both, depending on their size (Fryer 1957). The metazooplankton experienced sudden declines in August or September that coincided with those of the phytoplankton (Fig. 2D).

Gypsum blooms and sulfide-induced crashes

The simultaneous and catastrophic demise of phytoplankton and metazooplankton occurred when, throughout the water column, oxygen concentrations were extremely low and sulfide concentrations were very high (from *ca.* 1 mg l⁻¹ at surface to 5 mg l⁻¹ at depth, Watts *et al.* 2001). Hydrogen sulfide is likely produced in the hypolimnion by dissimilatory sulfate reduction (Finlay *et al.* 1991; Miracle *et al.* 1992). These events were also closely associated with or followed by so-called “green tide” events where the Sea turns from its usual olive or brownish color to a bright pale green as viewed from the boat or satellite (Tiffany *et al.* 2007a). The change in water color appears to be due to suspended gypsum crystals (CaSO₄·2H₂O), strong backscatterers of light across all wavelengths, that form *in situ* in the water column as sulfide is oxidized to sulfate (Watts *et al.* 2001; Swan *et al.* 2007b; Tiffany *et al.* 2007a).

The gypsum signal associated with sulfide eruptions at the Salton Sea is visible from space, may first have been noted and photographed by Gemini 5 astronauts L. Gordon Cooper, Jr. and Charles Conrad, Jr. in August 1965 (<http://science.ksc.nasa.gov/mirrors/images/images/pao/GT5/10074094.jpg>), and is evident in much satellite imagery since then. A companion paper (Tiffany *et al.* 2007a) documents spatial and temporal patterns of these gypsum blooms for the period 1998-2006.

In September of 1998 and 1999, unusually high normalized water-leaving radiances (L_{WN}) were observed by SeaWiFS imagery in large mid-lake patches for the 510, 555 and 670 nm wavebands. This was especially true for the green (555 nm) where values of 3-10 mW cm⁻² μm⁻¹ sr⁻¹ were reached,

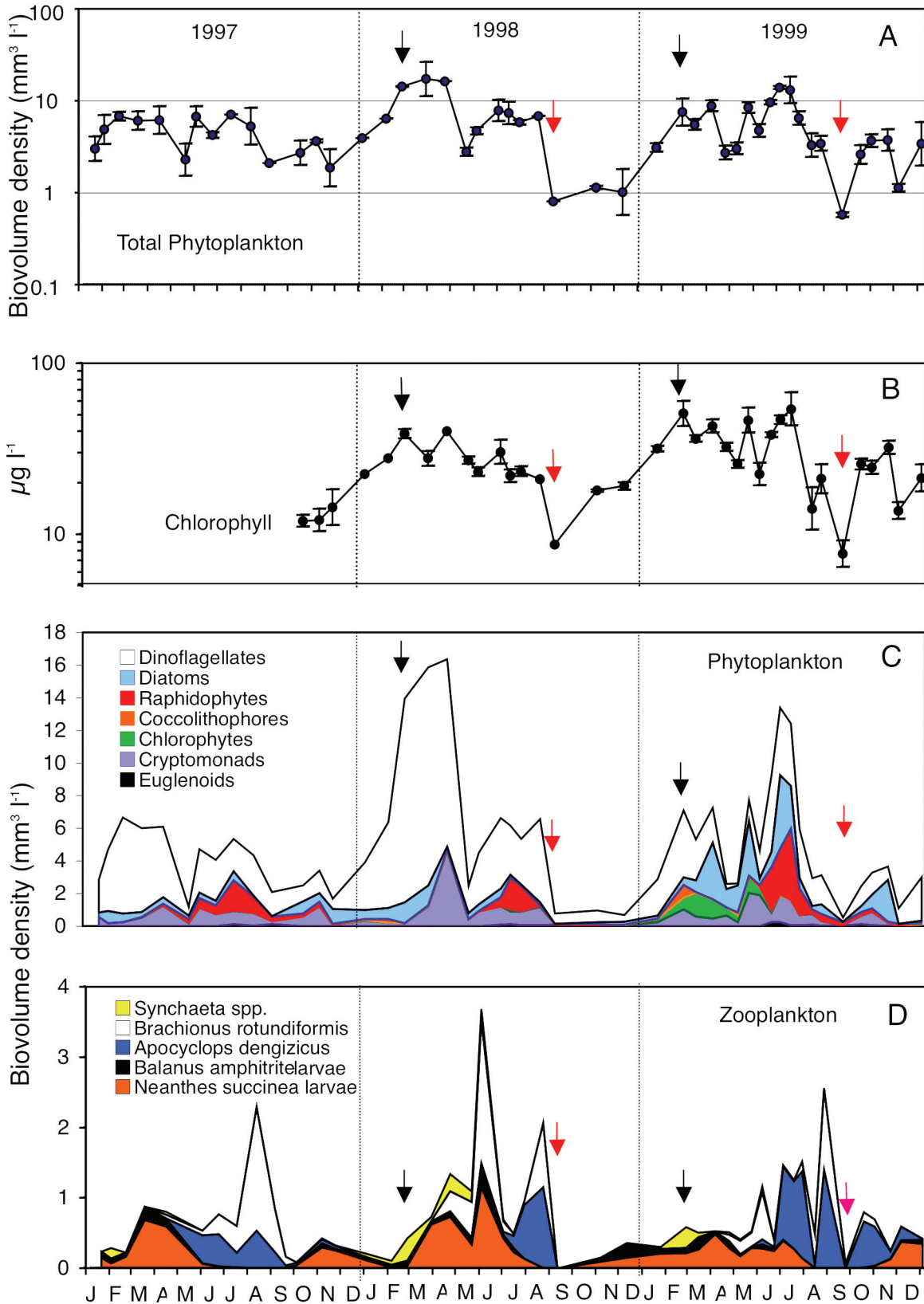


Figure 2.—Geometric mean ($\times/÷$ 1 SEF) plankton densities and chl-a concentrations for three mid-lake stations (S-1, S-2 and S-3), 1997-1999. (A) Total phytoplankton biovolume density. (B) Chl-a concentration. (C) Biovolume densities for seven dominant phytoplankton groups. (D) Biovolume densities for five dominant metazooplankton taxa (from Tiffany *et al.* 2002). Arrows explained in text.

but large signals were also observed in the 510 nm and 670 nm bands (Fig. 3). Negative water-leaving radiances were observed over some parts of the lake (black areas in Fig. 3); these are commonly seen in level 2 images of turbid coastal waters due to continental aerosols and high chlorophyll concentrations (Hu *et al.* 2000). On 12 Sep 1998 (Fig. 2, earliest red arrows), a single station was sampled by boat (S-1 in the northern basin), the water was very green, and recently dead tilapia were common at the surface. The entire water column there was anoxic (Watts *et al.* 2001) and phytoplankton biovolume density was very low ($0.8 \text{ mm}^3 \text{ l}^{-1}$). On 25 Sep 1999, oxygen concentrations at stations S-1, S-2 and S-3 were $< 0.6 \text{ mg l}^{-1}$ at all depths. Phytoplankton biovolume was very low at these stations ($0.6\text{-}1.0 \text{ mm}^3 \text{ l}^{-1}$) relative to what it had been on the preceding sampling date ($4\text{-}11 \text{ mm}^3 \text{ l}^{-1}$) (Fig. 10). Copepod density also showed a dramatic dip on this date at each of these same stations (Tiffany *et al.* 2002: fig. 4). The three mid-lake stations were within the large patch of bright green signal detected by the satellite sensor on 24 Sep 1999, just a day before our field sampling operations (Fig. 3).

It has been suggested that patchy bright signals seen at the Salton Sea are due to algal blooms (Cohn 2000; Jacques Descloitres, MODIS Rapid Response Team, <http://visibleearth.nasa.gov>). To further test this idea, images from late February of 1998 and 1999 (Fig. 2A-C, black arrows), when phytoplankton was especially abundant at the mid-lake stations ($\sim 5\text{-}14 \text{ mm}^3 \text{ l}^{-1}$), were processed and compared to those from September. On these dates (or within one day of these dates) SeaWiFS normalized water-leaving radiances were highest for the 555 nm waveband, reaching values of about $1\text{-}2 \text{ mW cm}^{-2} \mu\text{m}^{-1} \text{ sr}^{-1}$ (Fig. 3). These values, however, are far lower than for the same waveband in mid-lake observed in September of either year at these stations. Somewhat lower radiances ($< 1 \text{ mW cm}^{-2} \mu\text{m}^{-1} \text{ sr}^{-1}$) were observed for the other wavebands, 510 and 670 nm, as expected due to the greater absorption by chlorophyll of these wavelengths (Kirk 1983). So it is apparent that the intense signals observed in September are not due to chlorophyll content of surface waters (see also Tiffany *et al.* 2007a).

Dynamics of individual taxa

Dinophyceae

Dinoflagellates were generally the dominant group except for periods in 1999 when diatoms became unusually abundant (Fig. 2C, 4, 5A, 5B). The former usually accounted for more than 50%, and at times, usually in winter, over 80%, of total phytoplankton biovolume (Fig. 4). The increase in total phytoplankton biovolume in spring was mainly due to increased dinoflagellate abundance. Dinoflagellates were also relatively important in August-September when the overall phytoplankton biovolume density was low.

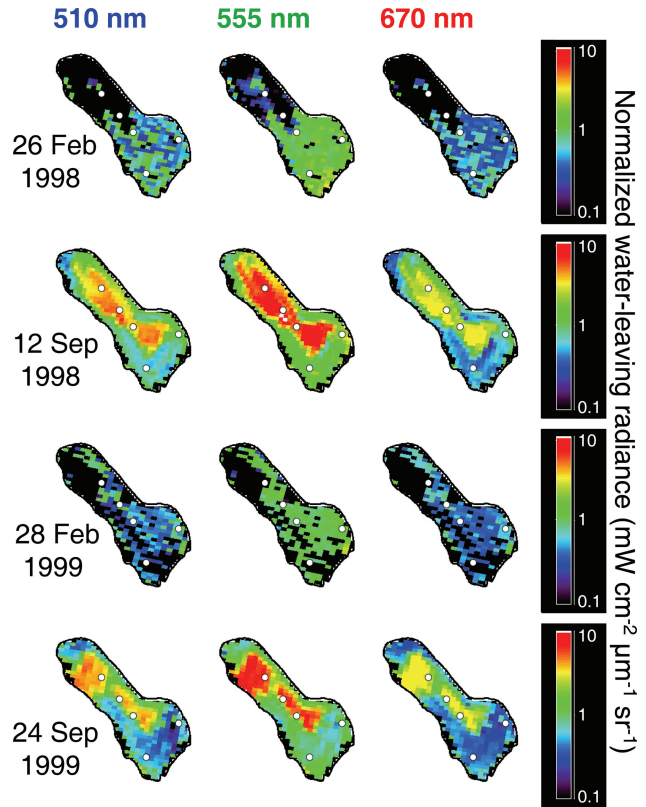


Figure 3.—Normalized water-leaving radiances for three selected wavebands and four dates in 1998 and 1999. Small white circles show location of sampling stations.

Dinoflagellates can be both autotrophic and heterotrophic and may be able to feed on smaller taxa such as cryptomonads, other dinoflagellates and ciliates. Some of the dinoflagellates present in the Salton Sea such as *Protoperdinium brevipes* and *Oblea* sp. have no chloroplasts, *i.e.*, are holozoic, and thus must ingest other organisms (Steidinger and Tangen 1997); others have chlorophyll but may utilize grazing or predation as a supplementary source of nutrition, *i.e.*, are mixotrophic (Kimor 1981; Gaines and Elbrächter 1987).

The particular species present varied seasonally (Fig. 5A) but two dinoflagellate species, *Gyrodinium uncatenum* and a small number of cells of a similar dinoflagellate enumerated along with it, *Gyrodinium instriatum*, often dominated phytoplankton biovolume and were present year-round. Both these species are known to form cysts and are typically found in estuaries (Tyler *et al.* 1982; Coats *et al.* 1984; Anderson *et al.* 1985; Steidinger and Tangen 1997), and the shallow waters of the Salton Sea likely encourage growth of species that produce cysts. *Gyrodinium uncatenum/instriatum* was present year round in high numbers and has a large cell size (Table 1, Figs. 5A and 6A). *Gyrodinium* often accounted for 40-80% of total phytoplankton biovolume, especially in

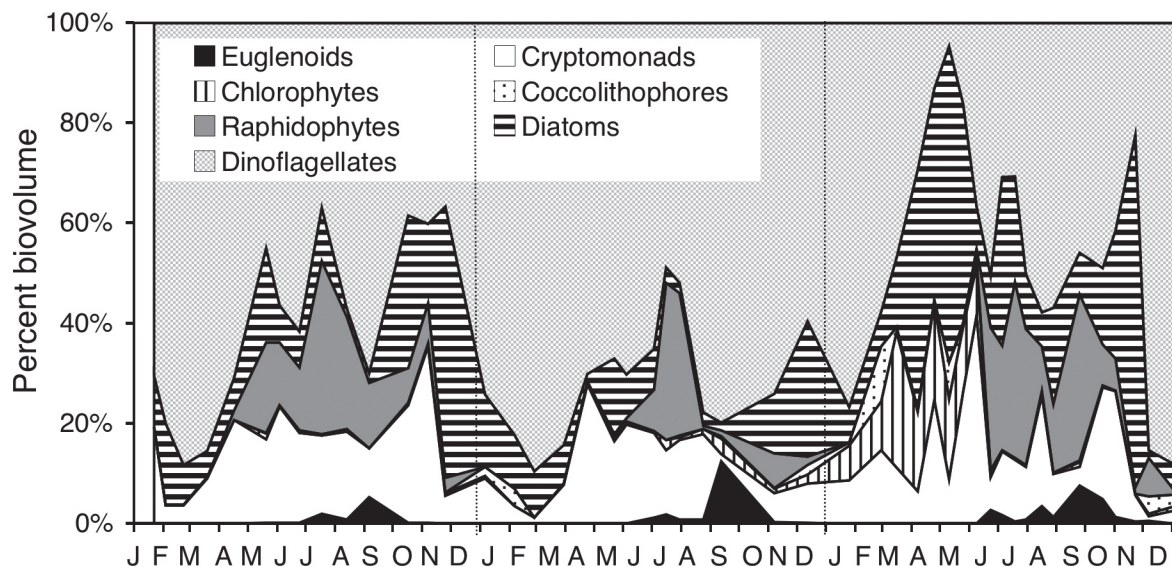


Figure 4.-Percent composition of phytoplankton by major taxa, 1997-1999, for three mid-lake stations (S-1, S-2 and S-3).

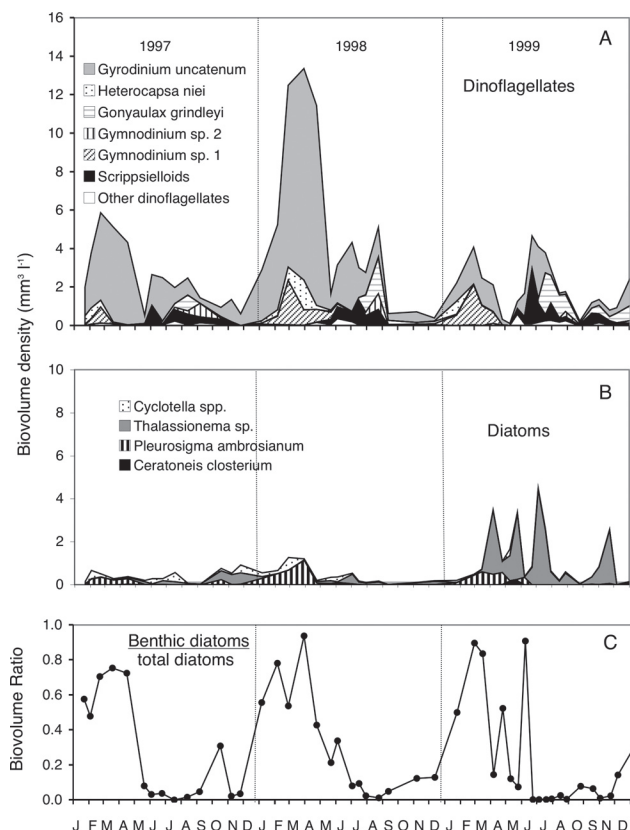


Figure 5.-Dinoflagellates and diatoms at the three mid-lake stations (S-1, S-2 and S-3), 1997-1999. (A) Biovolume densities for dominant dinoflagellate taxa. (B) Biovolume densities for dominant diatom taxa. (C) Ratio of benthic diatom biovolume to total diatom biovolume.

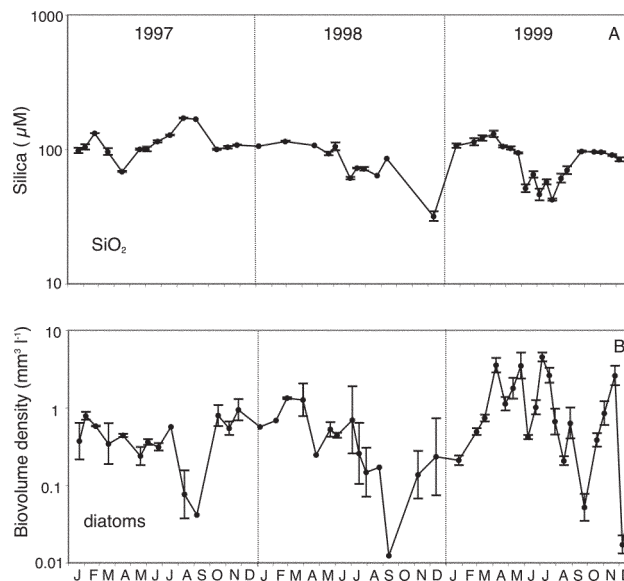


Figure 6.- (A) Geometric mean silicon concentration (\times/\div 1 SEF), top 12 m of the water column. (B) total mean mid-lake diatom biovolume density for three mid-lake stations (S-1, S-2, and S-3), in 1997-1999.

winter and spring. In 1998 *G. uncatenum/instriatum*, along with *Gymnodinium* sp. 1 and *Heterocapsa niei*, two other dinoflagellate taxa usually found in spring, became unusually abundant (Table 1, Figs. 5A, 7A). Unusually windy conditions characterized the spring of that year and the water column heated more rapidly than in 1997 or 1999 (Watts *et al.* 2001: fig. 2C).

Heterocapsa niei, a dominant species in the 1950s (Carpelan 1961a), was most abundant January to March each year and was often present at other times of year in much reduced numbers (Figs. 5A and 7F). It became very abundant at times, with mean densities up to 8,390 cells ml⁻¹, but, due to its small size (Table 1), did not usually make a large contribution to total phytoplankton biovolume (Fig. 5A). This species, cosmopolitan in both temperate and tropical marine waters, is known to form blooms in estuarine systems from spring to fall (Steidinger and Tangen 1997). In the Salton Sea it has been reported in densities as high as 310,000 cells ml⁻¹ (Reifel *et al.* 2001) and sometimes made up > 99% of the biovolume in nearshore samples (Reifel *et al.* 2002).

Another dinoflagellate found in winter was *Gymnodinium* sp. 1 (Figs. 5A and 7B). This species became undetectable in summer and fall. In contrast, *Gymnodinium* sp. 2 appeared to be primarily confined to August-November (Figs. 5A and 7C). It is relatively large (Table 1), but never became especially abundant.

Oblea sp., an armored heterotrophic species, mostly occurred in the first six months of each year but was never abundant. This genus is known to produce cysts (McQuoid *et al.* 2002).

Every August a dominant phytoplankton was the very large *Gonyaulax grindleyi* (Table 1, Figs. 5A and 7E). Interestingly, we found high densities of this species in the Salton Sea in February 2003 (up to 2,240 cells ml⁻¹ in surface samples). Therefore its near absence during January-June 1997-1999 is not likely due to an inability to thrive under the physical conditions of winter and spring. It can form red-tide blooms (Reinecke 1967), forms cysts (Steidinger and Tangen 1997), and is known to produce yessotoxins (Satake *et al.* 1997, 1999).

Scrippsielloid dinoflagellates, mostly represented by *Scrippsiella trochoidea*, were commonly found from May-October (Figs. 5A and 7D). *S. trochoidea* is cosmopolitan in marine environments and produces calcareous cysts. A species of *Pentaparsodinium* has been detected in the Salton Sea and may have contributed to this category, as well as may have other armored species such as *Bysmatrum* sp. and a possibly undescribed dark thecate species (Karen Steidinger, personal communication).

Other dinoflagellates present contributed little to total biovolume due to their small size or low numbers (Fig. 5A). These included *Oxyrrhis marina* (Fig. 7G), reported to be common in intertidal rock pools (Johnson 2000), *Prorocentrum minimum* (Fig. 7H), *Gonyaulax spinifera* (Fig. 7I), a known cyst-former (Dale 1983), *Protoperidinium brevipes* (Fig. 7K), *Gonyaulax cf. turbynei* (Fig. 7L), *Amphidinium cf. operculatum* and small, unidentified dinoflagellates < 20 µm length. Most of these were most abundant in summer.

Bacillariophyceae

Diatoms were important members of the phytoplankton, sometimes representing > 60% of total phytoplankton biovolume (Fig. 4). Planktonic diatoms were likely never limited by silica, as they are at times in many eutrophic marine systems such as Chesapeake Bay (Conley and Malone 1992), as mean silica concentration was always greater than 30 µM and more often closer to 100 µM (Fig. 6). These concentrations are well above those (*ca.* 2-5 µM) that potentially limit diatom growth (Conley and Malone 1992; Egge and Aksnes 1992; Dugdale *et al.* 1995). There was an increase in abundance and relative importance of diatoms over the three-year period (Figs. 2C, 4 and 5B). This was largely due to a single species, *Thalassionema* sp., that became extremely abundant in 1999. The huge increase in diatom biovolume density in mid-1999 appears to have caused a concomitant drop in silica concentration (Fig. 6). Silica concentrations were in the range of 100-120 µM in April-May but dropped to 40-50 µM in June-May 1999.

Thalassionema has previously been regarded as an exclusively marine genus (Grete Hasle, personal communication). The *Thalassionema* found in the Salton Sea is morphologically similar to *Thalassionema frauenfeldii* (Grunow) Grunow (Lange and Tiffany 2002). Occasionally it was found in stellate colonies, but was more often seen as solitary cells. *Thalassionema* sp. was often dominant in the plankton, at times comprising about 30-70% of total phytoplankton biovolume (Figs. 5B, 8A). After the late summer mixing events, most of the few intact frustules of *Thalassionema* sp. in the water column appeared to have abnormally small, "pinpoint" chloroplasts and probably were moribund or dead. Sudden fluxes to the sediment of siliceous diatom cell walls must occur on these occasions and "diatom graveyards," sediment layers up to 1 cm thick consisting 80-90% of this diatom, have been observed in laminated sediments from the Sea (Fig. 12). This particular massive deposit of *Thalassionema* sp. valves came from a core collected in June 1999 and lay 85 mm below the sediment surface. These valves may well be from a 1998 mortality event, possibly the one we documented on 12 Sep 1998.

The second most abundant diatom, *Pleurosigma ambrosianum*, was abundant in the winter and spring but, due to the

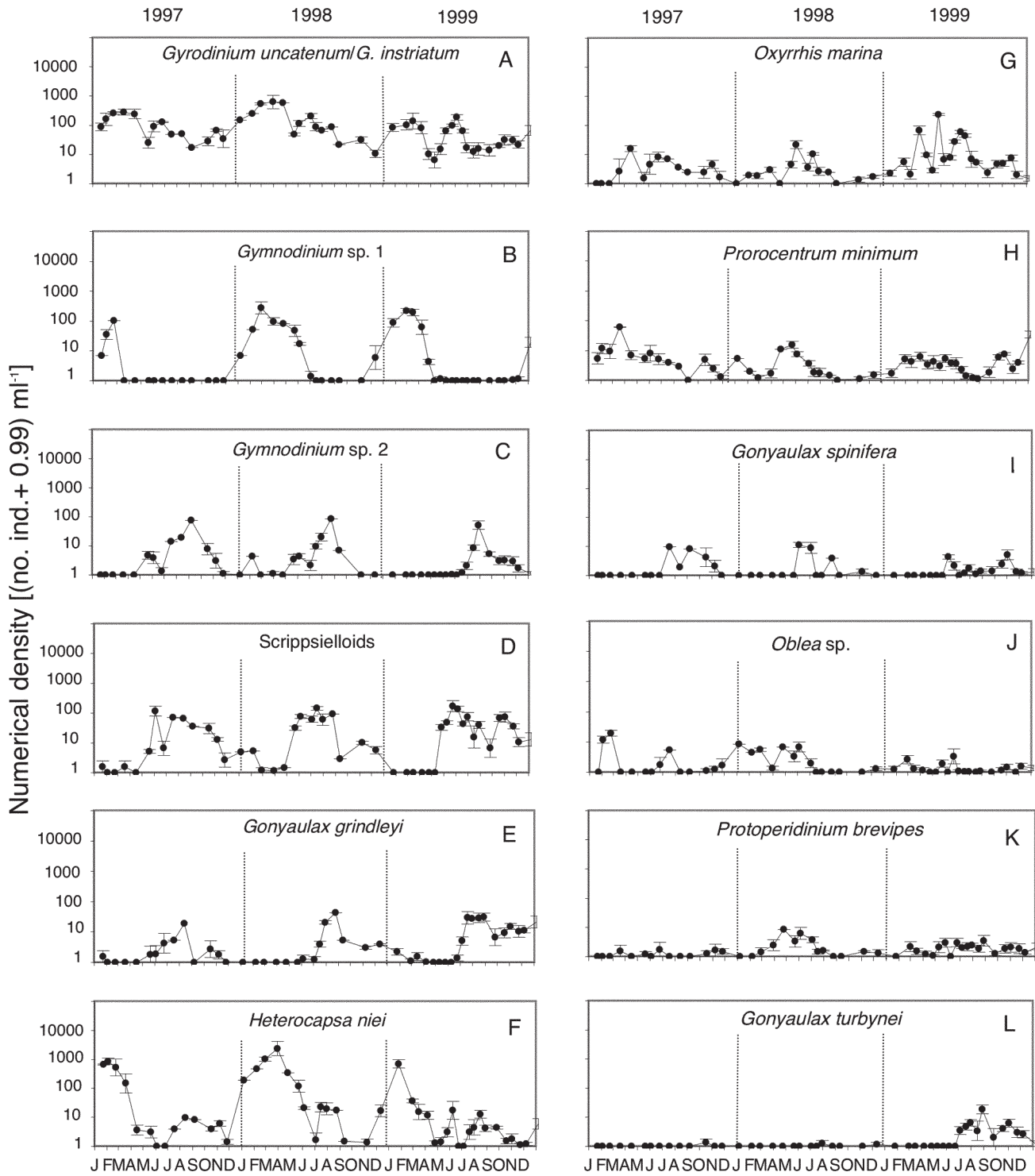


Figure 7.-Numerical densities (geometric mean $\times \pm 1$ SEF) of individual dinoflagellates at three mid-lake stations, 1997-1999.

Phytoplankton dynamics in the Salton Sea, California, 1997-1999

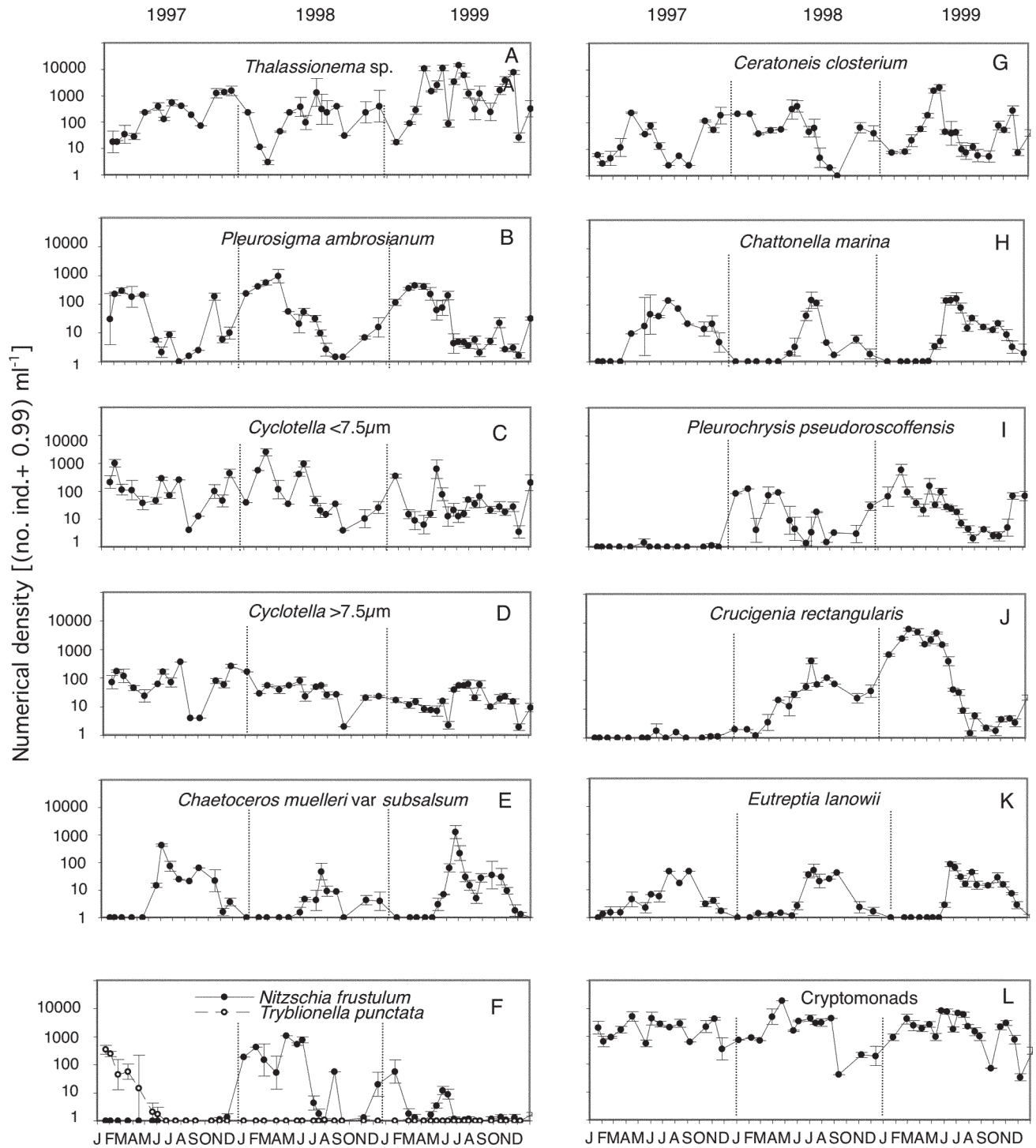


Figure 8.-Numerical densities (geometric mean \times/\div 1 SEF) of individual diatoms and other common taxa at three mid-lake stations, 1997-1999.

large number of dinoflagellates present then, never made up more than 20% of total phytoplankton biovolume (Figs. 5B, 8B). *Pleurosigma* species are usually considered benthic but are occasionally found in plankton (Round *et al.* 1990; Sterrenburg *et al.* 2003). *P. ambrosianum* may be able to maintain a planktonic population in winter due to the greater degree of mixing then and to its lightly silicified valves (Sterrenburg *et al.* 2000; Lange and Tiffany 2002). *Pleurosigma* species are sometimes recorded in marine plankton samples (Sterrenburg *et al.* 2003). Sterrenburg *et al.* (2003) speculated that *P. gracilitatis* Sterrenburg, Meave et Tiffany, common off the Pacific coast of Mexico, and *P. ambrosianum*, both lightly silicified diatoms, might use oil or gas bubbles to stay in the euphotic zone as well as kept in suspension by wind-mixing.

Other than some freshwater *Cyclotella* species, presumably washed in by rivers (Lange and Tiffany 2002), the genus *Cyclotella* was represented by two species, *C. choctawhatcheana* and *Cyclotella* sp. These were combined in the biovolume estimates because they overlap in size and have very similar appearance under the light microscope. Together these two species occasionally made up a significant portion of the diatom biovolume, *e.g.*, in summer 1997 and the first half of 1998 (Fig. 5B). *Cyclotella* cells < 7.5 µm, and therefore likely to be *C. choctawhatcheana*, were often abundant in spring, especially in 1998 (Fig. 8C). *Cyclotella* cells > 7.5 µm, most of which are probably *Cyclotella* sp., achieved their highest density in July 1997 and showed a tendency to decrease in abundance over the three-year period (Table 1, Fig. 8D). A recent increase in *C. choctawhatcheana* in surface sediments has been correlated with increasing cultural eutrophication in Chesapeake Bay (Cooper 1995) and the Baltic Sea (Weckström *et al.* 2004).

Other diatom species commonly found were either extremely small or had low numbers in the plankton. One of the small species, *Chaetoceros muelleri* var. *subsalsum*, possesses long setae and is often found in saline or brackish inland waters (Johansen and Rushforth 1985). It was detected primarily in warm months and vegetative cells of this species sometimes became very abundant (Fig. 8E). It likely overwinters as spores (Johansen and Rushforth 1985), and resting spores of this species were occasionally seen in the plankton and also in sediments of the lake (Lange and Tiffany 2002).

Ceratoneis closterium, a weakly silicified species commonly found in coastal marine habitats (formerly *Cylindrotheca closterium*, Jahn and Kusber 2005), was found throughout the year, though was scarce in late summer (Fig. 8G). This species, usually considered benthic, has formed blooms in a bay of the Black Sea with densities up to 7,400 cell ml⁻¹ (Turkoglu and Koray 2004).

Other diatom species usually described as benthic were found in the plankton in winter. *Tryblionella punctata* was

seen solely during January-March 1997 (Fig. 8F), and the very small *Nitzschia frustulum* in winter to early summer of both 1998 and 1999 (Fig. 8F). Two species of *Fallacia*, *Fallacia pygmaea* (Kützing) A.J. Stickle and D.G. Mann and *F. forcipata* (Greville) A.J. Stickle and D.G. Mann, indistinguishable under the light microscope and both present in the Salton Sea (Lange and Tiffany 2002), were detected sporadically in very low numbers. Presumably, these more heavily silicified diatoms, like *Pleurosigma ambrosianum*, could be maintained in the water column by the greater degree of mixing by wind and convectional mixing that occurs mostly in winter.

An indication of the effect of mixing was seen in the ratio of benthic diatom biovolume to total diatom biovolume in the phytoplankton samples. Species typically considered planktonic included: the two *Cyclotella* species, *Thalassionema* sp. and *Chaetoceros muelleri* var. *subsalsum*. Species typically considered benthic or epipelagic were: *Pleurosigma ambrosianum*, *Ceratoneis closterium*, *Tryblionella punctata*, *Nitzschia frustulum* and the two *Fallacia* species. This ratio varied seasonally with the highest value each year in late winter and lowest in June or July (Fig. 5C).

Raphidophyceae

The raphidophyte, *Chattonella marina*, is a large motile phytoplankter with two flagella and no cell wall. Some authorities believe *Chattonella* species are favored by stratification (Ono *et al.* 1999; Waite and Lindahl 2006) such as occurs during summer in the Salton Sea. This potentially toxic species was first noted in the Salton Sea when it was detected in high densities in summer of 1997 (Tiffany *et al.* 2001). It usually began to make its appearance in May or June of each year (Fig. 8H). It constituted about 20-30% of the total phytoplankton biovolume during most of the warmer months (Fig. 4). It was not observed from January to March or April. In 1997, *C. marina* appeared early and maintained dense populations from May to November, whereas in 1998 its density was only high in June and early July. Generally warmer water temperatures in early spring 1997 may have caused *Chattonella marina* to appear sooner that year (Fig. 8H). *C. marina* forms cysts that reside in the sediments (Imai and Itoh 1987). It is thought that excystment of this species is dependent on bottom water temperatures warming to a particular temperature (perhaps about 20 °C). The lake was more highly stratified during March-May 1997, probably due to lower wind speeds, and temperatures in the upper strata were higher than in 1998 or 1999. Nearshore, in areas with shallow depths, bottom temperatures thus rose earlier in 1997 than in 1998 and 1999. These areas could have seeded the *Chattonella* populations lake-wide. The presence of this alga is known to have an adverse effect on fish populations, however a connection to Salton Sea fish kills has not been

definitively made (Tiffany *et al.* 2002). *C. marina* generally disappeared by January.

Prasinophyceae

Tetraselmis sp. was sometimes seen nearshore, in Varner Harbor and in shoreline pools at densities up to 3,500 cells ml⁻¹ but was not detected in mid-lake phytoplankton samples. Many species of *Tetraselmis* are coastal or found in salt marshes and tide pools (Thronsen 1997).

Prymnesiophyceae

A coccolithophore, *Pleurochrysis pseudoroscoffensis*, was first noted in nearshore sediment samples in 1997. This species is known to have a benthic pseudofilamentous stage (Gayral and Fresnel 1983). During January-April 1998 it was seen in the plankton in low numbers (Fig. 8I). In 1999 it became fairly abundant February through May and was increasing again in December 1999 at the end of our study (Figs. 2C, 4 and 8I). *P. pseudoroscoffensis* had a tendency to form extensive films or scums on the water surface, as we first observed in early 1999 (Reifel *et al.* 2001; 2002), about the same time high densities were first observed in the plankton. Other prymnesiophytes, *Chrysochromulina* sp. and a *Prymnesium*-like form, were seen in low numbers in live samples (Karen Steidinger, personal communication) but were not detected in phytoplankton enumerations.

Chlorophyceae

Non-motile chlorophytes were seen in low numbers in 1997-1998. In 1999 there was an extensive bloom of *Crucigenia rectangularis* lasting from January to June that constituted up to 20% of total phytoplankton biovolume during that period (Figs. 4 and 8J). *Oocystis* spp. were consistently seen in the plankton but always in low numbers, generally < 20 colonies ml⁻¹, except on 25 April 1999 when its density ranged from 60-140 colonies ml⁻¹. No motile green algae were detected in the plankton during 1997-1999. Species of the genus *Dunaliella*, commonly found in saline habitats, were not seen in plankton samples but occasionally were observed in hypersaline pools adjacent to the Salton Sea. *Dunaliella* spp. may not be favored in phosphorus-limited environments (Javor 1989).

Euglenophyceae

Only one euglenoid, *Eutreptia lanowii* was observed in the phytoplankton during 1997-1999 (Figs. 2C, 4, 8K) although several other species, *Eutreptia viridis* Perty and the colorless *Astasia* sp. were occasionally found nearshore. The colorless *Pleuronema* sp. was probably also present in the plankton in 1999 (Eugene Small, personal communication) but was not recognizable in the Lugol's solution-preserved

samples. *Eutreptia lanowii* contributed significantly to total phytoplankton mostly at times of minimum phytoplankton biovolume (Fig. 4), perhaps because it, relative to other phytoplankters, was less sensitive to high sulfide levels likely to have been present then. This species was a dominant during a fish and invertebrate kill in 1988 when hypoxic conditions prevailed in Sandy Hook Bay, Hudson-Raritan Estuary, New Jersey (R. Reid *et al.* 2002). It has also been reported in bloom densities in the Black Sea, associated with eutrophication (Bodeanu and Ruta 1998).

Cryptophyceae

At least eight cryptomonad species are known to inhabit the Salton Sea (Barlow and Kugrens 2002). Due to their small size and the fact that scanning electron microscopy is necessary to differentiate them (Barlow and Kugrens 2002), they have been combined in this analysis. Even though very small (usually in the range of 5-15 µm in length), cryptomonads occasionally contributed up to 20-30% of total phytoplankton biovolume as they were often the most numerous taxon, with densities ranging up to 18,000 cells ml⁻¹ (Table 1, Figs. 2C, 4, and Fig. 8L).

Ebriidea

Ebriidians are a marine group of uncertain classification, possibly related to dinoflagellates, with two flagella and an internal siliceous skeleton. No *Hermesinum adriaticum*, the sole ebriidian known from the Salton Sea, were seen in routine plankton samples although they have been observed in high density in the past (Carpelan 1961a; A. Loeblich III, personal communication). Skeletons of this taxon were found, however, in surficial sediments as well as in a qualitative plankton sample prepared for scanning electron microscopy. It may be extant in the Sea but, if so, in densities lower than detection limit of our sampling protocols (Tiffany 2002).

Cyanobacteria

Small prokaryotic unicells, such as *Synechococcus* sp. and *Synechocystis* sp. were very likely present as these have been observed in shoreline plankton samples at the Salton Sea (Wood *et al.* 2002), but our method did not permit their enumeration. Filamentous cyanobacteria, such as *Oscillatoria* sp., *Geitlerinema* sp. and *Lyngbya* sp. were very rarely encountered mid-lake and appear to have been almost completely restricted to benthic nearshore environs during our study.

Spatial variation

Phytoplankton abundance generally varied in a similar way at all five stations during 1999 (Figs. 9 and 10). It increased

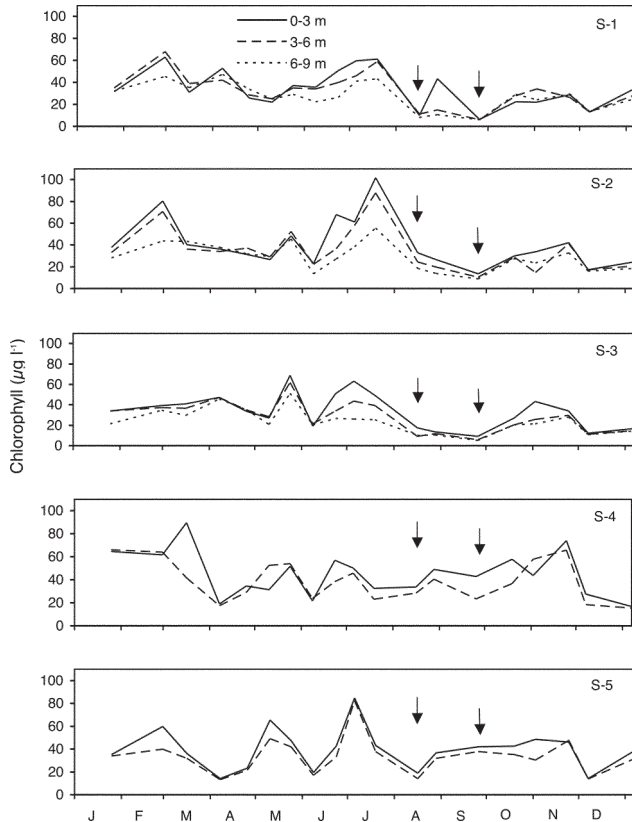


Figure 9.-Chl-*a* concentrations, by stratum, at five stations in 1999. Arrows discussed in text.

from late January to early April, the spring bloom period, and decreased in late April. All five stations experienced an order of magnitude decrease in phytoplankton biovolume density from mid-November to mid-December.

On several dates in January, March and April 1999, phytoplankton biovolume density at station S-4 was two to four times higher than that at the other four stations (Fig. 10). This station is downcurrent of the mouths of the New and Alamo Rivers and likely receives fresh nutrients from these sources, stimulating phytoplankton growth there (Reifel *et al.* 2007).

Major crashes in phytoplankton abundance sometimes hit certain stations and not others. This phenomenon was detected on two dates in 1999 (arrows in Figs. 9 and 10). On 16 Aug, stations S-1, S-3 and S-5 had lower mean phytoplankton biovolume and surface chl-*a* than did stations S-2 and S-4 (arrows in Figs. 9 and 10). Surface oxygen concentrations (0-2 m) on that date were $\leq 3 \text{ mg l}^{-1}$ at stations S-1, S-3 and S-5 and *ca.* 6 mg l^{-1} both S-2 and S-4 (Watts *et al.* 2001; Tiffany *et al.* 2002: fig. 4). Density of copepodites of *Apocyclops dimorphus* also was very low at the stations with lower oxygen concentrations.

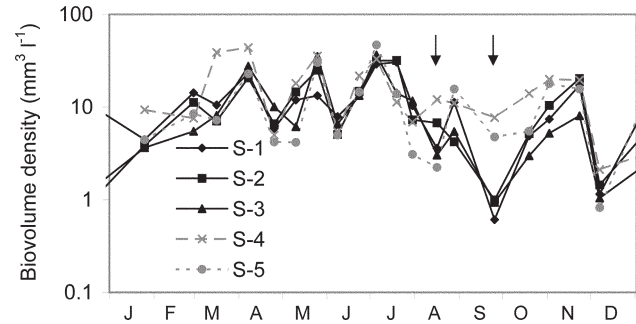


Figure 10.-Phytoplankton biovolume density (0-6 m) for five stations in 1999.

On 25 Sep 1999, phytoplankton abundance crashed at the three mid-lake stations (S-1, S-2 and S-3) but remained high at the shallow, better-oxygenated stations (S-4 and S-5). Surface oxygen concentrations at stations S-4 and S-5 were 16.6 and 5.9 mg l^{-1} respectively while most of the water column at stations S-1, S-2 and S-3 was anoxic and surface oxygen concentrations only ranged from 0.27 to 0.61 mg l^{-1} . Massive concurrent mortality of mid-lake zooplankton occurred at these three stations (but not at the shallow stations) with the density of *Apocyclops dimorphus* copepodites dropping by about three orders of magnitude from the previous sampling date (Tiffany *et al.* 2002: fig. 4). There was little or no evidence of zooplankton or phytoplankton mortality at the shallow stations, S-4 and S-5. *Thalassionema* sp. was the most abundant diatom in mid-lake waters just before the anoxic event; the many empty valves of *Thalassionema* sp. seen in mid-lake samples from 25 Sep 1999, provided further evidence of sudden demise of phytoplankton.

On a lake-wide basis the presumed areal extent and location of anoxic surface waters during the warm season can be detected using the gypsum crystal signal as seen by satellite (Tiffany *et al.* 2007a). SeaWiFS imagery obtained for 24 Sep 1999, just a day before our field sampling, showed about 50% of the lake surface exhibited a very intense signal ($3\text{-}10 \text{ mW cm}^{-2} \mu\text{m}^{-1} \text{ sr}^{-1}$ at 555 nm) (Fig. 3). The three mid-lake stations were within the bright region, while stations S-4 and S-5 were well outside of it. At and surrounding these shallow stations, relatively low water-leaving radiances prevailed for all three wavebands ($\leq 1 \text{ mW cm}^{-2} \mu\text{m}^{-1} \text{ sr}^{-1}$). Normalized water-leaving radiances at stations S-4 and S-5 spectrally resembled those seen lake-wide in February 1998 and 1999 and appear to be typical of Salton Sea waters laden with phytoplankton. On 24 Sep 1999, rather than being restricted to the middle of the lake, the northwest shore of the lake appears to have been also affected by sulfide and/or anoxia as evidenced by the gypsum signal there (Fig. 3). Advected shoreward, these waters may cause mortality of benthic or sessile organisms such as the polychaete worm *Neanthes succinea* Frey and

Leukart or the barnacle, *Balanus amphitrite* Darwin (Dexter *et al.* 2007).

Discussion

Our findings bear on a number of phenomena and issues. These include the origin of this phytoplankton assemblage, the paucity of cyanobacteria, the influence of polymixis, turbulence, sulfide events and grazers on phytoplankton dynamics. Brief analysis of these follows.

Origin of Salton Sea species

As is the case of many microbial groups present in the Salton Sea most of its phytoplankton species appear to be of coastal marine origin. The source of at least some of the species is likely to have been ocean waters introduced with the stocking of game fish into the lake in the 1940s and 1950s. Also, migratory birds, attracted by the productivity of the Sea, can carry algal cysts and live cells on their feet or feathers. Some species important in the Salton Sea in 1997-1999, especially *Chattonella marina* and some dinoflagellates, have not been reported from it in past studies and may have arrived via this route. On the other hand, the total volume of lake water examined for phytoplanktoners in ours and all previous studies is on the order of 1 L while the volume of the Sea is $\sim 8 \times 10^{12}$ L. Thus there doubtless are many species long resident in the Salton Sea that never have been detected – and never will be.

A number of phytoplankton species observed form cysts or resting stages that can reside for months in the sediments and return to the water column when conditions are favorable. Neritic phytoplankton species with a phase residing in sediment should be favored in this shallow lake over those lacking these (Taylor 1980). Dinoflagellate cysts and *Chaetoceros* resting spores have been observed in the Salton Sea sediments and occasionally in its plankton. *Chattonella marina* is a known cyst-former and has recently been reported from the Pacific coast of Mexico and the Gulf of California (Band-Schmidt *et al.* 2004), the latter a likely source for the Salton Sea population of this delicate species.

Smayda and Reynolds (2001, 2003) proposed rules of community assembly for marine dinoflagellates along gradients of nutrient and light availability. According to their scheme, under conditions of ample nutrients and light, intermediate-sized gymnodinioids and peridinioids/prorocentroids (their types I and II) should be favored. These encompass many of the dinoflagellate species found in the Salton Sea. They also suggest that the particular species within a group which succeeds in producing planktonic blooms is stochastic, depending on instantaneous availability in the species pool and aperiodic excystment of species from the sediments (their Assembly Rule V). Thus, the “winning” dinoflagellate species

during a bloom in the Salton Sea may be one which happens to have cysts available with an appropriate dormancy period and excystment temperature requirements.

Eukaryotes vs. prokaryotes

Quantitative enumerations of unicellular planktonic cyanobacteria in the Salton Sea have only been determined in a single study, in 1999 (Wood *et al.* 2002). Assuming cell diameters of $\sim 2 \mu\text{m}$ and using densities reported by Wood *et al.* (2002), nearshore samples had a cyanobacterial biovolume density on the order of $0.02 \text{ mm}^3 \text{ l}^{-1}$. This is less than 1% of the usual biovolume density of eukaryotic phytoplankton (cells $\geq 5 \mu\text{m}$) in the Salton Sea, which ranged from about $1\text{-}16 \text{ mm}^3 \text{ l}^{-1}$ (Fig. 2A). Interestingly, in spring 2005 filamentous cyanobacteria (*Oscillatoria*, *Arthrospira* and *Geitlerinema*) became a dominant group in the mid-lake phytoplankton representing 3-10% of the phytoplankton biomass (Anderson *et al.* 2007). Cyanotoxins (microcystins) from picoplanktonic *Synechococcus* and filamentous cyanobacteria were reported in samples collected in 1999-2001 mostly near river outflows and near shore (Carmichael and Li 2006).

In contrast, planktonic cyanobacteria often make up 15-90% of the total phytoplankton biomass in estuaries such as San Francisco Bay (Ning *et al.* 2000), Neuse River, North Carolina (Pinckney *et al.* 1998) and Pensacola Bay, Florida (Murrell and Lores 2004). Iriarte and Purdie (1994) suggest that cyanobacteria are less important in eutrophic than oligotrophic temperate estuaries. The Salton Sea certainly is more similar to the former category.

Wind, polymixis and nutrient resupply

As a wind-driven, discontinuous warm polymictic lake the Salton Sea and all processes and populations in it exhibit very dynamic behaviors. During fall and winter thermal stratification is minimal and the water column well mixed by convective circulation even in the absence of strong wind (Watts *et al.* 2001). It is weakly thermally stratified most of the time during spring, summer and early fall though experiencing sporadic complete mixing events during those seasons in response to strong winds. It is the highly variable strength and irregular timing of wind events that make seasonal succession and year-to-year differences so unpredictable in such a lake.

The dramatic observed differences among the three years in total phytoplankton and in abundances of individual species were, in part, a reflection of this phenomenon. Some species appeared to increase over the three-year period, some decreased, and some were most abundant in 1998 (Table 1). 1998 had the highest spring densities of both phytoplankton and metazooplankton. That year was exceptionally windy in spring and the lake warmed faster in spring as a consequence

(Watts *et al.* 2001). Increased availability of nutrients and an accelerated metabolism in warmer water would be expected to increase phytoplankton production. *Gyrodinium uncatenum/instriatum*, *Heterocapsa niei*, *Gymnodinium* sp. 1, and *Cyclotella* spp. all achieved higher densities in March 1998 than they did in March of 1997 and 1999 (Figs. 5A, 5B), contributing to the high biovolume.

According to Margalef's "Mandala" schematic (1978, 1979) high nutrient-low turbulence conditions favor dinoflagellates, while the opposite conditions favor diatoms. High turbulence seems to adversely affect division of dinoflagellate cells (Sullivan *et al.* 2003). In tropical lagoons in Belize, with conditions of low turbulence, high nutrients and higher temperatures and salinities than the surrounding ocean waters, dinoflagellates dominate as predicted by Margalef (Faust *et al.* 2005). Phytoplankton in the Salton Sea, however, seems to behave differently. Dinoflagellates dominated the Salton Sea most of the time, even during times when turbulence is likely to have been high (winter and spring before stratification). A diatom, *Thalassionema* sp., dominated during stratified, lower turbulence periods, especially in summer, 1999. One reason for this reversal of the "Mandala" may be that active feeding on large algal cells by the planktivorous fish, tilapia, occurs primarily in the warmer seasons due to the physiology of the fish. Smayda (2000) suggested that not all dinoflagellate blooms in coastal upwelling regions adhere to traditional theories of phytoplankton community assembly, especially in regions such as the Southern Benguela current with its great temporal variability in wind-driven upwelling (Pitcher and Boyd 1996).

Diatoms usually considered benthic were often found in mid-lake phytoplankton samples. The phenomenon of benthic species occurring in the plankton (tychoplankton) may result from strong wave action and turbulence in nearshore waters where large populations of benthic diatoms have been observed in the Salton Sea (Lange and Tiffany 2002). These cells then become available to herbivores within the water column.

Although the Salton Sea water column was usually stratified in summer, which could lead to nutrient depletion in upper strata, occasional strong windstorms broke down stratification for short periods (Watts *et al.* 2001). Heat was injected into deeper strata (*e.g.*, > 12 m) as evidenced by the gradually increasing temperatures at depth throughout the spring and summer (Watts *et al.* 2001). This presumably allowed nutrients to be brought up intermittently from bottom waters, and that, combined with the relatively steady influx of agricultural wastewaters, made nutrient depletion in the euphotic zone an improbable explanation for reduced phytoplankton densities observed in fall.

Influence of sulfide irruptions

Sudden mass mortality of plankters and other organisms, and the irregularity of sulfide events, make the dynamics of this system very unpredictable. High sulfide conditions may persist in this lake for days. Sulfide is quite toxic to most aerobic organisms (Theede *et al.* 1969; Bagarinao 1992). For example, Admiraal and Peletier (1979) found that > 90% of cells of a common Salton Sea diatom, *Ceratoneis closterium*, were killed by sulfide concentrations of 2.9 mg l⁻¹ in 48 h.

Relatively rapid recovery of phytoplankton populations from sulfide events in the Salton Sea may often occur because, during any one event, only a portion of the lake experiences these conditions, as evidenced by satellite imagery (Fig. 3). Mixing and advection from unaffected areas allows the inoculation of phytoplankters into depleted mid-lake regions. Algal cells can multiply rapidly in the warm waters and quickly re-establish the plankton communities after sulfide levels subside. Death and decomposition of phytoplankters, zooplankters and even fish also release nutrients into the water column. Indeed, by 19 Oct 1999, mid-lake mean phytoplankton biovolumes and chl-*a* concentrations had rebounded to levels similar to those observed on 29 Aug 1999 before one of the crashes occurred (Figs. 2A-C), and even the slower-growing zooplankton experienced some measure of recovery in mid-lake by same date (Fig. 2D).

Similar sulfide irruptions, accompanied by anoxia and massive plankton mortality, have been documented in at least two other systems. At a eutrophic, steep-sided, meromictic, coastal salt lake in Croatia, Lake Rogoznica, anoxic sulfide-laden waters from the monimolimnion are brought up to the surface on rare occasions. The halocline usually present in this lake breaks down, and a whitish color is imparted to the lake, reportedly by elemental sulfur particles (Krišnić *et al.* 2000; Barić *et al.* 2003). In September 1997, phytoplankton and zooplankton populations crashed dramatically during such an event and essentially the entire phytoplankton community perished; no nearshore, shallow water refuge from sulfide was available from which survivors could quickly disperse to re-establish populations as is the case for the Salton Sea. An atypical community of "microflagellates" developed after the crash rather than the more typical diatom and dinoflagellate assemblage.

Sulfide irruptions (H₂S concentrations as high as 0.11 mg l⁻¹ at the surface and 3.4 mg l⁻¹ at 13 m) and anoxic events (surface oxygen concentration as low as 0.9 ml l⁻¹) also occur in marine waters off Namibia, Africa, near the upwelling zones of the Benguela Current (Weeks *et al.* 2004; Bakun and Weeks 2004). These events cause great mortality of fish and invertebrates such as lobsters. Surface waters are described as appearing "milky turquoise." One such irruption was blamed for the death of two billion young hake, *Merluccius capensis* Castelnau (Woodhead *et al.* 1998). SeaWiFS images of these

events bear strong resemblance to those of fish-killing sulfide irruptions and gypsum blooms at the Salton Sea (Tiffany *et al.* 2007a). Weeks *et al.* (2004) report the presence of elemental sulfur granules in the Benguela waters, whereas we instead find an abundance of tiny suspended gypsum crystals during “green tides” at the Salton Sea.

Tilapia grazing

Grazing by the omnivorous fish, tilapia, may have influenced both seasonal and year-to-year variations in Salton Sea phytoplankton populations. This tilapia is an omnivorous fish feeding on phytoplankton, zooplankton, benthos and detritus (Mironova 1969; Maitipe and DeSilva 1985) and has been shown to strongly affect Salton Sea planktonic and benthic organisms and nutrient cycling in microcosm experiments (González 1997; González *et al.* 1998; Hart *et al.* 1998; Simpson *et al.* 1998).

There are indications that tilapia do not feed at temperatures below 15 °C (Kelly 1956) and mean water temperatures in the Salton Sea do not rise to 15 °C until about March (Watts *et al.* 2001). This suggests the dip in phytoplankton density in April each year may be related to increasing feeding activity by tilapia as lake water temperatures rise. By mid-summer, however, the fish vacate the middle of the lake due to poor conditions there produced by sulfide irruptions (Costa-Pierce and Riedel 2000; Riedel *et al.* 2002; Caskey *et al.* 2007). The retreat of this grazer may help explain the rebound in mid-lake phytoplankton abundance between April and July. Phytoplankton abundance may increase in early winter partly due to reduced grazing by tilapia during the colder months when water temperatures drop to 13-14 °C (Watts *et al.* 2001; Holdren and Montañó 2002).

Tilapia abundance decreased during 1997-1999 as only one age class of adult tilapia, produced in 1995, dominated in the Salton Sea during our study (Riedel *et al.* 2002; Caskey *et al.* 2007; Hurlbert *et al.* 2007). This cohort declined in numbers on every occasion when low temperatures or low oxygen and high sulfide conditions caused high fish mortality. Tilapia made up > 95% of > 14,000,000 fish observed in fish kills during 1997-1999 (Hurlbert *et al.* 2007). The dramatic increase in abundance of some large phytoplankters, such as *Thalassionema* sp. (Fig. 8A), *Crucigenia rectangularis* (Fig. 8J) and *Gonyaulax grindleyi* (Fig. 7E), over the period 1997-1999 may have been due to decreasing grazing pressure by this fish. Abundance of large ciliates also increased throughout this period, perhaps for the same reason (Tiffany *et al.* 2007b). Tilapia remove large algal cells and colonial forms more effectively than individual small cells and cause reduction in overall phytoplankton abundance when exclusively filter-feeding (David Brune, personal communication). There was no clear indication of total phytoplankton abundance increasing from 1997 to 1999 (Fig. 2). In the Salton Sea mi-

croecosystems, however, tilapia caused 30-90% reductions in total phytoplankton abundance (González 1997).

Tintinnid-dinoflagellate interactions and grazing by invertebrates

Grazing by *Favella* sp., a tintinnid ciliate, likely had an effect on dinoflagellates $\leq 35 \mu\text{m}$ on some occasions. The tintinnid became especially abundant, up to 1500 ml⁻¹, in spring 1999 (Tiffany *et al.* 2007b). It is known to feed on dinoflagellates, especially *Heterocapsa* spp. (Stoecker *et al.* 1981, 1995; Yoo and Lee 1987; Kamiyama 2005). *Heterocapsa niei*, decreased earlier in 1999 than in the previous two years. An abrupt decline in *Favella* sp. in July 1999 coincided with an increase in the raptorial cyclopoid *Apocyclops dimorphus* that likely fed upon it (Tiffany *et al.* 2007b). This release from tintinnid grazing pressure, in addition to the vacating of mid-lake by tilapia, may have contributed to a peak in phytoplankton abundance in summer 1999. Interestingly, *Favella* is known to be itself preyed upon by at least one large dinoflagellate species present in the Salton Sea, *Gyrodinium instriatum*, complicating the picture (Uchida *et al.* 1997).

Grazing by metazooplankters and protozoans likely has a major influence on the phytoplankton community. Metazooplankton biovolume increased dramatically in April probably in response to the warming temperatures and abundant algal food (Tiffany *et al.* 2002). The increase in abundance of metazooplankton in summer may limit the growth of some algal populations then. The main herbivore in summer, *Brachionus rotundiformis* Tschugunoff, feeds most efficiently on picoplanktonic algae and bacteria in the size range 0.3-2 μm (Vadstein *et al.* 1993; Heerkloß and Hlawa 1995) and almost certainly is unable to ingest large diatoms, *e.g.*, *Thalassionema* sp., the raphidophyte *Chattonella marina* or the dinoflagellate *Gonyaulax grindleyi*. These larger forms thus may be favored when *B. rotundiformis* is abundant. The August-September decline in metazooplankton, caused by sulfide irruptions, may contribute to the subsequent increases in phytoplankton abundance by a reduction in grazing pressure.

Changes over the last 50 years

Differences between the phytoplankton of the 1950s, late 1960s and the late 1990s consisted of changes in species composition and seasonal patterns in abundance. Some of the same phytoplankton species reported by Carpelan (1961a) and Bain *et al.* (1970) persist in the Sea. In particular, many of the dominant species found in this study were present in the Salton Sea over 40 years earlier. Examples are the diatoms *Thalassionema* sp., *Cyclotella* sp., *Pleurosigma ambrosianum* and *Ceratoneis closterium*, the dinoflagellates *Heterocapsa niei* and *Prorocentrum minimum* and the

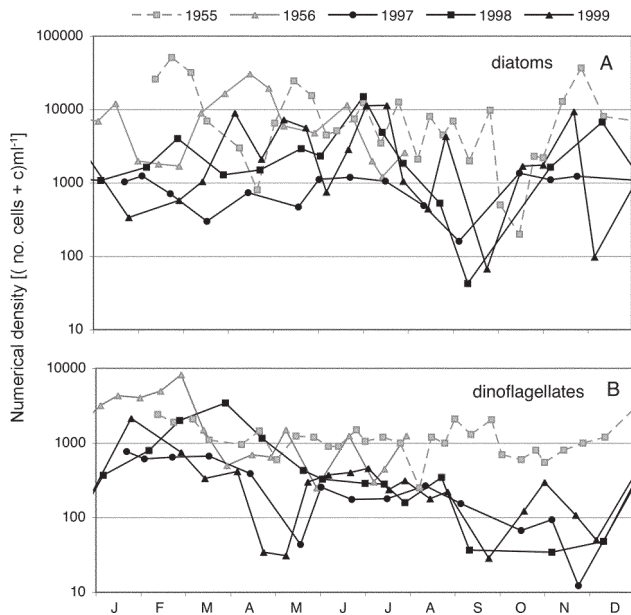


Figure 11.—Comparison of total diatom (A) and dinoflagellate (B) numerical density for 1955 and 1956 with that for 1997-1999. Values for the 1950s are from Carpelan (1961). Due to different protocols, $c = 40$ for the 1955-1957 study, $c = 0.99$ for the 1997-1999 study.

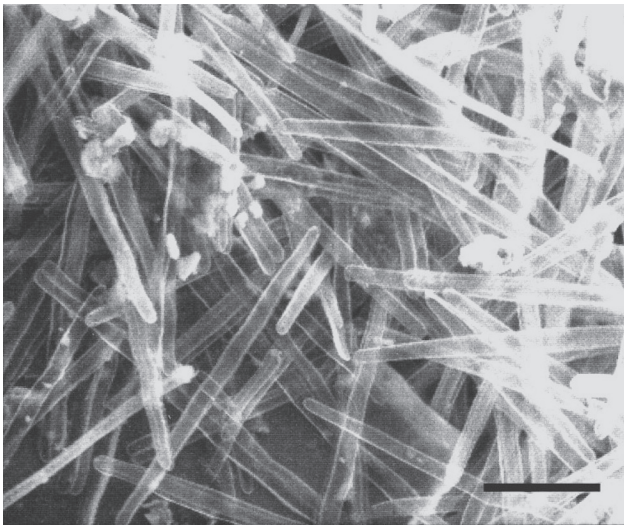


Figure 12.—Scanning electron microscope image of a "diatom graveyard" dominated by *Thalassionema* sp., core taken 17 June 1999. Scale bar = 20 μm .

euglenoid *Eutreptia lanowii*. These species must either be able to tolerate higher salinities or have gradually adapted over the years to the increasing salinity.

Many other species not previously reported are now abundant in the Sea such as *Chattonella marina*, a number of dinoflagellates, such as *Gonyaulax grindleyi*, *G. spinifera* and *Oblea* sp., and diatoms such as *Chaetoceros muelleri*

var. *subsalsum*. These species could have been present in the past but in numbers too low to detect. Alternatively, they may have been introduced in the interim.

Some species seen in the past, for example the ebridiid *Hermesinium adriaticum* and the dinoflagellate *Prorocentrum compressum*, were not detected in this study. Whether these are no longer extant in the Sea or are present in levels too low to detect is unknown.

High densities of phytoplankton were reported in both Carpelan (1961a) and Bain *et al.* (1970). Surface water chl-*a* values of 35-50 $\mu\text{g l}^{-1}$ in 1968-1969 (Bain *et al.* 1970) correspond fairly closely to those often observed in our study although we have recorded higher values (up to 100 $\mu\text{g l}^{-1}$) and some much lower values (as low as 7 $\mu\text{g l}^{-1}$ following strong wind events). Highest phytoplankton densities in the past studies occurred in January and February, as they did in 1997-1999.

Some physical factors such as temperature and mixing regimes have probably not changed greatly since the 1950s and 1960s, but chemical ones such as oxygen and sulfide levels have. Water temperatures in 1997-1999 were similar to those found in the 1950s (Watts *et al.* 2001). Oxygen concentrations, however, showed greater fluctuations in the present study than in the past, with supersaturation due to photosynthesis common in the winter and persistent anoxia in late summer (Watts *et al.* 2001). Surface water at Carpelan's offshore deep station was low in oxygen on only one occasion (16 Sep 1955) when it dipped to 0.55 mg l^{-1} and was more usually in the range of 3-8 mg l^{-1} . Sulfide concentrations in the lake during our study were likely much higher as periods of anoxia were more extreme than observed during Carpelan's study. If sulfide mortality events occurred 40-50 years ago, they were less extreme or of shorter duration and had little effect on phytoplankton as crashes in total phytoplankton density were not reported by Carpelan (1961a) or Bain *et al.* (1970) for any time of year. Bain *et al.* (1970) sampled about once a month and population crashes easily could have occurred between sampling dates without being observed. Carpelan sampled more frequently, about every two weeks. His station was located about 7 km WSW of our Station S-1 (Fig. 1) in 11-12 m of water. In order to compare our results to his, the total diatom and dinoflagellate numerical densities were tallied for S-1 for 1997-1999 and compared to those reported by Carpelan (Fig. 11). The precipitous drops in plankton abundance we have documented in August or September do not appear to have occurred during 1955-1956 with the possible exception of late Sept to Oct of 1955 when diatom density dropped by more than an order of magnitude and dinoflagellate density dropped by about 70%.

As implied earlier, arrival of tilapia in the lake likely influenced the phytoplankton. A thriving sportfishery existed during Carpelan's study, but none of the fish present then were

considered planktivorous in the adult stage. At the time of the Bain *et al.* (1970) study tilapia may have just invaded the Sea but likely not yet exerted an effect. Since these studies, tilapia has exhibited boom and bust patterns of population density in the Salton Sea (Hurlbert *et al.* 2007). When both abundant and actively feeding, tilapia has probably structured the phytoplankton assemblage by selectively feeding on certain size fractions and by lowering overall phytoplankton abundance. As a factor accidentally mitigating for the high nutrient inputs to the lake, tilapia may have slowed the lake's march to a hypereutrophic state. Without this fish the Salton Sea might have even greater environmental problems.

Conclusions

It is clear that the Salton Sea is in critical need of "restoration," but the question is restoration to what? It is an artificial waterbody in that an engineering accident formed the lake in its present incarnation and agricultural activities have maintained it since and caused its salinity and nutrient levels to rise. The organisms in the lake, however, are "natural" and the lake has proved to be beneficial to waterbirds, a sportfishery, and other water-based recreation.

If the salinity continues to rise, the planktonic assemblage should be expected to change. Most of the phytoplankton species are of estuarine or coastal origin and these are often euryhaline and can tolerate a wide range of salinity. However, an increase in salinity can be expected to cause some of the present organisms to disappear and a less species-rich flora to develop. Some hypersaline waters may be expected to retain primarily marine species up to a salinity of *ca.* 100 g l⁻¹ (Por 1980). At higher salinities, only strictly halophilic organisms usually prevail. Such species as the chlorophyte *Dunaliella* spp. (Javor 1989) and cyanobacteria such as *Aphanothece halophytica* (Felix and Rushforth 1979) may be favored if the salinity rises to this degree in the Salton Sea.

Conversely, if the salinity of the lake or a portion of it were lowered to that of seawater, as is currently planned under the proposed Salton Sea Authority Plan (www.saltonsea.ca.gov), many of the phytoplankton species presently found would probably persist, as most of them are reported from waters of normal ocean water salinities. Thus, potentially toxic species such as *Gonyaulax grindleyi* or *Chattonella marina* might still present a threat. However, considering the high algal diversity we have documented in the Salton Sea and the variety of biotic and other abiotic variables influencing it, it is difficult to predict which species would prevail under any future scenario.

Reduction of nutrient input could certainly lead to improved conditions, depending on the level of internal loading (Swan *et al.* 2007a), and a lowering of total algal biomass is a goal worth striving for. Major anoxia events with concomitant

high sulfide concentrations might lessen in frequency if there were less algal biomass sinking and decaying after blooms. This could reduce the frequency of mass mortality events and odor problems. Loss or recovery of the planktivorous tilapia may have the strongest influence on future phytoplankton assemblages. These likely have been kept in check by this fish when it has been present in large numbers.

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