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SALINE WATER

Influence of river inflows on plankton distribution around the southern perimeter of the Salton Sea, California

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Abstract The influence of river inflows (2.5–5 g l^{-1}) on phytoplankton and zooplankton was assessed with samples collected at 17 sites around the 50 km perimeter of the southern basin of the Salton Sea (41–45 g l^{-1}) along the 5 m isobath on 2 September and 11 December 2000. Phytoplankton generally increased in abundance downcurrent of the points of inflow, but patterns in downcurrent abundance varied widely among species. Several diatom species showed large increases; *Chaetoceros muelleri* var *subsalsum*, *Cylindrotheca closterium* and *Thalassionema* sp. increased up to 800-fold in abundance by ca. 20 km downcurrent from inflow points in September. In contrast, the dinoflagellates *Gyrodinium uncatenum* and *Prorocentrum minimum* increased 6- and 4-fold, respectively, in December, and *Gonyaulax grindleyi* actually decreased downcurrent of the rivers in September. In September, patterns in downcurrent abundance were correlated with the ratio of cell surface area to cell biovolume, with species with high ratios showing the largest increases. Zooplankton abundances did not show regular trends downcurrent of river inflows except for the larvae of *Balanus amphitrite*, which increased in density ca. 100-fold. This increase most likely reflected the abundance of adult-colonized rocky substrates near river inflow points. The strong upcurrent trends documented for some species seemed to have been due to the injection of nutrient-rich water from central to nearshore areas and near-site mortality due to the presence of hydrogen sulfide. This study gives a first glimpse of the complexity of the responses of nearshore plankton to river

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Saline Waters and their Biota

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inflow and provides evidence for how changes in factors such as current speed, nutrient supply and salinity stratification may influence plankton dynamics.

Keywords diatoms · dinoflagellates · phytoplankton · salt lakes · sulfide · turbulence · zooplankton

Introduction

Saline lakes are important, and often overlooked, economic, recreational, scientific and ecological resources (Williams, 1993; Melack, 2002). Most are located in semi-arid regions characterized by highly variable precipitation and stream inputs (Hammer, 1986). Many have experienced large physical, chemical and biological changes due to alterations of inflows by both man and nature (Williams, 1993, 1996). Changes in water supply to a saline lake can disrupt its hydrological balance causing fluctuations in water level, salinity and stability (Romero & Melack, 1996; Williams, 1996). These physical and chemical changes may then trigger shifts in primary productivity and in the species composition of plankton, benthos, fish and even birds (Jellison & Melack, 1993; Jehl, 1994).

River inflows and surface runoff into saline waters can stimulate phytoplankton growth simply by supplying nutrients (Granéli & Moreira, 1990; Paerl, 1997), or by increasing water column stability and forming semi-stable lenses of freshened water with high nutrient concentrations (Smayda, 1997). Less-saline, nutrient-rich inflows may favor specific groups of phytoplankton and may alter species composition (Granéli & Moreira, 1990). Phytoplankton communities in nearshore areas can thus be quite different from those found in midlake regions. Horne et al. (1971), for example, described a dense dinoflagellate-dominated bloom that occurred around the periphery of Clear Lake, California, following a period of high runoff while cyanobacteria were dominant offshore. Cannon (1990) described a dinoflagellate bloom that was largely confined to the edges of the Port River, Australia. When phytoplankton and zooplankton are closely coupled, zooplankton populations can also respond when phytoplankton production increases (Li et al., 2000).

Study site

The Salton Sea is a 980 km^2 saline (41–45 g l^{-1}) lake located in arid southeastern California, USA. It is a shallow, closed-basin lake with a mean depth of 8 m and a maximum depth of 15 m (see Cohen et al., 1999; Watts et al. 2001; Holdren & Montaño, 2002 for maps). Midlake chlorophyll *a* (chl *a*) concentrations in the Salton Sea range from 0.7–100 μg l^{-1} and nearshore values range up to 560 μg l^{-1} (M. A. Tiffany, unpublished data; K. M. Reifel, unpublished data). Dinoflagellates and diatoms make up 50 to >90% of the settleable phytoplankton, by biovolume, throughout the year (Reifel et al., 2002; M. A. Tiffany, unpublished data). In late winter when total phytoplankton abundance is highest, dinoflagellates dominate, and in summer a raphidophyte (*Chattonella marina* (Subrahmanyan) Hara et Chihara), dinoflagellates and diatoms are co-dominants (M. A. Tiffany, unpublished data). A copepod (*Apocyclops dengizicus* Lepeschkin) and a rotifer (*Brachionus rotundiformis* Tschugunoff) dominate the zooplankton community in summer, and larvae of the polychaete worm, *Neanthes succinea* Frey et Leukart, and the barnacle, *Balanus amphitrite* Darwin, dominate in winter and spring (Tiffany et al., 2002).

The New and Alamo rivers enter at the lake's southern margin (Fig. 1) and contribute approximately 77% of the inflow to the Salton Sea (Cohen et al., 1999; Watts et al., 2001). Agricultural and municipal wastewaters supplied by these two rivers and, at the northern end, the Whitewater River constitute the bulk of inflows (Bain et al., 1970; Cohen et al., 1999). The effects of these freshwater inflows on the plankton communities in the Salton Sea are expected to be important due to large salinity differences between inflows and lake water and higher nutrient concentrations in the inflows.

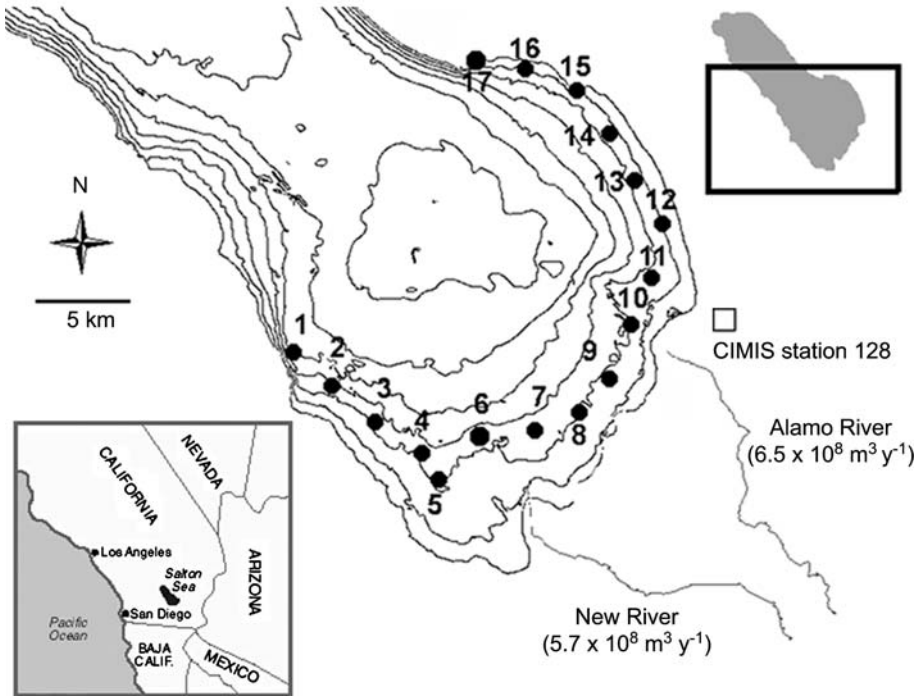

Fig. 1 Map of the Salton Sea indicating southern nearshore sampling sites 1–17 (•) and California Irrigation Management Information System (CIMIS) station 128 (□). Isobaths are at 2 m intervals. Approximate annual inflows for 2000 are indicated for the two major rivers in the southern region (USGS National Water Information System, http://waterdata.usgs.gov/nwis)

During periods of calm weather, inflows from the New and Alamo Rivers often create differences in salinity of up to 3 g l^{-1} between near-surface and 1 m depth even a few kilometers offshore, and larger differences have occasionally been documented (Arnal, 1961; Watts et al., 2001). The layer of less-saline water increases water column stability and may decrease the frequency and magnitude of mixing events that occur in these areas relative to the rest of the lake (Watts et al., 2001).

External nutrient loading to the lake is high (1.6 g P m^{-2} $year^{-1}$, 12 g N m^{-2} $year^{-1}$; J. M. Watts, unpublished data). In the Salton Sea, the molar ratio of total nitrogen (TN) to total phosphorus (TP) is high (between 70 and 190) indicating that phosphorus is most likely the limiting macronutrient for phytoplankton growth (Holdren & Montaño, 2002; J. M. Watts, unpublished data). During 1999, TP concentrations in the rivers were approximately one order of magnitude higher than those in the lake (annual means of 0.41, 0.70 and 0.021 mg l^{-1} for the Alamo River, New River and Salton Sea, respectively; Holdren & Montaño, 2002). Approximately 54 and 61% of TP in the Alamo and New Rivers, respectively, consisted of orthophosphate, which is directly utilized by phytoplankton. In contrast, concentrations of orthophosphate in the Salton Sea were frequently below the detection limit (0.005 mg l^{-1} in Holdren & Montaño, 2002; J. M. Watts, unpublished data). These factors would be expected to influence the formation, density and duration of algal blooms in the southern region of the Salton Sea.

In the southern basin, currents move in a roughly circular counterclockwise pattern (Arnal, 1961; Cook et al., 2002). This counterclockwise gyre is predominantly wind-driven. Although both the New and Alamo rivers enter the lake in the southern basin, water from these rivers flows over shallow sandbars at their mouths and through multiple shallow channels. The inflows

therefore do not have a strong influence over the gyre current except by creating vertical salinity gradients. The gyre current influences the distribution of nutrients and freshwater inputs, and organisms affected by both. Although winds of 2.9 m s^{-1} resulted in the formation of gyres in a hydrodynamic model of the Salton Sea (Cook et al., 2002), the critical wind speed needed to generate currents in the southern basin has not been determined. When the gyre is present, inflow water will be carried away from the river mouths in an easterly and then northerly direction. Watts et al. (2001) detected vertical salinity gradients 10 km upcurrent from the mouth of the Alamo River, and Arnal (1961) documented a tongue of lower-salinity surface water that extended along the shoreline >40 km from the river mouths.

The southern nearshore area is an important habitat for wildlife at the Salton Sea, and this area differs from the rest of the lake in both its physical properties (Watts et al., 2001) and biological communities (Carpelan, 1961; Reifel et al., 2002). Migratory waterbirds utilize this area during winter months, and colonial waterbird nesting areas are located at the New and Alamo river deltas (McCaskie, 1970; Shuford et al., 2002). Tilapia (*Oreochromis mossambicus* Peters), orangemouth corvina (*Cynoscion xanthulus* Jordan et Gilbert), bairdiella (*Bairdiella icistia* Jordan et Gilbert) and sargo (*Anisotremus davidsoni* Steindachner), the dominant fish species in the Salton Sea, can be found in high densities nearshore, especially near the New and Alamo rivers, during summer and fall. All fish seek refuge in the nearshore areas in spring and summer when midlake areas periodically experience low dissolved oxygen and high hydrogen sulfide concentrations throughout the water column (Costa-Pierce & Riedel, 2000; Riedel et al., 2002; Caskey et al., 2007). Reproduction of the four main fish species also occurs mainly in nearshore areas and areas near river inflow (Matsui et al., 1991; Riedel et al., 2002). Large mortality of tilapia and other fish found in the Salton Sea are common (Bain et al., 1970; Riedel et al., 2002; Caskey et al., 2007), and phytoplankton may contribute to this mortality (Tiffany et al., 2001; Reifel et al., 2002).

Because of the importance of the southern nearshore regions to both fish and birds and because phytoplankton might be related to mortality involving these groups, a study of plankton distribution in the southern basin was undertaken. The objective was to characterize the nearshore phytoplankton and zooplankton around the southern end of the Salton Sea, along the 5 m isobath, and to assess the influence of freshwater inflows on these populations.

Materials and methods

Samples were collected at 17 sites located in the southern basin approximately every 3 km along the 5 m isobath beginning at 115°50.0′ N, 33°12.0′ W and ending at 115°43.4′ N; 33°20.6′ W (Fig. 1). This transect was chosen to include areas directly offshore from inflows as well as areas both upcurrent and downcurrent from the inflow points. Samples were collected once during late summer (2 September 2000) and once during winter (11 December 2000). Sites 1–17 were visited in order of site number between 1000 and 1500 in September and 0830 and 1230 in December. On the first date, two samples were taken at site 11 (11A and 11B) approximately 5 m apart on either side of a transition from brownish-red water to lighter, apparently silt-laden water.

Collection of plankton

Integrated water samples were collected from the 0–2 m stratum at each site for phytoplankton abundance and pigment analyses using a 3 m sampling tube. This stratum represents the majority of the euphotic zone (B. K. Swan, unpublished data). Samples for enumeration were preserved in 1% (final concentration) Lugol's solution. Samples (60–100 ml) for pigment analysis were filtered through Whatman GF/F (0.7 μm) filters in the field using a syringe filter apparatus. Filters were stored in liquid nitrogen (–196°C) until analyzed. For the determination of zooplankton abundance and composition at each site, samples were collected at a depth of 2.5 m using a 32-l Schindler trap equipped with a 55 μm mesh

net and were preserved in 5% (final concentration) buffered formaldehyde.

Taxonomic and pigment analysis

Preserved phytoplankton samples were enumerated using the Utermöhl method (Lund et al., 1958). Lugol's preserved samples were settled in 25 ml settling chambers for at least 24 h before analysis. Cells in two crossed diameters were enumerated using a Leitz inverted microscope at a total magnification of 400×. For species present in high densities, only 10–15 fields of view were enumerated. All cells larger than 5 μm in length were counted and identified to genus or species. Because zero values cannot be plotted on a log scale, the constant 1.1 was added to each datum. This constant represents the smallest non-zero value possible, given the sampling and counting protocols and reporting units (no. ind. ml^{-1}) used. Cell biovolumes and surface areas were calculated by measuring at least 25 individuals of each species and using formulas for simple geometric shapes.

Zooplankton samples were counted using a compound microscope at 40× (or 100× for especially abundant taxa) and a modified, 40 mm × 50 mm Sedgwick-Rafter chamber. The whole chamber was counted when a species was scarce (less than ~10 individuals per 40 mm × 4 mm transect). When a species was intermediate in abundance (less than ~10 individuals per field of view), 4–10 transects were counted. When a species had greater than ~10–15 individuals per field of view, 4–10 fields of view were counted. For graphical representations, the constant 0.031 was added to each datum. This constant also represents the smallest non-zero, per liter value possible given the sampling procedure. For graphing purposes, data for *Synchaeta* aff. *vorax* and *Synchaeta* sp., for the nauplii and copepodids of *Apocyclops dengizicus* and for the nauplii and cyprids of *B. amphitrite* were combined. Zooplankton biovolumes were estimated by measuring 40 individuals of each species and using simple geometric shapes.

Chl *a* concentrations were measured to obtain an independent measure of phytoplankton abundance. Pigment analysis was done using high performance liquid chromatography (HPLC). Filters were extracted in 90% acetone for 24 h and then sonicated with a microprobe system to enhance extraction efficiencies. An internal pigment standard (canthaxanthin, which is not normally found in samples) was used to correct for volume changes during the extraction and injection processes. The method of Wright et al. (1991) was used. Pigment compounds were separated on an ODS-2 column using a three solvent gradient system at a flow rate of 1 ml min^{-1}. Pigment peaks were detected by two absorption detectors; a ThermoQuest UV2000 which measures absorption at 436 and 450 nm and a ThermoQuest UV6000 which measures from 390 to 550 nm every 1 nm. In addition, a fluorescence detector (ThermoQuest FL3000, Ex 404 nm; Em 680 nm) was used to detect and quantify the various chlorophyll degradation products, which usually occur at low concentrations.

Meteorological and physical data

Hourly measurements of wind speed were obtained for the seven days preceding and the days of sampling in the southern basin (26 August-2 September and 4–11 December, 2000) from California Irrigation Management Information System (CIMIS) meteorological station 128 located 0.5 km from the southeastern shoreline of the Salton Sea at 33°13′12″ N; 115° 34′48″ W (Fig. 1). Average daily flow rates for the New and Alamo rivers were obtained for the two sampling dates from the USGS National Water Information System (http://www.waterdata.usgs.gov/nwis). Although nutrient data were not collected during the present study, daily loading of TN and TP from the rivers was estimated using concentrations from Holdren & Montaño (2002).

At each site, measurements of temperature, dissolved oxygen and specific conductance were taken at 1 m intervals from the surface (~15 cm below surface) to a depth of 4–5 m using a YSI model UPG6000 Sonde, which housed a factory-calibrated thermistor (accuracy: ± 0.15°C), a rapid pulse oxygen probe (accurate to 0.2 ± 0.01 mg l^{-1}), and a 4 electrode cell specific conductance probe (accurate to 0.01 ± 0.01 m S cm^{-1}). The thickness

of the euphotic zone (surface to depth of 1% light penetration) was determined from vertical profiles of down-welling photosynthetically active radiation (PAR; wavelengths of 400–700 nm) measured at each site. PAR was measured as μmoles quanta m^{-2} s^{-1} using a Li-Cor LI-1000 data logger and Li-Cor Instruments cosine corrected quantum sensors at 0.5 m intervals from the surface to 4–5 m. Secchi disk depth was also measured at each station.

The critical depth (z_c) is the mixed-layer depth beyond which carbon loss due to respiration by the phytoplankton of the whole water column exceeds its carbon gain from photosynthesis (Sverdrup, 1953; Talling, 1957; Kirk, 1994). Net phytoplankton growth cannot occur when the mixed layer exceeds z_c. The critical depth can be calculated as a function of the euphotic layer; the ratio of z_c to the lower boundary of the euphotic zone ranges from 6 to 10 (Wofsy, 1983; Fichez et al., 1992). To estimate z_c, the depth of the euphotic zone was multiplied by six, which should give a conservative estimate.

Regression analyses of plankton densities

A least squares linear regression of $\log_{10}$ density as a function of distance (km) along the southern transect was performed for each phytoplankton and zooplankton species and for total phytoplankton and total zooplankton abundances. Slopes were calculated, and their statistical significance assessed. Sites 1–6 were not included in the analysis because these sites are upcurrent of inflow points of the New and Alamo rivers (Fig. 1), and phytoplankton density in these areas most likely is not directly influenced by river inflows. Percent increase in abundance per km of transect (D) was calculated from the slope (b) of the regression line using the equation: $D = 10^b–1$. A linear model was used as a simple descriptive device to complement the graphical presentation of patterns in abundance. We do not assume that any populations would actually have had a constant rate of change along the transect.

To explore the relationship between the cell surface area to biovolume (S/B) ratio and rate of change in abundance downcurrent of river inflows, least squares linear regression analyses of D as a function of the S/B ratio (μm^2 μm^{-3}) were performed for each sampling date, both for all phytoplankton species taken together and for each major group (diatoms, dinoflagellates and other) taken separately. Only species present at all or nearly all sites were used in the analysis (12 and 11 species, respectively, for the September and December sampling dates). All regression analyses were performed using SYSTAT™ v. 9.0 (SPSS, 1998).

Results

Physical and meteorological conditions

In September, inflow rates were high (Table 1). In addition, wind speeds averaged 5.6 m s^{-1} and gusts of up to 10 m s^{-1} were noted during the 24 h prior to sampling. These wind speeds are considerably higher than those that resulted in the formation of gyre currents in the hydrodynamic model (2.9 m s^{-1}; Cook et al., 2000). Evidence of both the inflow waters themselves and their trajectories can be seen in the reductions in Secchi disk depth (Fig. 2a) and in the large gradients in specific conductance (Fig. 3a) that were present at sites 9, 11B, 12 and 13. On this date, the gyre current appeared to push the incoming freshwater downcurrent along the shoreline before it was able to flow out into the lake. The sites furthest downcurrent (sites 15–17) showed no vertical gradients in specific conductance but were less-saline than sites at the start of the transect (sites 1–4). Dissolved oxygen was generally low, especially upcurrent of river inflows (sites 1–7) where concentrations were at or below 5 mg l^{-1} (Fig. 3c). Average water temperatures from 0–2 m were high (27.7°C). Temperature stratification was observed at many sites downcurrent from the inflows and was probably facilitated by salinity stratification (Fig. 3b). Upcurrent from inflows, water temperature was about 28°C, but at many downcurrent sites it was 1–2°C lower, probably reflecting the lower temperature of inflow waters. The last few sites sampled that day had warm surface waters. Although the depth of light penetration was at times very shallow (Fig. 2b), z_c either equaled or exceeded water depth at all sites.

Table 1 Flow rates, nutrient concentrations and estimated nutrient loading for the New and Alamo rivers and wind speed for 2 September and 11 December, 2000

Variable	2 September 2000			11 December 2000		
	New River	Alamo River	Total	New River	Alamo River	Total
Discharge rate ($\times 10^6$ m^3 d^{-1})[a]	1.39	1.68	3.07	1.31	1.42	2.73
Total phosphorus						
concentration (mg l^{-1})[b]	1.01	0.53	–	1.16	0.74	–
estimated loading ($\times 10^6$ g d^{-1})[c]	1.40	0.89	2.29	1.52	1.06	2.58
Total nitrogen						
concentration (mg l^{-1})[b]	5.3	2.3	–	4.7	3.4	–
estimated loading ($\times$l0^6 g d^{-1})[c]	7.4	3.9	11.3	6.2	4.8	11.0
Wind speed[d]						
mean (m s^{-1})	–	–	5.6	–	–	1.6
maximum (m s^{-1})	–	–	10.2	–	–	2.5

[a] hourly flow rates averaged over 24 h, from USGS National Water Information System (http://waterdata.usgs.gov/nwis)

[b] from Holdren & Montaño (2002); ''summer'' concentrations used for September and ''winter'' concentrations used for December

[c] estimated using flow rates from USGS and nutrient concentrations from Holdren & Montaño (2002)

[d] from CIMIS station 128, averaged over the 24 h prior to sampling

In December, inflow rates and wind speeds were lower than on the September date (Table 1). If the gyre was present, it was likely weaker allowing incoming freshwater to flow further out away from the rivermouths and mix to some extent with the more saline water before being pushed downcurrent. Vertical salinity gradients were present beginning at site 7, but the magnitude of these gradients was not as great as those in September (Fig. 4a). Also, Secchi disk depths were similar across sites (Fig 2a). Dissolved oxygen concentrations were high (6–10 mg l^{-1}) except at site 5 where concentrations were 2–4 mg l^{-1} (Fig. 4c). Average water temperatures from 0–2 m were about 11°C lower than they were in September (16.6°C). Temperature profiles for sites downcurrent from the inflows showed a slight warming of the salinity-stabilized surface waters (Fig. 4b). Although the depth of light penetration was at times shallow (Fig. 2b), z_c exceeded water depth at all sites. Estimated nutrient loading rates were high, with TN loading being greater in September and TP loading being higher in December (Table 1).

Downcurrent patterns in phytoplankton abundance

In September, phytoplankton abundance, measured as chl *a*, increased immediately downcurrent of the rivers and remained constant or decreased beyond site 10 (Fig. 5a). The phytoplankton consisted of a mixture of dinoflagellates, diatoms, raphidophytes, cryptomonads and other taxa. Patterns in downcurrent abundance varied among individual species, and these variations were correlated with the cell *S*/*B* ratio (Figs. 5b–d and 6, Table 2). Three diatom species, *Chaetoceros muelleri* var *subsalsum* Johansen et Rushforth, *Cylindrotheca closterium* and *Thalassionema* sp., increased in abundance by 40–800-fold between sites 7 and 17 in September (Fig. 5c). These species have the highest *S/B* ratios of any species considered in this study (Table 2). Among dinoflagellates, *Gonyaulax grindleyi* Reinecke, the species with the lowest *S/B* ratio, actually decreased downcurrent of the rivers (Fig. 5b; Table 2).

By December, large changes in the phytoplankton had taken place. Averaged (geometric mean) over all sites, total phytoplankton biovolume density was three times higher in December (28×10^6 μm^3 ml^{-1}) than in September (8.9×10^6 μm^3 ml^{-1}), and chl *a* was 2.3 times greater in December (110 μg l^{-1}) than in September (47 μg l^{-1}). Chl *a* again appeared to increase immediately downcurrent of the rivermouths and trended upward all the way to sites 16–17 (Fig. 5a). Dinoflagellates constituted > 85% of total phytoplankton biovolume at all sites,

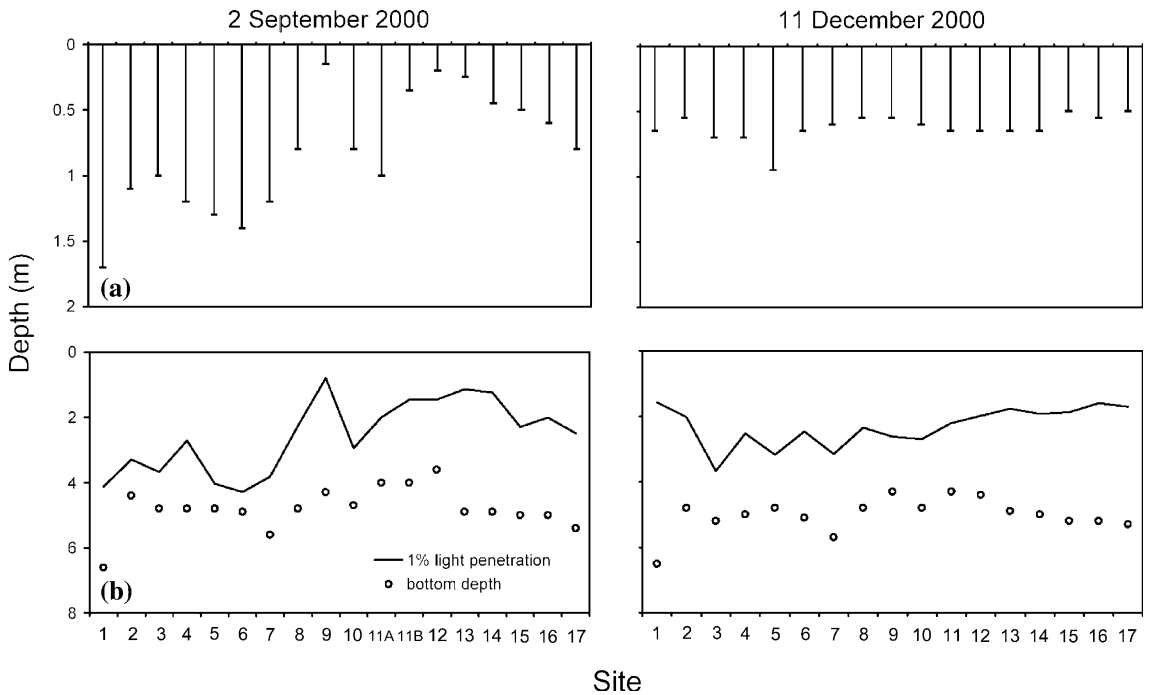

Fig. 2 Secchi disk depth (a) and depth of 1% light penetration and bottom depth (b) at each site on 2 September and 11 December 2000. Light data for site 12 on 11 December was lost

and other taxa, such as diatoms, were scarce (Fig. 5b–d).

In December, trends of individual species downcurrent of the river inflows were variable but were not correlated with the cell *S/B* ratio (Figs. 5b–d and 6, Table 2). Among dinoflagellates, *Gyrodinium uncatenum* and *Prorocentrum minimum* showed the largest changes, increasing 6- and 4-fold in density, respectively, between sites 7 and 17 (Fig. 5b; Table 2). *Cyclotella* spp., the only diatom that showed a definite trend along the transect, decreased in abundance downcurrent slightly but consistently, with a mean density of 268 ind. ml^{-1} for sites 7, 8 and 9 and of 194 ind. ml^{-1} for sites 15, 16 and 17. For other diatom species, the relationship between density and distance downcurrent of the river-mouths in December was weak (Fig. 5c; Table 2).

Downcurrent patterns in zooplankton abundance

In September only one zooplankter showed a regular trend downcurrent of the river inflows: the larvae of *B. amphitrite* increased in density ca. 100-fold between sites 7 and 17 (Fig. 5e; Table 2). This species composed a small percentage (up to 5%) of the total metazooplankton biovolume on this date, while the rotifer *Brachionus rotundiformis* and the copepod *Apocyclops dengizicus* constituted > 85% of total metazooplankton biovolume. Though neither *A. dengizicus* nor *B. rotundiformis* showed consistent trends along the transect, their abundances did show a slight negative correlation ($r = -0.40$; $p = 0.22$) beginning at site 7, the former tending to decrease along the transect and the latter tending to increase (Fig. 5e).

In December, the larvae of *B. amphitrite* and *Neanthes succinea* together constituted >85% of metazooplankton biovolume. They showed somewhat similar trends over the downcurrent portion of the transect, their abundances rising slightly from site 9 or 10 to maxima at site 14 and then declining (Fig. 5e). A somewhat irregular tendency existed for *A. dengizicus* to increase and of *B. rotundiformis* to decrease between sites 7 and 17 (Fig. 5e). These were the reverse of the

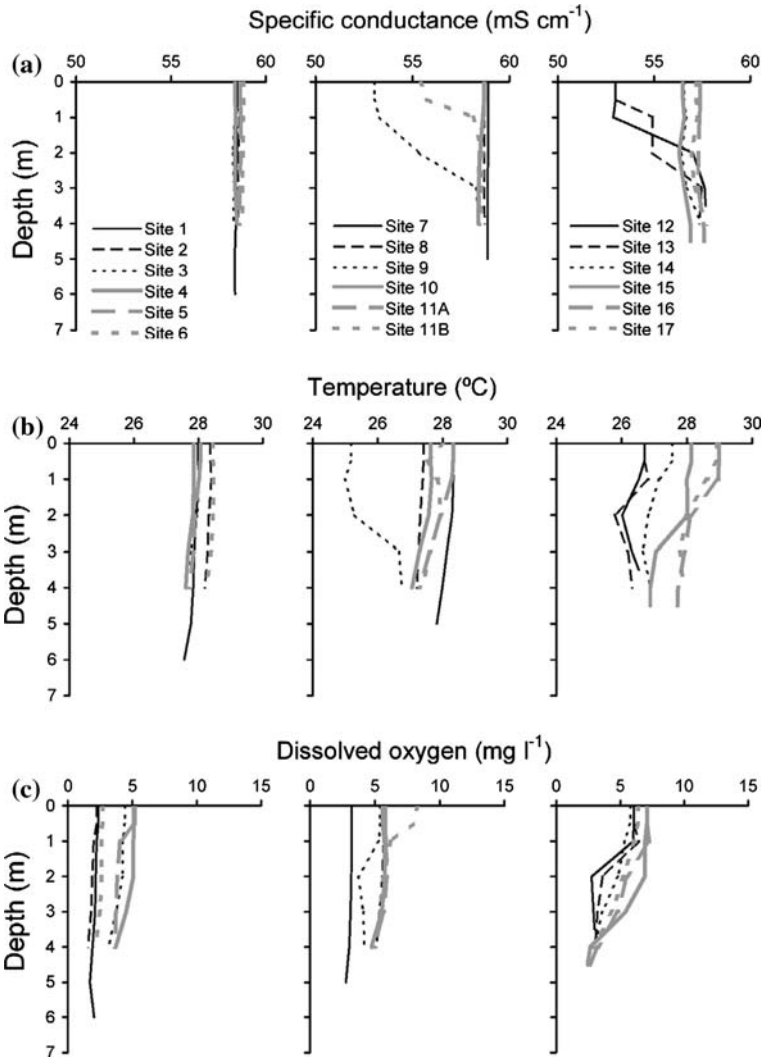

Fig. 3 Specific conductance (a), temperature (b) and dissolved oxygen (c) profiles taken at each site on 2 September 2000

September trends, but again represented weak evidence for a negative correlation ($r = –0.16$; $p = 0.63$) between the abundances of these two species.

Upcurrent patterns in plankton abundance

Several distinct patterns were also apparent upcurrent of the rivers, between sites 1 and 6 (Fig. 5). In September, the dominant diatoms *Chaetoceros muelleri* var *subsalsum* and *C. closterium*, two species with low *S/B* ratios, increased steadily in abundance along the entire transect beginning at site 1. In contrast, depressed densities of the diatom *Thalassionema* sp., of all dinoflagellates and of *A. dengizicus* and *B. rotundiformis* were observed at sites 2, 5 and 6. Relative to adjacent sites, these reductions were up to 100-fold for phytoplankters and up to 15-fold for zooplankters. These variations corresponded to depressed oxygen levels at sites 1, 2 and 6 (Fig. 3c).

In December, chl *a* concentration, all dinoflagellates, the diatoms *C. closterium* and *Thalassionema* sp., cryptomonads and the larvae of *N. succinea* showed steady decreases in abundance between sites 1 and 5 (Fig. 5). Oxygen concentration showed a parallel trend, dropping

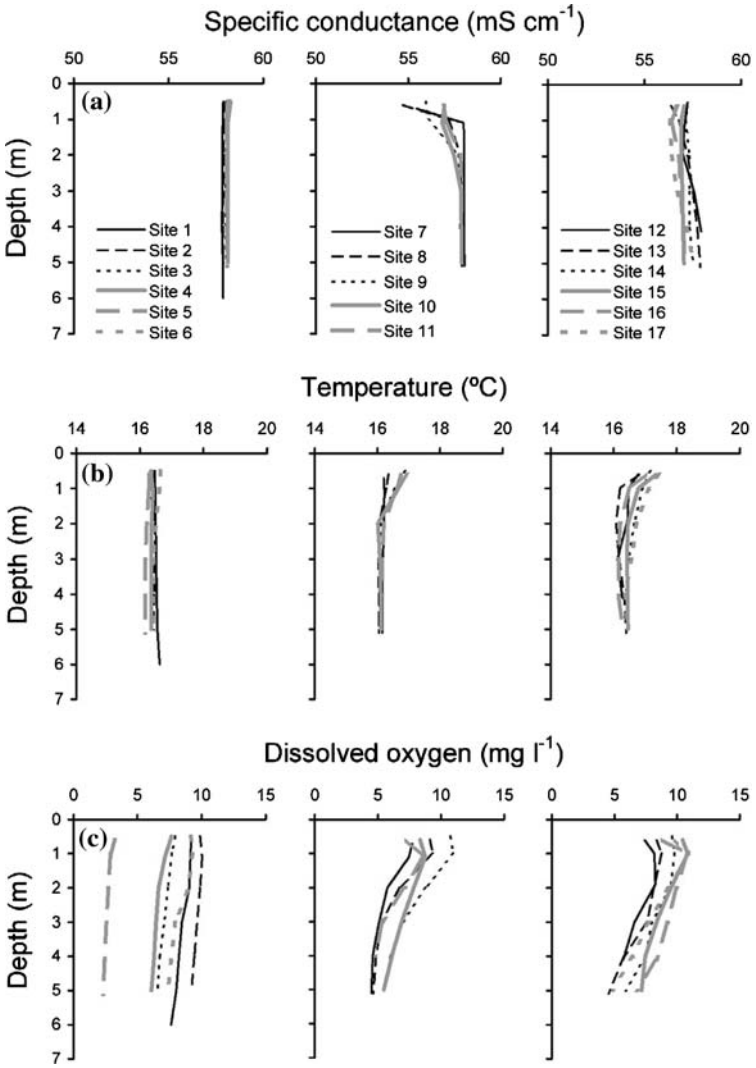

Fig. 4 Specific conductance (a), temperature (b) and dissolved oxygen (c) profiles taken at each site on 11 December 2000

from ca. 10 mg l^{-1} at site 2 to ca. 3 mg l^{-1} at site 5, rebounding to ca. 9 mg l^{-1} at site 6 (Fig. 4c). One ''rebel'' diatom (*Cyclotella* spp.) showed the reverse trend, increasing steadily in density from site 1 to site 6 (Fig. 5c).

Discussion

Variations in plankton abundance documented around the southern perimeter of the Salton Sea were greater than the typical 1- to 4-fold variations among mid-lake stations (Tiffany et al., 2002; unpublished data). These variations can be explained by a number of factors: nutrient inputs and salinity gradients created by the New and Alamo river inflows, cell morphology, hydrogen sulfide, and injection of plankton-depleted water from the lake center.

Light limitation is unlikely

Susceptibility of phytoplankton to stimulation by nutrient-rich inflows could be reduced if light was limiting; this appears not to be the case in this study. Light penetration is

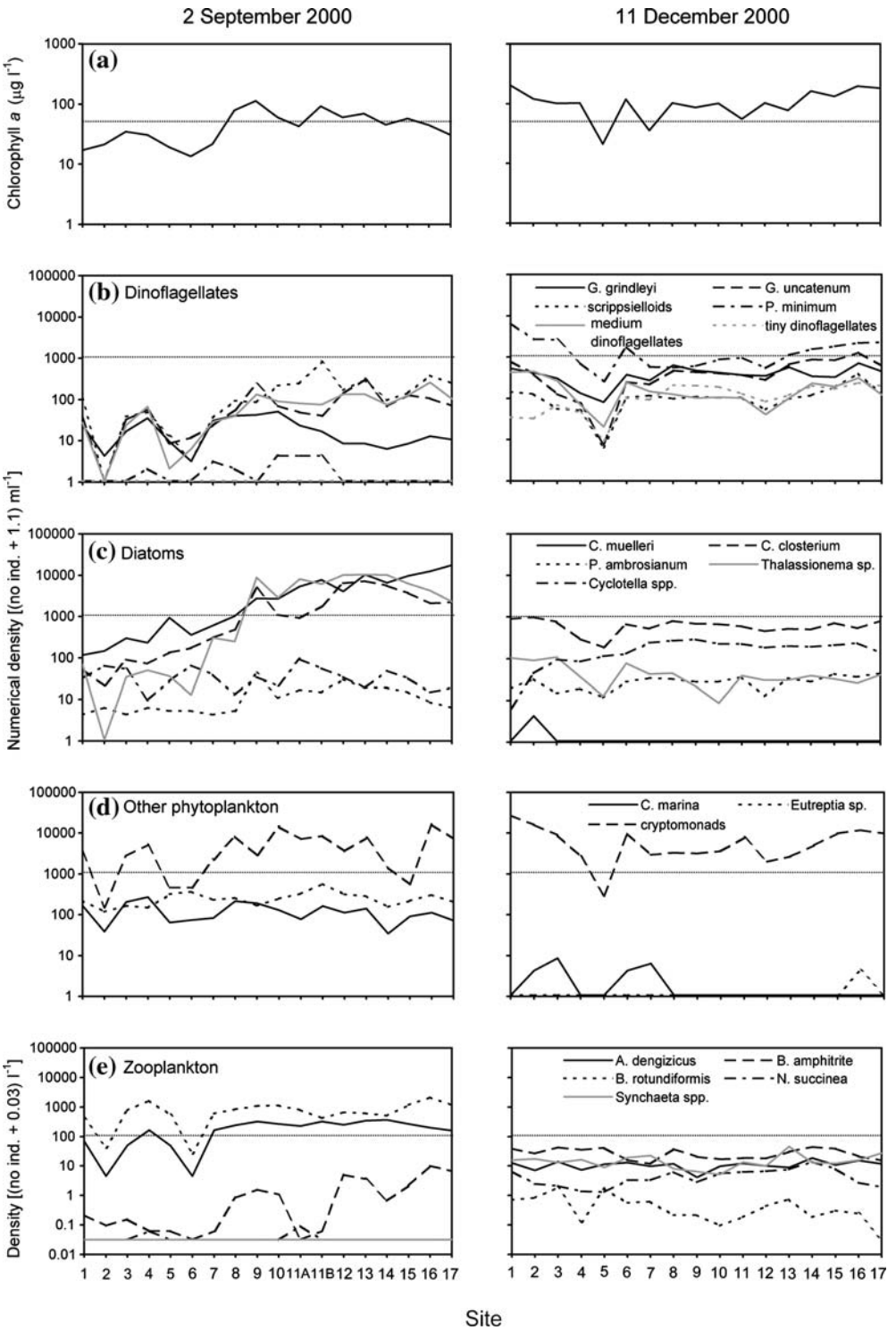

Fig. 5 Chlorophyll *a* concentration (a) and numerical density of dinoflagellates (b), diatoms (c), other phytoplankton (d) and zooplankton (e) as a function of position along the transect for 2 September and 11 December 2000. ''Medium dinoflagellates'' refers to unidentified dinoflagellates greater than 12 μm and ''tiny dinoflagellates'' refers to unidentified dinoflagellates less than 12 μm in length. On 2 September, the zooplankton sample for site 8 was lost

influenced both by phytoplankton themselves and by suspended clay, silt or other particulate matter that can be brought in by river inflow. Although Secchi disk depth was at times shallow, at nearly every site on both dates, z_c exceeded water depth.

Role of nutrient inputs and salinity gradients

The salinity of the New and Alamo rivers (2.5–5 g l^{-1}) is much lower than that of the lakewater (41–45 g l^{-1}). Thus inflows tend to create vertical salinity and density gradients (Figs. 3a, c). Density gradients due to salinity increase the stability of the water column (Arnal, 1961; Watts et al., 2001), and increased water column stability is often an initial factor in the formation of phytoplankton blooms (Margalef et al., 1979; Steidinger & Haddad, 1981; Smayda, 1997). The magnitude and spatial variation of vertical density gradients created by inflow waters depends on several factors including the rate of flow from the rivers and the strength of the gyre current.

Coupled with increased stability is the input of nutrients by the rivers. Loading of phosphorus from both the New and Alamo rivers was estimated to be higher in December than in September (Table 1). This may explain the higher concentrations of chl *a* and total phytoplankton biovolume in December. TP concentrations in the New and Alamo Rivers are 10–16-fold higher than those in the Salton Sea (annual means of 1.1, 0.72 and 0.069 mg l^{-1} for the New River, Alamo River and Salton Sea, respectively; Holdren & Montaño, 2002). Thus even a slight mixture of river water with Salton Sea water would increase phosphorus availability to phytoplankton. Differences in water temperature, currents and turbulence between the two sampling dates were probably responsible for some differences in phytoplankton spatial variation, but specific effects of these cannot be discerned.

Influence of surface area to biovolume ratio

The differences among species in their responses to river inflow observed in September were strongly correlated with cell *S/B* ratios among all major phytoplankton groups. There are several reasons why cells with high *S/B* ratios would show stronger responses to the river inflows than cells with low *S/B* ratios. Small or elongated cells (cells with high *S/B* ratios) are generally able to absorb both light and nutrients at a higher rate per unit mass than large cells or cells with low *S/B* ratios (Malone, 1980; Kirk, 1994; Tang, 1995). In addition, among non-motile cells such as diatoms, cells with low *S/B* ratios generally have higher sinking rates causing them to sink out of surface waters faster than species with high *S/B* ratios (Walsby & Reynolds, 1980; Reynolds, 1984). *Cyclotella* sp., the species with the lowest *S/B* ratio of all diatoms in the study, actually decreased in abundance downcurrent of the river inflows in December (Fig. 5c; Table 2).

Diatom-dinoflagellate differential responses to mixing

For both diatoms and dinoflagellates in September, the rate at which a species tended to increase downcurrent from inflows increased with its *S/B* ratio (Fig. 5a). Since all dinoflagellates shown had *S/B* ratios lower than any of the diatoms, there was no direct evidence of how the downcurrent responses of a dinoflagellate and a diatom of the same *S/B* ratio would compare. Extension of the regression lines in Fig. 6a would suggest, however, that the dinoflagellate would increase downcurrent more rapidly than the diatom. For example, the regression lines indicate that with a $S/B = 1.0$, a diatom would be expected to increase in density by about 1 percent per km and a dinoflagellate by about 8 percent per km.

These variations may reflect the differential effect of the salinity stratification present along most (sites 8–13) of the downcurrent portion of the sampling transect. Such stratification would have reduced water column mixing, which would likely affect diatoms and dinoflagellates differently. Increases in diatom abundances resulting from nutrient loading could have been dampened due to an increase in the numbers that sank out of surface waters due to the reduction in mixing. Dinoflagellates, on the other hand, would have maintained their vertical position, by swimming, under low turbulence conditions.

Table 2 Cell biovolumes, ratio of surface area to biovolume, percent increases per km downcurrent and results of regression analyses for log abundance (A) as a function of distance (X) downcurrent from site 7 (n=12 or 13 sites)

Species	Cell volume (μm^3)	Surface area to volume ratio (μm^2) (μm^{-3})	Regression analyses					
			September			December		
			% incr.			% incr.		
			Per km[a]	R^2	p[b]	Per km[a]	R^2	p[b]
Dinophyceae								
Gonyaulax grindleyi	45,000	0.12	–5.8	0.60	< 0.01	0.69	0.04	0.54
Gyrodinium uncatenum	17,000	0.29	2.8	0.12	0.28	4.2	0.58	0.01
scrippsielloid dinoflagellates	8,300	0.36	4.2	0.24	0.11	2.6	0.24	0.13
Prorocentrum minimum	1,100	0.49	np	np	np	5.2	0.83	< 0.01
medium dinoflagellates	970	0.74	4.2	0.48	0.01	1.2	0.11	0.32
tiny dinoflagellates	562	0.89	np	np	np	1.9	0.13	0.28
total dinoflagellate biovolume	–	–	0.23	0.01	0.83	1.9	0.34	0.06
Bacillariophyceae								
Cyclotella sp.	216	0.92	–1.1	0.03	0.58	–1.4	0.51	0.01
Pleurosigma ambrosianum	1,200	1.14	0.69	0.01	0.80	0.93	0.07	0.43
Thalassionema sp.	340	1.62	7.2	0.25	0.10	0.46	0.01	0.77
Cylindrotheca closterium	110	2.48	6.4	0.32	0.06	< 0.01	< 0.01	0.92
Chaetoceros muelleri	160	3.82	10	0.84	< 0.01	np	np	np
total diatom biovolume	–	–	7.4	0.49	0.01	–0.46	0.17	0.22
Raphidophyceae								
Chattonella marina	13,000	0.32	–2.5	0.21	0.13	np	np	np
Cryptophyceae								
cryptomonads	247	1.18	–0.46	0.00	0.90	4.2	0.47	0.02
Euglenophyceae								
Eutreptia sp.	2,400	0.63	–0.23	0.01	0.80	np	np	np
Total phytoplankton	–	–	1.2	0.10	0.33	2.1	0.37	0.05
Chlorophyll *a*	–	–	–0.92	0.04	0.54	4.2	0.66	< 0.01
Metazooplankton								
Apocyclops dengizicus	8,630	–	–0.23	0.01	0.81	1.9	0.22	0.15
Balanus amphitrite larvae	19,600	–	14	0.43	0.03	0.93	0.06	0.48
Brachionus rotundiformis	1,130	–	2.3	0.18	0.20	–3.2	0.27	0.13
Neanthes succinea larvae	47,600	–	np	np	np	–0.23	0.002	0.89
Synchaeta spp.	–	–	np	np	np	2.6	0.17	0.21
total zooplankton biovolume	–	–	1.9	0.24	0.13	1.4	0.18	0.19

[a] Calculated as 10^b-1 where log$A$ = a + bX

[b] Significance level of estimated slope (b)

np = not present

Stimulation of potentially toxic phytoplankton

Three species known to produce toxins in other systems (*P. minimum*, *G. grindleyi* and *Chattonella marina*) were observed during the study. Many dieoffs of fish and birds have occurred at the Salton Sea, although none have been conclusively linked to blooms of these taxa (Tiffany et al., 2001; Reifel et al., 2002). Two of these species, *G. grindleyi* and *Chattonella marina*, decreased in abundance downcurrent of river inflow points. The third species, *P. minimum*, appeared to be stimulated by river inflow increasing approximately 4-fold in density between sites 7 and 17. As *P. minimum* has the highest *S/B* ratio of the three species, this pattern is consistent with the pattern found among all phytoplankton species (Fig. 6).

The southern nearshore environments are complex and productive, not just because that zone receives inflows but also because the shoreline is complex, with two, long finger deltas extending into the lake, multiple embayments and thousands of hectares of shallow water habitat used by a wide variety of waterbirds and juvenile fish. Comparisons of nearshore phytoplankton with those found in midlake are difficult. No

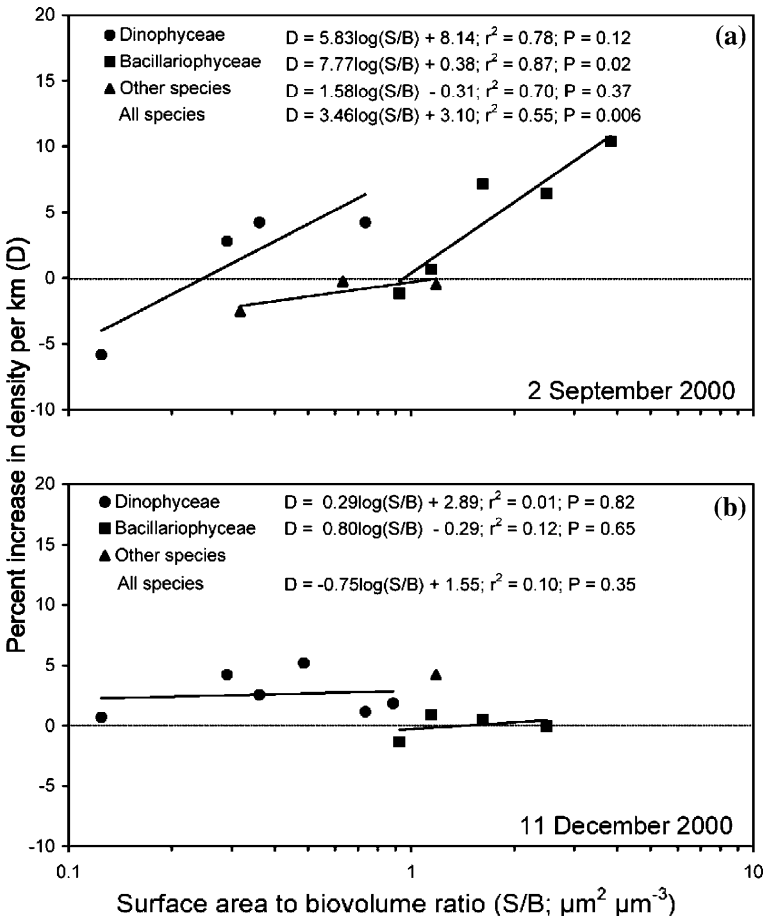

Fig. 6 Percent increase per km downcurrent from the New River as a function of the surface area to biovolume ratio for all phytoplankton taxa for 2 September (a) and 11 December (b) 2000. Regression analysis based on data for sites 7–17

midlake data were collected during 2000, and many taxa show large year-to-year variation in abundance (M. A. Tiffany, unpublished data). The data collected during this study, however, provide evidence that at least certain potentially toxic taxa were more abundant in the southern nearshore zone than in midlake. For example, maximum abundances of *P. minimum* recorded in midlake during 1997–1999 ranged from 90–100 cells ml^{-1} (M. A. Tiffany, unpublished data), and densities observed in this study on the December date range from 550–6,600 cells ml^{-1}.

Zooplankton patterns: predation and substrate availability

The slight negative correlation between abundances of *Apocyclops dengizicus* and *Brachionus rotundiformus* could reflect a predator-prey interaction. An inverse relationship between densities of the two species was also seen in a study of temporal changes in zooplankter abundances (Tiffany et al., 2002).

The almost 100-fold increase in the larvae of *B. amphitrite* downcurrent of the New and Alamo rivers in September was likely the result of increased production of larvae at sites near and downcurrent from the points of inflow. Much of the shoreline between the New and Alamo rivers consists of rock dikes, covered with adult barnacles. Larvae produced by these adults are carried offshore of this area. Elsewhere along the Sea's shoreline, hard substrates are scarce. At midlake sites, *B. amphitrite* is generally scarce (< 0.1 ind. l^{-1}) during summer and early fall (Tiffany et al., 2002) as it was at sites 1–7 on the September date in this study. This may reflect repeated episodes of sulfide-caused mortality of larvae and adults as well as intense zooplanktivory by tilapia and other fish that crowd nearshore waters in summer and early

fall (Riedel et al., 2002; Tiffany et al., 2002; Caskey et al., 2007). Therefore, the effect of additional larvae carried offshore from the diked shorelines was marked in September but undetectable in December when *B. amphitrite* are 10–100-fold more abundant than in September in midlake waters (Fig. 5E; Tiffany et al., 2001).

The increase in the density of *B. amphitrite* larvae may represent an increase in food supplies for zooplanktivorus fish at and downcurrent of the points of inflow during summer months. As described above, fish likely utilize the nearshore areas as refuges from midlake waters that periodically experience low oxygen and high hydrogen sulfide levels during the summer. Although *Brachionus rotundiformis* and *Apocyclops dengizicus* would make up the majority of the summertime food supply for zooplanktivorus fish such as tilapia and bairdiella due to their high abundances, *B. amphitrite* larvae may also become important over limited areas downcurrent from the diked shorelines.

Plankton kills and upcurrent patterns

The strong trends documented for some species upcurrent of inflow points (sites 1–6) seemed to have been due to two phenomena: the injection of plankton-decimated, nutrient-rich water from central to nearshore areas and additional near-site mortality due to the presence of hydrogen sulfide.

In September, the two diatom species with the highest *S/B* ratios, *Chaetoceros muelleri* var. *subsalsum* and *Cylindrotheca closterium*, showed 3-fold increases in abundance between sites 1 and 6. Extra nutrients may have been supplied to the nearshore region near site 1 through the injection of nutrient-enriched water from the lake's center following large-scale mortality events in midlake plankton (Tiffany et al., 2001; Watts et al., 2001). Decomposition of dead plankton after such an event could have contributed dissolved nutrients to the water column, and the counterclockwise gyre in the southern basin could have brought this nutrient-rich water from the lake's center to the western shore in the area of site 1. There, it could have been 'seeded' with inocula from less-affected plankton populations of shallow, nearshore areas. In the presence of decomposition-released nutrients, species with high *S/B* ratios, like these two diatoms, are the type that would be expected to respond most rapidly.

The large reductions in both phytoplankton and zooplankton noted at particular upcurrent sites (1, 5 and 6) in September (Fig. 5) were perhaps due to the presence of hydrogen sulfide as suggested by the low oxygen concentrations documented at these sites. Hydrogen sulfide is toxic to most aerobic organisms even at low concentrations (Bagarinao, 1992). Possibly, fingers or eddies of hydrogen sulfide-rich, plankton-poor water had intruded at these points from further out in the lake.

Conclusion

This study gives only a first glimpse of the complexity of the responses of plankton to river inflow. Samples were collected along a single transect of sites, almost of all of which are greater than 1 km from the shore. Nearshore areas are important nesting and foraging areas for waterbirds. However, most waterbird use is confined to a strip less than 1 km from the shore where shoreline complexity (e.g., deltas, embayments) is likely to create complex patterns in plankton populations that are undocumented in this study. Nevertheless, this study shows that nearshore plankton populations can be affected by river inflows and can differ from those found in the midlake.

Various proposals for the restoration of the Salton Sea involve different shoreline configurations and inflow points, different degrees of phosphorus reduction in inflow waters, and different inflow volumes. Each proposed project would create different dynamics for nearshore plankton populations. This precludes any meaningful speculation as to what specific changes in nearshore plankton populations may occur as a result of restoration measures. However, this study does provide evidence for how changes in several factors, such as current speed, species composition and nutrient supply, may influence plankton dynamics in these regions.

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References

Arnal, R. E., 1961. Limnology, sedimentation and microorganisms of the Salton Sea, California. Bulletin of the Geological Society of America 72: 427–478.

Bagarinao, T., 1992. Sulfide as an environmental factor and toxicant: tolerance and adaptations in aquatic organisms. Aquatic Toxicology 24: 21–62.

Bain, R. C., A. M. Caldwell, R. H. Clawson, H. L. Scotten & R. G. Willis, 1970. Salton Sea California: water quality and ecological management considerations. U. S. Department of the Interior, Federal Water Quality Administration, Pacific Southwest Region, 54 pp.

Cannon, J. A., 1990. Development and dispersal of red tides in the Port River, south Australia. In Granéli E., B. Sundström, L. Edler & D. M. Anderson (eds), Toxic marine phytoplankton. Elsevier Science Publishing, New York, 110–115.

Carpelan, L. H., 1961. Phytoplankton. In Walker B. W. (ed.), The ecology of the Salton Sea, California in relation to the sportfishery. California Department of Fish Game, Fish Bulletin 113: 33–42.

Caskey, L.L., R.R. Riedel, B. Costa-Pierce, J. Butler & S.H. Hurlbert, 2007. Population dynamics, growth, and distribution of tilapia (*Oreochromis mossambicus*) in the Salton Sea, 1999–2002, with notes on bairdiella (*Bairdiella icistia*) and orange mouth corvina (*Cynoscion xanthulus*). Hydrobiologia 576: 185–203.

Cohen, M. J., J. I. Morrison & E. P. Glenn, 1999. Haven or hazard: the ecology and future of the Salton Sea. Pacific Institute, Oakland, California, 64.

Cook, C. B., G. T. Orlob & D. W. Huston, 2002. Simulation of wind-driven circulation in the Salton Sea: implications for indigenous ecosystems. Hydrobiologia 473(Developments in Hydrobiology 161): 59–75.

Costa-Pierce, B. A. & R. Riedel, 2000. Fisheries ecology of the tilapias in subtropical lakes of the United States. In Costa-Pierce B. A., & J. E. Rakocy (eds), Tilapia aquaculture in the Americas, Vol. 2. The World Aquaculture Society, Baton Rouge, Louisiana, 1–20.

Fichez, R., T. O. Jickells & H. M. Edmonds, 1992. Algal blooms in high turbidity, a result of the conflicting consequences of turbulence on nutrient cycling in a shallow water estuary. Estuarine, Coastal & Shelf Science 35: 577–592.

Granéli, E. & M. O. Moreira, 1990. Effects of river water of different origin on the growth of marine dinoflagellates and diatoms in laboratory cultures. Journal of Experimental Marine Biology Ecology 136: 89–106.

Hammer, U. T., 1986. Saline lake ecosystems of the world. Junk, Dordrecht, 616 pp.

Holdren, G. C. & A. Montaño, 2002. Chemical and physical characteristics of the Salton Sea, California. Hydrobiologia 473 (Developments in Hydrobiology 161): 1–21.

Horne, A. J., P. Javornicky, & G. R. Goldman, 1971. A freshwater ''red tide'' on Clear Lake, California. Limnology & Oceanography 16: 684–689.

Jehl, J. R. Jr., 1994. Changes in saline, alkaline lake avifaunas in western North America in the past a years. In Jehl J. R. Jr., & N. K. Johnson (eds), Studies in Avian Biology, no. 15. Cooper Ornithological Society, Los Angeles, California, 258–272.

Jellison, R. & J. M. Melack, 1993. Algal photosynthetic activity and its response to meromixis in hypersaline Mono Lake, California. Limnology & Oceanography 38: 818–837.

Kirk, J. T. O., 1994. Light and photosynthesis in aquatic ecosystems, (2nd edn). Cambridge University Press, Cambridge, 509.

Li, M., A. Gargett & K. Denman, 2000. What determines seasonal and interannual variability of phytoplankton and zooplankton in strongly estuarine systems? Estuarine, Coastal & Shelf Science 50: 467–488.

Lund, J. W. G., C. Kilpling & E. D. LeCren, 1958. The inverted microscope method of estimating algal numbers, and the statistical basis of estimation by counting. Hydrobiologia 11: 143–170.

Malone, T. C., 1980. Algal size. In Morris I. (ed.), The physiological ecology of phytoplankton. University of California Press, Berkley, 433–463.

Margalef, R., M. Estrada & D. Blasco, 1979. Functional morphology of organisms involved in red tides, as adapted to decaying turbulence. In Taylor D. L. & H. H. Seliger (eds), Toxic dinoflagellate blooms. Elsevier North Holland, New York, 89–94.

Matsui, M. L., A. Bond, G. Jordan, R. Moore, P. Garrahan, K. Iwanaga & S. Williams, 1991. Abundance and distribution of the ichthyoplankton in the Salton Sea in relation to water quality. Final Performance Report, California Department of Fish and Game.

McCaskie, G., 1970. Shorebird and waterbird use of the Salton Sea. California Fish and Game 56: 87–95.

Melack, J. M., 2002. Ecological dynamics in saline lakes. Verhandunglen Internationale Vereinigung für theoretische und Angewandte Limnologie 28: 29–40.

Paerl, H. W., 1997. Coastal eutrophication and harmful algal blooms: importance of atmospheric deposition and groundwater as ''new'' nitrogen and other nutrient sources. Limnology & Oceanography 42: 1154–1165.

Reifel, K. M., M. P. McCoy, T. E. Rocke, M. A. Tiffany, S. H. Hurlbert & D. J. Faulkner, 2002. Possible importance of algal toxins in the Salton Sea, California. Hydrobiologia 473 (Developments in Hydrobiology 161): 275–292.

Reynolds, C. S., 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge, 384 pp.

Riedel, R., L. Caskey & B. A. Costa-Pierce, 2002. Fish biology and fisheries ecology of the Salton Sea, California. Hydrobiologia 473 (Developments in Hydrobiology 161): 229–244.

Romero, J. R. & J. M. Melack, 1996. Sensitivity of vertical mixing in a large saline lake to variations in runoff. Limnology & Oceanography 41: 955–965.

Shuford, W. D., N. Warnock, K. C. Molina & K. K. Sturm, 2002. The Salton Sea as critical habitat to migratory and resident waterbirds. Hydrobiologia 473 (Developments in Hydrobiology 161): 255–274.

Smayda, T. J., 1997. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. Limnology & Oceanography 42: 1137–1153.

SPSS, Inc., 1998. SYSTAT^{TM} for Windows: statistics. SPSS, Inc., Chicago, Illinois.

Steidinger, K. A. & K. Haddad, 1981. Biologic and hydrographic aspects of red tides. BioScience 31: 814–819.

Sverdrup, H. U., 1953. On conditions for the vernal blooming of phytoplankton. Journal du Conseil International pour l'Exploration de la Mer 18: 287–295.

Talling, J. F., 1957. The phytoplankton population as a compound photosynthetic system. New Phytologist 56: 133–149.

Tang, Y., 1995. The allometry of algal growth rates. Journal of Plankton Research 17: 1325–1335.

Tiffany, M. A., S. B. Barlow, V. E. Matey & S. H. Hurlbert, 2001. *Chattonella marina* (Raphidophyceae) a potentially toxic alga in the Salton Sea, California. Hydrobiologia 466 (Developments in Hydrobiology 162): 187–194.

Tiffany, M. A., B. K. Swan, J. M. Watts & S. H. Hurlbert, 2002. Metazooplankton dynamics in the Salton Sea, California, 1997–1999. Hydrobiologia 473 (Developments in Hydrobiology 161): 103–120.

Walsby, A. E. & C. S. Reynolds, 1980. Sinking and floating. In I. Morris (ed), The physiological ecology of phytoplankton. Blackwell Scientific Publications, 371–412.

Watts, J. M., B. K. Swan, M. A. Tiffany & S. H. Hurlbert, 2001. Thermal, mixing and oxygen regimes of the Salton Sea, California, 1997–1999. Hydrobiologia 466 (Developments in Hydrobiology 162): 159–176.

Williams, W. D., 1993. Conservation of salt lakes. Hydrobiologia 267: 291–306.

Williams, W. D., 1996. What future for saline lakes? Environment 38: 12–39.

Wofsy, S. C., 1983. A simple model to predict extinction coefficients and phytoplankton biomass in eutrophic waters. Limnology & Oceanography 28: 1144–1155.

Wright, S. W., S. W. Jeffrey, R. F. C. Mantoura, C. A. Llewellyn, T. Bjornland, D. Repeta & N. Welslehmayer, 1991. An improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. Marine Ecology Progress Series 77: 183–196.