Long-term trends and causal factors associated with Microcystis *abundance and toxicity in San Francisco Estuary and implications for climate change impacts*

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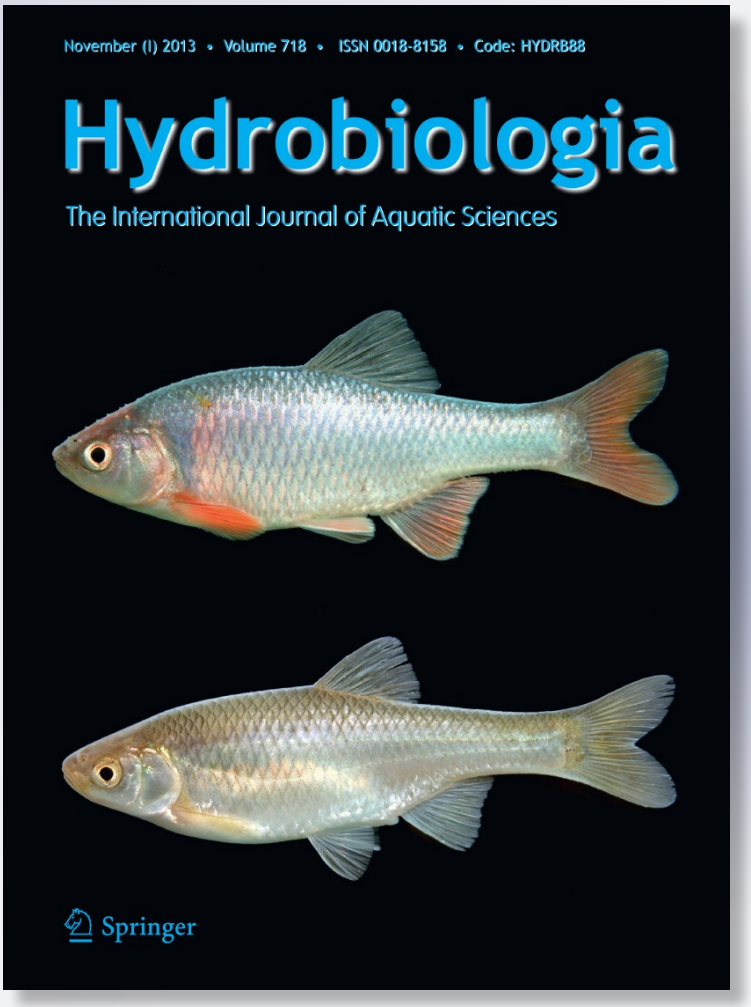

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PRIMARY RESEARCH PAPER

Long-term trends and causal factors associated with *Microcystis* abundance and toxicity in San Francisco Estuary and implications for climate change impacts

P. W. Lehman · K. Marr · G. L. Boyer · S. Acuna · S. J. Teh

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Abstract The impacts of climate change on *Microcystis* blooms in San Francisco Estuary are uncertain because factors associated with the abundance and distribution of *Microcystis* blooms since their inception in 1999 are poorly understood. Discrete and continuous data collected between 2004 and 2008 were used to assess what factors controlled bloom initiation and persistence, if there was an impact of the bloom on mesozooplankton abundance and toxicity or dissolved organic carbon concentration, and how these might vary with climate change. *Microcystis* abundance was greater in dry years than wet years and both total microcystins concentration and the microcystins content of mesozooplankton tissue increased with abundance. The bloom began in the upstream portions of the estuary and spread farther west during dry years. Bloom initiation required water temperature above 19°C and surface irradiance in the visible range above 100 W m^{-2}. The bloom persisted during a wide range of water quality conditions but was closely correlated with low turbidity. The intensity of *Microcystis* blooms will likely increase with climate change due to increased water temperature and low streamflow during droughts. Elevated water temperature earlier in the spring could also extend the duration of *Microcystis* blooms by up to 3 months.

Keywords *Microcystis* · Climate change · Microcystins · Cyanobacteria · Environmental factors · Estuary

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Introduction

Cyanobacteria are common in freshwater aquatic ecosystems worldwide and are an increasing concern due to their long-term increase in frequency and intensity since the 1960s (Carey et al., 2012). *Microcystis*, the most common cyanobacterium in freshwater, has also spread into estuaries including Chesapeake Bay, San Francisco Bay, and Neuse River Estuaries in the United States; the Swan River Estuary in Australia; and the Guadiana River Estuary in Spain and Portugal (Paerl, 1988; Sellner et al., 1988; Rocha et al., 2002; Robson & Hamilton, 2003; Lehman et al., 2005). *Microcystis* is a local health threat to humans and wildlife directly in contact with the blooms because it usually contains microcystins, hepatotoxins that

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promote tumor and liver cancer (Zegura et al., 2003; International Agency for Research on Cancer, 2006; Ibelings & Havens, 2008). However, *Microcystis* toxins can also be a regional health threat. In southern California, microcystins flushed seaward from an inland freshwater lake concentrated in marine mollusks and caused liver cancer in sea otters which rely on mollusks as a food source (Miller et al., 2010). The surface scum produced by *Microcystis* blooms is also well known to affect water quality conditions by impeding recreation, reducing esthetics, lowering dissolved oxygen concentration, and causing taste and odor problems in drinking water (Paerl et al., 2001).

The abundance, frequency, and distribution of *Microcystis* and other cyanobacteria are expected to increase with climate change (Carey et al., 2012). The high Q_{10} of *Microcystis* allows it to grow rapidly compared with other primary producers at high water temperature which is expected to increase with the increased frequency, intensity, and duration of heat waves in North America (Carey et al., 2012; Paerl & Paul, 2012). High water temperature also increases thermal stratification which in turn enhances nutrient limitation near the surface and reduces vertical mixing. Such conditions favor buoyant species like *Microcystis* that can vertically migrate to harvest nutrients throughout the water column (O'Neil et al., 2012). Vertical migration to the surface and tolerance of high light conditions also enable *Microcystis* to adapt to limiting light conditions during blooms which are expected to increase with warmer water temperature (Reynolds, 2006). Similarly vertical migration to the surface enables *Microcystis* to use atmospheric carbon dioxide when dissolved inorganic carbon in the water column becomes limiting during blooms (Reynolds, 2006; Elliott, 2012). Climate change is also expected to increase the frequency, intensity, and duration of high precipitation events as well as droughts (IPCC, 2007). These conditions will further promote *Microcystis* and other cyanobacteria over other primary producers because of their ability to compete well for increased nutrients associated with high runoff from precipitation and to tolerate increased light, salinity, water temperature, stratification, and bloom conditions during drought (Elliott, 2012; O'Neil et al., 2012; Paerl & Paul, 2012).

In San Francisco Estuary (SFE), *Microcystis* colonies have formed widespread surface scums or blooms at varying levels each year since they first became established in 1999 (Lehman et al., 2005, 2008, 2010). Blooms commonly begin in the central delta and spread seaward into brackish water environments with streamflow and tide (Lehman et al., 2005). *Microcystis* blooms pose a threat to human and ecosystem health in SFE because they commonly contain the highly toxic hepatotoxin, microcystin-LR, and microcystins are present throughout the lower food web in clams, mesozooplankton, and juvenile fish (Lehman et al., 2005, 2008, 2010; Acuna et al., 2012a, b). Laboratory bioassays demonstrated that both short and long-term exposure to dissolved and dietary microcystins impact the health and survival of native zooplankton and fish (Ger et al., 2009; Deng et al., 2010; Acuna et al., 2012a, b). Further, the presence of *Microcystis* was associated with a shift in phytoplankton and cyanobacteria species composition, suggesting it may affect the structure as well as the function at the base of the food web (Lehman et al., 2010). Persistent elevated nutrient concentrations in SFE and poor correlation between nutrient concentration and cell abundance suggest that nutrients do not control the year to year variations in *Microcystis* (Lehman et al., 2008). Instead, physical factors such as streamflow and water temperature appear to be of greater importance (Lehman et al., 2008). The importance of environmental factors is confounded by the multiple genotypes and strains of *Microcystis* in SFE (Moisander et al., 2009; Baxa et al., 2010).

It is unknown how *Microcystis* blooms will vary with climate change in SFE. It is hypothesized that *Microcystis* bloom intensity and duration will increase with the elevated water temperature (Paerl & Huisman, 2008). Continuous monitoring data have already demonstrated an increase in water temperature at multiple stations in the Delta since 2000 (Brooks et al., 2012). Models suggest that this long-term increase in water temperature will continue (Cloern et al., 2011). It is further hypothesized that *Microcystis* blooms will increase with the projected increase in the frequency and intensity of drought conditions throughout California with climate change (Cloern et al., 2011). Understanding the current and future causes of *Microcystis* blooms are particularly important in SFE where the blooms are hypothesized to be a contributing factor in the decline of many species of interest including striped bass, the endangered delta smelt, longfin smelt, and mesozooplankton since 2000 (Sommer et al., 2007).

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The purpose of this study was to characterize the trend in *Microcystis* blooms and the associated physical, chemical, and biological factors between 2004 and 2008 and to use this information to gain insight into the causal factors and the potential future variation of *Microcystis* blooms and their toxins with climate change. The study will address the questions: (1) Did *Microcystis* abundance, microcystin toxin concentration or dissolved organic carbon concentration vary with wet and dry conditions? (2) Did the toxin content in the lower food web animals vary with wet and dry conditions? (3) What environmental factors controlled initiation and persistence of the blooms? To address these questions, physical, chemical, and biological data were compiled from five stations sampled monthly to semimonthly during four independent research studies conducted on the *Microcystis* bloom in 2004, 2005, 2007, and 2008; only the data from 2004 and 2005 have been published previously. Additional water temperature and surface irradiance data were obtained from a fixed continuous monitoring station located near Antioch.

Methods

Site description

The SFE consists of an inland delta that flows into a chain of marine bays downstream—Suisun, San Pablo, and San Francisco—and creates one of the largest estuaries on the west coast of North America. The estuary is formed by two rivers, the Sacramento River on the north and the San Joaquin River on the south. These rivers converge to form a delta with 200 km^2 of waterways (Fig. 1). The estuary contains many kinds of habitats from freshwater shallow flooded islands that are 2 m deep in the center of the delta, wide brackish water bays in Suisun Bay, and deep river channels 13 m deep. Water flow in the

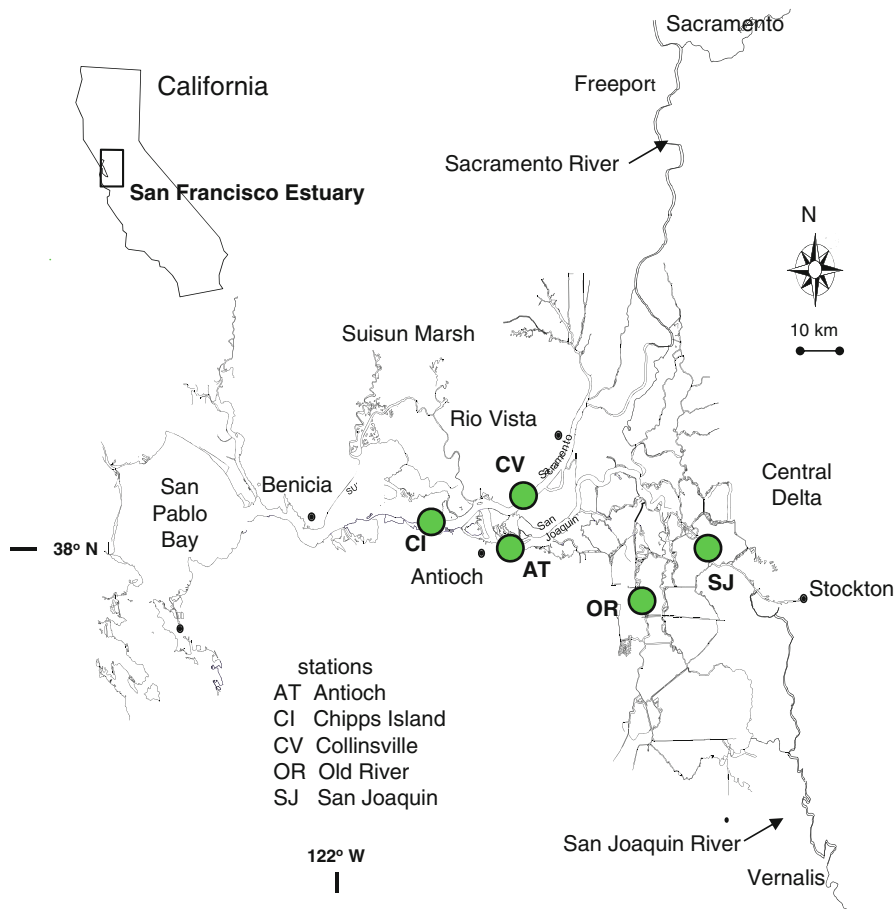

Fig. 1 Location of five stations sampled during *Microcystis* blooms in summers between 2004 and 2008

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channels is influenced by the semidiurnal tide which commonly has a 1.5-m amplitude and up to 6 km excursion. A combination of tide, streamflow, and agricultural diversion keeps the river channels and brackish bays mixed to the bottom. The estuary is turbid with maximum photic zone depth of 2 m. *Microcystis* blooms occur throughout the freshwater and brackish water regions of the estuary between June and October (Lehman et al., 2005). Elevated *Microcystis* abundance usually occurs in the center of the delta in association with the San Joaquin River but the greatest abundance on any given day can occur anywhere throughout the region.

Sampling

Data used in this analysis were combined from research studies that sampled the same five stations (CI, AT, CV, SJ, and OR) biweekly during the summers of 2004, 2005, 2007, and 2008 (Fig. 1). Sampling was conducted between June and October for 2004, 2007, and 2008 and August and September for 2005. For each study, *Microcystis* tissue was collected from the first 0.5 m of the water column using a surface-water tow of a 0.50–0.75-m diameter plankton net fitted with a 75 µm mesh. A net tow was used for collection to get a representative sample of *Microcystis* colonies that were widely dispersed. Use of a wide diameter mesh allowed capture of most of the cyanobacterium colonies that were often 50 mm in diameter while reducing clogging of the net from heavy suspended sediment. Surface water for chemical analysis was collected at 0.3 m by a van Dorn or diaphragm pump sampler.

Concentrated samples from the net tow sample were filtered through GF/F glass fiber filters and processed for pigment or toxin concentration, with final concentration based on the volume of the net tow. Filters for chlorophyll *a* analysis were treated with 1% magnesium carbonate solution to prevent acidity, immediately frozen on dry ice and stored at −4°C until analysis for chlorophyll *a* and pheophytin concentration. Pigments were extracted in 90% acetone and measured using spectrophotometry (American Public Health Association et al., 1998). Filters with tissue for total microcystins analysis were immediately frozen on dry ice and stored at −80°C until processing for total toxic microcystins concentration using protein phosphate inhibition assay (PPIA; Lehman et al., 2005). The PPIA assay is an integrative bioassay that sums the inhibitory activity of all the different microcystins in the sample into a single value. The results are then expressed in terms of microcystin equivalents. For quality control purposes and to ensure that the changes in toxicity observed using the PPIA assay were not due to changes in toxin composition, 274 of the more 600 samples collected in 2007 and 2008 whose microcystin concentrations in the extract solution as determined by the PPIA assay exceeded 0.5 µg l^{-1} were also analyzed by liquid chromatography coupled with photodiode array and mass selective detection (LCMS-PDA) using established methods (Boyer, 2007).

Water samples for chloride, ammonium-N, nitrate plus nitrite-N, and SRP that were filtered through a 0.45-µm nucleopore filter as well as unfiltered whole water samples for total and volatile suspended solids and total organic carbon analysis were kept at 4°C or frozen until analysis (United States Environmental Protection Agency, 1983; United States Geological Survey, 1985; American Public Health Association et al., 1998). Water samples for dissolved organic carbon analysis were filtered through pre-combusted GF/F filters and kept at 4°C until analysis (American Public Health Association et al., 1998). Water temperature, pH, specific conductance turbidity, and dissolved oxygen concentration were measured at 0.3 m using a freshly calibrated Yellow Springs Instrument (YSI) 6600 water quality sonde. Photon flux (µmol photons m^{-2} s^{-1}) of the photosynthetically active radiation (PAR) was measured from the surface to 1% of the surface light level at 0.3 m intervals in the water column using a Li-COR spherical quantum sensor model LI-193. The total and median photon flux of PAR in the photic zone (PAR_{pz}) where *Microcystis* was most abundant was computed from the integrated (triangular) Li-COR values measured from the surface to the depth of 1% of the surface irradiance, reduced by 10% to correct for reflectance at the surface. Water transparency was also measured by Secchi disk depth.

Continuous high-frequency (15-min averaged) data were collected at a fixed monitoring station near AT. These data included water temperature measured with an YSI water quality sonde and surface irradiance (W m^{-2}) measured with an Eppley pyrheliometer (www.iep.water.ca.gov). Pyrheliometer irradiance

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was expressed as PAR by assuming PAR comprised 49% of the total surface irradiance.

Streamflow variables were obtained from the California Department of Water Resources DAYFLOW (www.water.ca.gov/dayflow) database containing both measured and computed values. Upstream San Joaquin River streamflow was described by measured streamflow past Vernalis (QSJR) while upstream Sacramento River streamflow was described by measured streamflow past Freeport (QSAC; Fig. 1). QWEST is a computed value that describes the amount of San Joaquin River streamflow that flows into the central delta past Jersey Point and reflects the inflow from the San Joaquin River and loss from water diversions between Vernalis and Jersey Point. QWEST streamflow values can be negative due to large net reverse streamflows from water diversions at the State (SWP) and Federal (CVP) pumping facilities. In a similar fashion, QRIO describes the amount of water that remains in the Sacramento River at Rio Vista after channel depletions between Freeport and Rio Vista. Unimpaired streamflows were used to classify water years 2004 and 2005 as wet versus 2007 and 2008 as dry (www.waterplan.water.ca.gov).

Biological samples

Microcystis cell abundance estimates were determined from plankton samples collected from the net tow. These samples were immediately stained and preserved with Lugol's solution. *Microcystis* cells were identified and enumerated at 700× using an inverted microscope in 2004 and 2005 (Utermöhl, 1958) or a Fluid Imaging Technologies FlowCAM digital flow cytometer in 2007 and 2008 (Sieracki et al., 1998). Microscope and FlowCAM cell abundance estimates were strongly correlated ($r = 0.88$, $P < 0.01$).

Mesozooplankton were collected by a 3 min diagonal tow of a 0.5-m diameter plankton net fitted with a 150 µm mesh. Zooplankton were kept at 4°C and separated by pipette from *Microcystis* in the water sample using a dissecting microscope within 48 h of sampling. Zooplankton tissue was rinsed in distilled water and frozen at −80°C until toxin analysis by protein phosphatase inhibition assay (PPIA). Zooplankton for identification and enumeration were dyed and preserved in 10% buffered formalin with rose Bengal dye. Species identification and enumeration were conducted using a dissecting microscope.

Data analysis

All statistical analyses were computed with non-parametric statistics using Statistical Analysis System (SAS, 2004) and Primer-e version 6 (Clarke, 1993; SAS Institute, 2004; Clarke & Gorley, 2006). SAS was used to compute simple Spearman rank correlations between single variables. PRIMER-e is a multivariate non-parametric permutation statistical method that was used to test the similarity of patterns in sample groups described by similarity matrices. Analyses mentioned in this study included determining the similarity between biological samples and suites of environmental samples with RELATE, distinguishing significant differences between groups of multivariate samples with ANOSIM, isolating the best match between biological and environmental (multivariate) similarity matrices with BEST and describing the associations among environmental variables and *Microcystis* abundance with principal components analysis (PCA). Similarity of the sample matrices is based on Spearman rank correlation coefficients.

Before PRIMER analyses, *Microcystis* cell abundance and chlorophyll *a* concentration were log transformed and then converted to similarity matrices using a Bray–Curtis Similarity Index which better represents the lack of normality and unequal variance distribution of these biological data (Clarke & Gorley, 2006). Environmental similarity matrices were computed from Euclidean distances that were computed from normalized variables (difference of the value from the mean and divided by the standard deviation). In addition, similarity matrices were only computed for variables that were not intercorrelated ($r > 0.70$). Chloride gram per liter was converted to salinity by the multiplier 1.80655 (American Public Health Association et al., 1998).

Results

Long-term trend

Microcystis abundance was greater during August and September (combined) of dry years than wet years (Fig. 2). Peak abundance occurred in August and September and median abundance exceeded ($P < 0.05$, ANOSIM) that in June or July by a factor of 1.2 (21,101 ± 2,386 cells ml^{-1} for June and July

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and 24,941 ± 32,836 cells ml^{-1} for August and September). Median *Microcystis* abundance in August and September was also greater ($P < 0.01$, ANOSIM) in the dry years 2007 and 2008 with 29,920 ± 21,433 cells ml^{-1} compared with the wet years 2004 and 2005 with 34 ± 311,506 cells ml^{-1} (Table 1). Abundance increased throughout the Delta in dry years and was greater at stations in both the central Delta (OR and SJ, $P < 0.05$) and western Delta near the confluence (AT, CI and CV, $P < 0.01$; Fig. 2).

Median chlorophyll *a* concentration within the 0.5-m surface layer was also greater in August and September during dry years ($P < 0.01$, ANOSIM; 36 ± 53 ng l^{-1} and 110 ± 132 ng l^{-1} for wet and dry years, respectively; Fig. 2 and Table 1). Among months, median chlorophyll *a* concentration was lowest for August 2004 ($P < 0.05$) but did not differ among years for September. Among stations, chlorophyll *a* concentration was greater in the central delta at SJ and OR than near the confluence at AT, CV, and CI (130 ± 82 ng l^{-1} and 20 ± 48 ng l^{-1}, respectively). Similar patterns of chlorophyll *a* concentration and *Microcystis* abundance were due to their correlation which was greater in dry years when *Microcystis* biomass increased ($r = 0.43$, $P < 0.01$ for 2004–2005 and $r = 0.78$, $P < 0.01$ for 2007–2008).

Median dissolved organic carbon concentration ranged from 1.7 to 2.3 mg l^{-1} during the peak of the bloom in August and September (Fig. 2). There was no significant difference in dissolved organic carbon concentration among all years during the peak of the bloom but abundance was greater for both months in the dry year 2008 than the wet year 2005 ($P < 0.05$; Table 1). Dissolved organic carbon concentrations also varied directly with the bloom and increased with all measures of the bloom intensity, *Microcystis* abundance, chlorophyll *a* concentration, and total microcystins concentration ($r = 0.44$, $r = 0.55$, $r = 0.60$, $P < 0.01$; respectively).

Total microcystins concentration was over an order of magnitude greater in dry years (Fig. 2; Table 1). Median total microcystins concentration was greater in 2005, 2007, and 2008 at 36 ± 55 ng l^{-1} than in 2004 at 2 ± 5 ng l^{-1} ($P < 0.01$, ANOSIM). Concentrations increased with *Microcystis* abundance and were greater for dry years when *Microcystis* was more abundant ($r = 0.81$, $P < 0.01$ for 2007–2008 and $r = 0.43$, $P < 0.01$ for 2004–2005). Median total

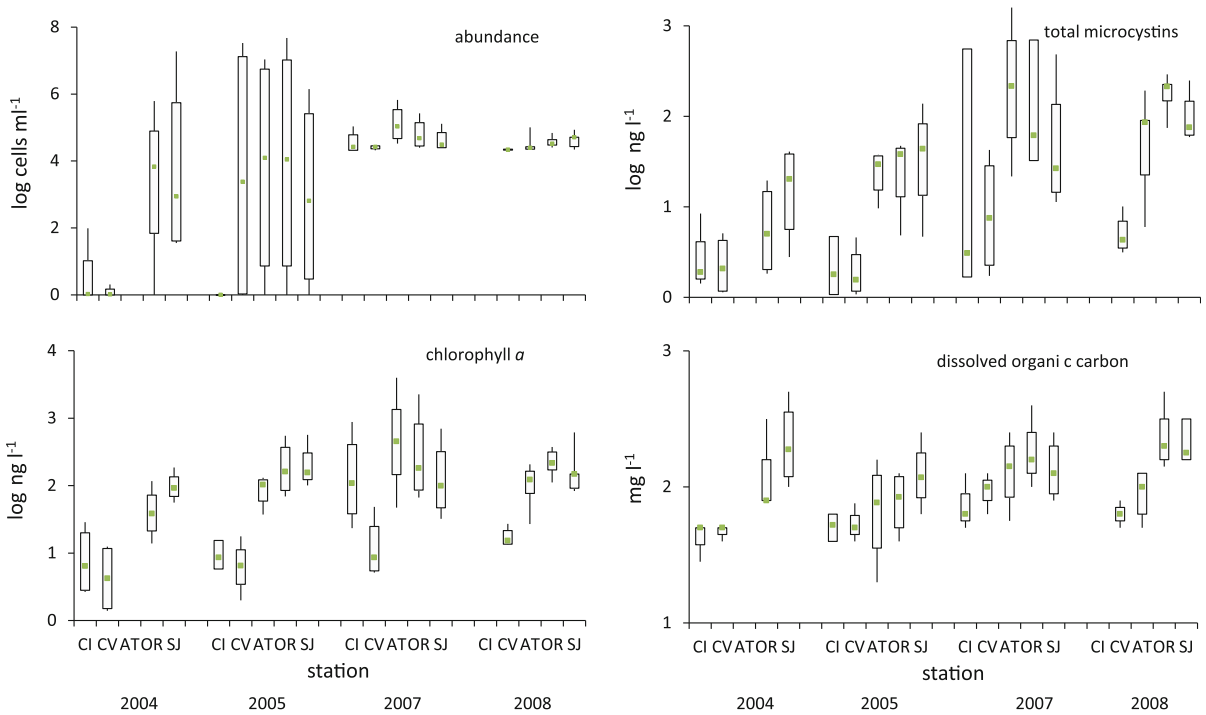

Fig. 2 Maximum, minimum, median and 25 and 75% quartiles for *Microcystis* cell abundance as well as chlorophyll *a*, total microcystins, and dissolved organic carbon concentration measured at five stations in the delta in the summer between 2004 and 2008

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microcystins concentration varied little among years during the peak of the bloom in August and September except for the greater concentration in August of 2007 ($P < 0.01$, ANOSIM). Among stations, total microcystins concentration was greater in the San Joaquin River at AT, SJ, or OR than the Sacramento River at CI or CV ($P < 0.05$, ANOSIM; 29 ± 33 ng l^{-1} and 0.79 ± 1.5 ng l^{-1}). Median total microcystins cellular content was 0.7 ± 1.4 pg $cell^{-1}$ and did not differ significantly between wet and dry years or among stations.

Although the total mesozooplankton carbon was similar among stations for the wet year 2005 and the dry year 2007 (Fig. 3), the maximum total microcystins content was somewhat greater in the dry year 2007 than the wet years 2004 or 2005 (Table 2). Mesozooplankton tissue contained 0.14–0.74 µg (g dry - weight)$^{-1}$ total microcystins in 2004 and up to 1.43 µg (g dry weight)$^{-1}$ in 2005. This was lower than the maximum 2.55 and 3.14 µg (g dry weight)$^{-1}$ measured at CI and CV in the dry year 2007. High variability and the relative nature of these values limited further conclusions.

Environmental conditions

A seasonal threshold response characterized the association between *Microcystis* and water temperature or light. *Microcystis* was present only when surface water temperature was 19°C or greater (Fig. 4). Peak abundance occurred near 23°C, but relatively high abundance persisted up to the maximum recorded water temperature of 25.6°C. These

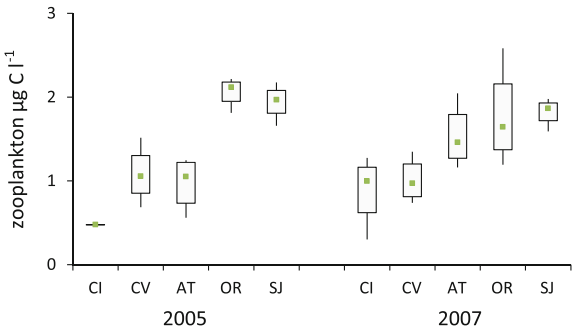

Fig. 3 Maximum, minimum, median and 25 and 75% quartiles for mesozooplankton carbon (µg C l^{-1}) collected by diagonal net tow at five stations sampled in 2005 and 2007 during the peak of the *Microcystis* bloom in August and September

water temperatures restricted the *Microcystis* bloom to the summer months between June and October. The daily average surface irradiance during this period was 167 ± 7 to 126 ± 7 W m^{-2} (Fig. 5a). Blooms disappeared in October or November once surface irradiance dropped below 98 ± 14 W m^{-2}. However, surface irradiance greater than 126 W m^{-2} occurred as early as March and suggested water temperature and not surface irradiance limited *Microcystis* growth between March and June.

Light within the water column was influenced by turbidity. *Microcystis* occurred when total suspended solids concentration was <50 mg l^{-1} (Fig. 4). These values were associated with an integrated average PARpz of over 50 µmol photons m^{-2} s^{-1}, with most blooms occurring when the average PARpz ranged between 50 and 200 µmol photons m^{-2} s^{-1} (Fig. 5b). The median extinction coefficient during blooms was 1.9 ± 0.41 m^{-1}.

In general, *Microcystis* occurred over a wide range of most physical and chemical conditions that were not linearly correlated with abundance (Fig. 4). *Microcystis* occurred in fresh to brackish water conditions where specific conductance was less than 12,000 µS cm^{-1}, salinity was between 0 and 3,500 and pH was between 7.5 and 9.6. Nutrient concentrations varied by a factor of 5 during the blooms with peak *Microcystis* abundance occurring near the low end of the range of concentrations for nitrate–N, SRP, or ammonium-N concentration (ranged from 0.1 to 0.4 mg l^{-1}, 0.03 to 0.09 mg l^{-1}, and 0.01 to 0.08 mg l^{-1}, respectively). *Microcystis* also occurred in the lower end of the range for DIN:DIP molar ratios from 5 to 22.

For streamflow, *Microcystis* was abundant in the San Joaquin River when QWEST ranged from positive 48 to negative 169 m^3 s^{-1} and QSJR ranged from 28 to 84 m^3 s^{-1} (Fig. 6). For the Sacramento River, *Microcystis* was associated with QRIO in the Delta between 113 and 3,030 m^3 s^{-1} and QSAC upstream between 300 and 600 m^3 s^{-1}. Peak abundance occurred at a narrower range of streamflows near negative 100 m^3 s^{-1} for QWEST and 250 m^3 s^{-1} for QRIO, 80 m^3 s^{-1} for QSJR and 500 m^3 s^{-1} for QSAC. Elevated chlorophyll *a* concentration occurred over an even wider range of streamflows than *Microcystis*; 20–80 m^3 s^{-1} for QSJR, negative 250–50 m^3 s^{-1} for QWEST, 200–600 m^3 s^{-1} for QSAC, and 100–450 m^3 s^{-1} for QRIO (not shown).

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Table 1 Comparison of median with 25 and 75% percentile confidence limits of physical, chemical, and biological data for the wet years 2004 and 2005 and dry years 2007 and 2008 measured during the peak of the *Microcystis* bloom in August and September

Variable	Wet year	Dry year	Significance level
Microcystis (cells ml^{-1})	34 ± 311,506	29,920 ± 21,433	0.05
Total microcystins (ng l^{-1})	3.8 ± 16.9	60.5 ± 90.9	0.01
Chlorophyll *a* (ng l^{-1})	36.4 ± 52.7	110.4 ± 132.6	0.01
Pheophytin (ng l^{-1})	7.2 ± 4.8	1.9 ± 13	ns
Water temperature (°C)	21.6 ± 1.2	21.8 ± 1.3	ns
Secchi disk depth (cm)	72 ± 42	88 ± 42	0.05
Specific conductance (μS cm^{-1})	1002 ± 2,325	1,438 ± 2,225	ns
Chloride (mg l^{-1})	232 ± 736	331 ± 671	ns
Total suspended solids (mg l^{-1})	7.5 ± 13	6 ± 4	ns
Volatile suspended solids (mg l^{-1})	2 ± 2	1 ± 1	0.01
Dissolved oxygen (mg l^{-1})	8.7 ± 0.5	8.5 ± 0.4	ns
pH	7.9 ± 0.1	8.0 ± 0.3	ns
Turbidity NTU	14.8 ± 14.4	7.1 ± 3.8	0.01
Ammonium (mg l^{-1})	0.03 ± 0.02	0.04 ± 0.01	ns
Nitrate (mg l^{-1})	0.26 ± 0.04	0.28 ± 0.06	0.05
Soluble reactive phosphorus (mg l^{-1})	0.06 ± 0.01	0.06 ± 0.01	ns
NP molar ratio	10.8 ± 1.3	12.0 ± 2.1	ns
Silica (mg l^{-1})	14.3 ± 0.75	14.5 ± 0.9	ns
Total organic carbon (mg l^{-1})	2.2 ± 0.4	2.2 ± 0.2	ns
Dissolved organic carbon (mg l^{-1})	1.8 ± 0.2	2.1 ± 0.2	0.01
Sacramento River-Freeport (m^3 s^{-1})	498 ± 28	433 ± 83	0.01
Sacramento River-Rio Vista (m^3 s^{-1})	275 ± 18	238 ± 63	0.01
San Joaquin River-Vernalis (m^3 s^{-1})	58 ± 22	28 ± 1	0.01
San Joaquin River-Jersey Point (m^3 s^{-1})	−94 ± 15	−88 ± 68	ns

Correlations between biological and environmental data

Microcystis abundance across the Delta was correlated with the suite of physical and chemical variables ($P < 0.01$, RELATE). About 72% of the variability in the environmental variables associated with the *Microcystis* bloom over time was characterized by five PCA axes (Table 3). The first two axes each described 22–23% of the variance in the environmental data with an additional 7–11% of the variation described by each of the additional three PCA axes. Of these, only PCA axes 1, 2, and 5 were significantly correlated with *Microcystis* abundance (Table 3).

An overlay of *Microcystis* abundance on the ordination of the first and fifth PCA axes suggested that *Microcystis* occurred during warm water temperature, low turbidity, and low streamflow conditions (Fig. 7). *Microcystis* abundance varied most closely with PCA axis 1 ($r = 0.41$, $P < 0.01$) which primarily described a combination of warm water temperature, low nitrogen concentration (total and ammonium), low QWEST flow, and low turbidity. *Microcystis* abundance was similarly correlated with axis 5 ($r = 0.39$, $P < 0.01$) which primarily described a combination of low San Joaquin River streamflow, low turbidity, and high dissolved oxygen concentration. There was also a somewhat lower, but negative correlation between *Microcystis* abundance and PCA axis 2 ($r = -0.20$, $P < 0.05$; not shown) which was largely the opposite of PCA axis 1. PCA axis 2 described conditions associated with high chloride and turbidity and low total organic carbon concentration, water temperature, and QWEST flow.

However, only a few of these variables accounted for most of the variation in *Microcystis* abundance

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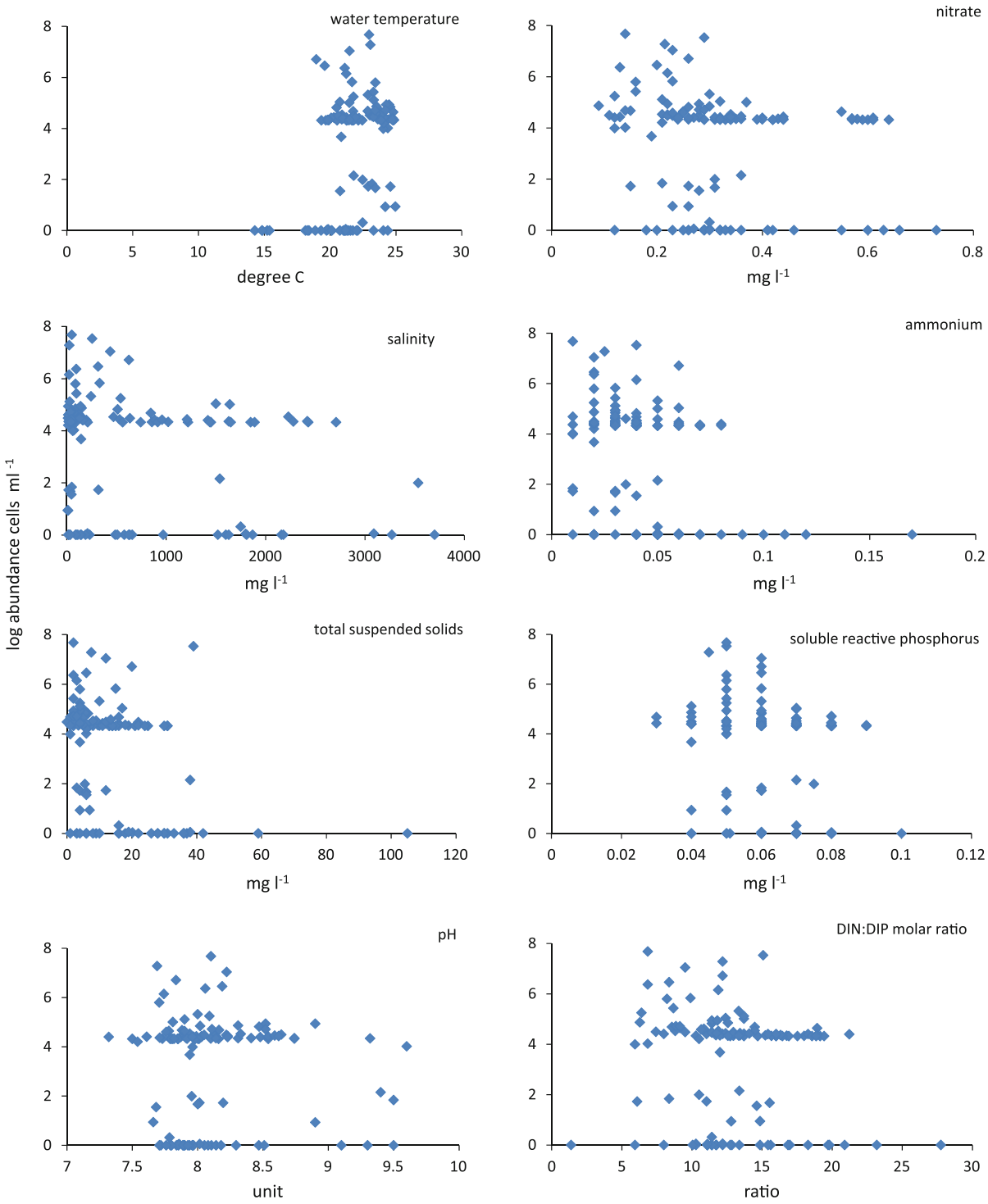

Fig. 4 Associations between *Microcystis* cell abundance and physical and chemical variables measured for five stations during summers between 2004 and 2008

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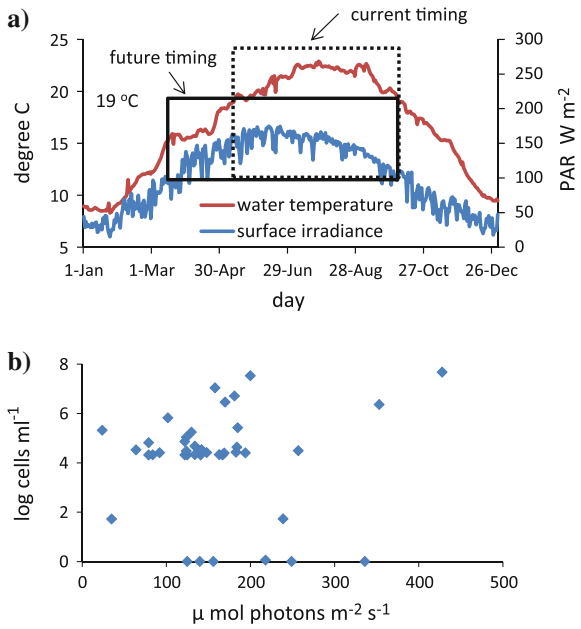

Fig. 5 **a** Average daily variation of PAR as surface irradiance (Eppley pyrheliometer) and water temperature at 1 m depth at Antioch for 2004, 2005, 2007, and 2008. **b** Average PAR (LiCOR) within the photic zone associated with *Microcystis* abundance at five stations in the Delta during summers between 2004 and 2008

based on BEST analysis which determines the best match between biotic and abiotic similarity matrices. The combination of turbidity and SJR described the largest variation in *Microcystis* abundance ($r = 0.47$, $P < 0.01$, BEST). However, most of this variation was due to the inverse correlation between *Microcystis* abundance and turbidity ($r = 0.35$, $P < 0.01$, BEST). Turbidity also accounted for most of the variation in *Microcystis* abundance during the peak of the bloom in August and September ($r = 0.40$, $P < 0.01$, BEST) and was produced by total suspended solids in the water column ($r = 0.79$, $P < 0.01$).

Chlorophyll *a* concentration was also correlated with the suite of physical and chemical variables across the Delta ($P < 0.01$, RELATE). Most of the variation was associated with turbidity and total nitrogen ($r = 0.42$, $P < 0.01$, BEST), with turbidity accounting for nearly all of the variance ($r = 0.41$, $P < 0.01$, BEST). Turbidity also described most of the variability in chlorophyll *a* concentration during the peak of the bloom in August and September ($r = 0.32$, $P < 0.01$, BEST). The inverse correlation between chlorophyll *a* concentration and turbidity occurred at all stations ($r = -0.39$ to $r = -0.65$, $P < 0.01$) except AT where chlorophyll *a* concentration was

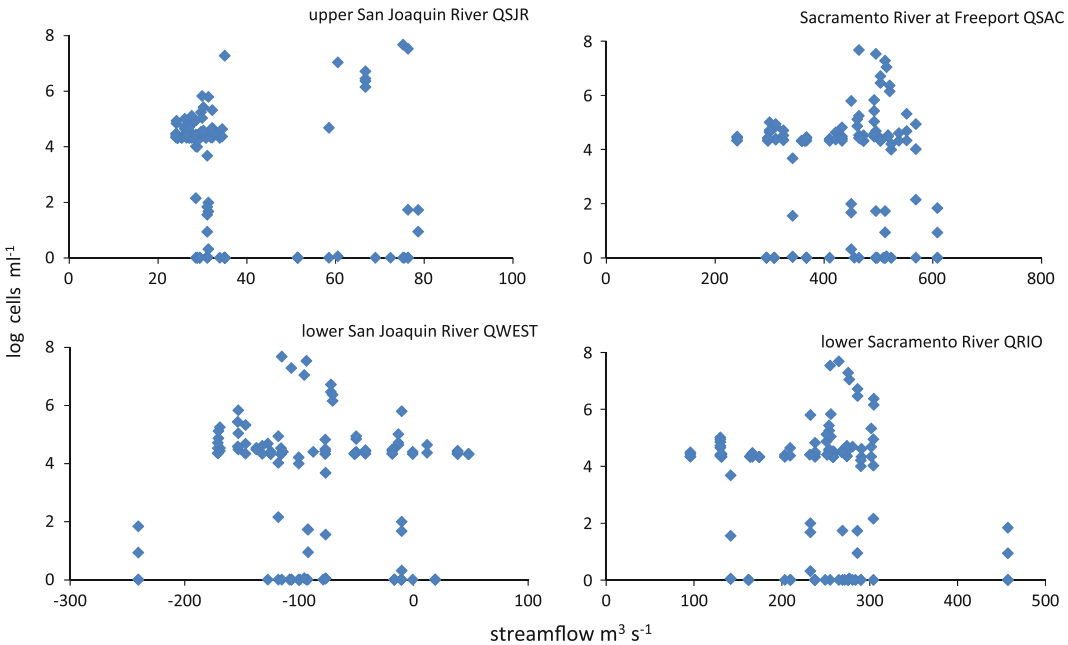

Fig. 6 Associations between *Microcystis* abundance and streamflow variables during the summer between 2004 and 2008

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Table 2 Median with 25 and 75% percentile confidence limits or detection limits for total toxic microcystins content in mesozooplankton [μg microcystins (μg dry weight)$^{-1}$] collected at five stations in 2004, 2005, and 2007

Date	Antioch	Chipps Is.	Collinsville	Old River	San Joaquin
August and October 2004			0.74 ± 0.79		0.14 ± 0.15
August and September 2005	<1.05	<3.99	<0.22	<3.14	1.43 ± 0.62
June 26, 2007	<0.67	0.25 ± 0.04	0.87 ± 0.11	<0.72	NA
July 10, 2007	<0.38	1.17 ± 0.12	<4.05	<0.81	0.68 ± 0.09
July 24, 2007	<1.58	<0.41	<15.00	<1.58	<0.66
August 7, 2007	<0.75	<12.00	<8.57	<0.87	<0.95
August 21, 2007	<0.98	<20.00	<0.52	<2.40	<0.38
September 4, 2007	<2.73	2.55 ± 0.04	3.14 ± 0.10	<3.75	<0.29
September 17, 2007	0.70 ± 0.25	<3.33	<0.40	<2.72	<0.72

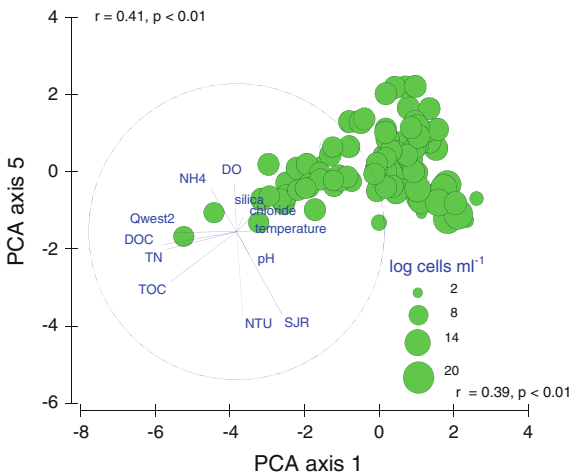

Fig. 7 Ordination of principal component axes 1 and 5 describing the associations among environmental factors overlaid with coincident *Microcystis* abundance (*circles*) for blooms in 2004, 2005, 2007, and 2008. All variables are normalized to the mean

more closely correlated with nitrate and total nitrogen concentration ($r = -0.58$ and $r = -0.60$, $P < 0.01$).

Similar to *Microcystis* abundance and chlorophyll *a* concentration, total microcystins concentration was correlated with the suite of physical and chemical variables (P <0.01, RELATE) at stations across the Delta. It was also correlated with turbidity ($r = 0.19$, $P < 0.01$, BEST), but the correlation was low. The similar direction of the correlations between total microcystins or *Microcystis* abundance and environmental conditions was probably due to their strong correlation ($r = 0.68$, P <0.01). In contrast, the total microcystins cellular content was not correlated with the suite of physical and chemical variables and weakly correlated with individual variables ($r = -0.21$, $r = -0.21$, and $r = -0.25$, $P < 0.05$ for dissolved oxygen concentration, turbidity, and the DIN:DIP molar ratio).

Streamflow

Streamflow probably directly affected the distribution and accumulation of *Microcystis* colonies in wet and dry years. The increased abundance of *Microcystis* in dry years was accompanied by 13–52% ($P < 0.01$) lower streamflows in both the Sacramento and San Joaquin Rivers (Table 1). The bloom also occurred when there was a combination of both cross delta streamflow from QRIO and water diversions from the south delta. The eastward movement of water across the delta from the Sacramento River into the San Joaquin River was suggested by the inverse correlation between QWEST at Jersey Point and streamflow at QRIO ($r = -0.70$, $P < 0.01$). Some of this water from QRIO replaced water diverted for agriculture in the lower San Joaquin River as suggested by the inverse correlation between QWEST and SWP or CVP ($r = -0.75$ and $r = -0.68$, $P < 0.01$). Diversions in the Delta were also linked to the overall wet and dry conditions in the Delta because agricultural water diversion increased directly with the magnitude of both QSJR and QSAC ($r = 0.84$ and $r = 0.62$, $P < 0.01$ for QSAC; and $r = 0.49$ and $r = 0.45$, $P < 0.01$ for QSJR with SWP and CVP, respectively).

Streamflow probably indirectly affected *Microcystis* abundance through impacts on the physical and chemical conditions in the Delta during wet and dry

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Table 3 Principal component analysis of non-correlated environmental variables measured during *Microcystis* blooms and the correlation between the principal component scores of these axes and *Microcystis* abundance for 2004–2008

Variable	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Water temperature	0.35	−0.26	−0.22	0.35	0.11
Dissolved oxygen	−0.11	0.11	0.00	−0.75	0.40
pH	0.06	0.05	−0.63	−0.35	−0.26
Turbidity	−0.33	0.32	−0.12	0.09	−0.44
Ammonium-N	−0.37	0.17	−0.07	0.09	0.14
Chloride	−0.27	0.42	0.03	0.10	0.01
Total dissolved inorganic nitrogen	−0.50	−0.15	0.04	0.08	−0.10
Dissolved organic carbon	−0.19	−0.54	0.03	−0.06	−0.02
Silica concentration	−0.13	0.21	−0.34	0.39	0.39
Total organic carbon	−0.27	−0.39	−0.29	−0.05	−0.35
QWEST flow	−0.34	−0.25	0.39	0.03	0.16
San Joaquin River streamflow	0.23	0.20	0.43	−0.06	−0.48
Percent variation	23	22	11	10	7
Correlation with *Microcystis* abundance	**0.41**	−0.20			**0.39**

Correlation coefficients are significant at the 0.01 level (bold text) and 0.05 level (plain text)

conditions. Water temperature decreased with streamflow in the San Joaquin River at QSJR and QWEST ($r = -0.18$, $P < 0.05$; $r = -0.27$, $P < 0.01$) and increased with streamflow in the Sacramento River QSAC and QRIO ($r = 0.28$, $P < 0.01$; $r = 0.23$, $P < 0.05$). Turbidity increased with streamflow at both QSAC and QRIO ($r = 0.26$, $P < 0.01$ and $r = 0.20$, $P < 0.05$) in the Sacramento River. Total and volatile suspended solids also increased with QRIO near the confluence at AT, CI, and CV ($r = 0.29$ and $r = 0.30$, $P < 0.05$) and with QSJR flow in the San Joaquin and Old River at stations SJ and OR ($r = 0.21$, $P < 0.01$; $r = 0.35$, $P < 0.01$). Nitrate, total nitrogen, SRP, and total and dissolved organic carbon in the Delta, increased with flow at QWEST ($r = 0.32$ to $r = 0.52$; $P < 0.01$). In contrast, nutrient concentrations decreased upstream at high streamflow. For the San Joaquin River, nitrate, total nitrogen, SRP, silica and dissolved organic carbon concentrations decreased with QSJR ($r = -0.26$ to $r = -0.33$, $P < 0.01$). Similarly, ammonium, nitrate, total nitrogen, SRP, and dissolved organic carbon decreased with high streamflow for the Sacramento River at QSAC ($r = -0.19$, $P < 0.05$; $r = -0.46$, $P < 0.01$; $r = -0.46$, $P < 0.01$; $r = -0.39$, $P < 0.01$; $r = -0.35$, $P < 0.01$) and QRIO ($r = -0.43$, $r = -0.43$, $r = -0.31$, $r = -0.36$, $P < 0.01$).

The influence of streamflow on environmental conditions may partially explain the differences in environmental conditions between wet and dry years (Table 1). Streamflow was relatively low in the upper Sacramento and San Joaquin Rivers at most locations and coupled with low water diversions for agriculture during dry years. These years were characterized by a 50% reduction in turbidity and volatile suspended solids as well as a 60% increase in specific conductance. A relatively smaller but significant increase in pH of 6% and decrease in nitrate concentration of 8% also occurred.

Discussion

Long-term trend

Microcystis abundance and toxin concentration increased over the study period and were greater during dry years. Dry years were generally characterized by low streamflow and low total suspended solids, but elevated water temperature and inorganic and organic nutrient concentrations (Lehman, 2000). These factors correlate well with *Microcystis* abundance in SFE (Lehman et al., 2008, 2010). *Microcystis* occurs in these conditions worldwide because it can outcompete other primary producers at elevated nutrient concentration and water temperature and light near the surface where it occurs during the day (Paerl et al., 2001). Dry conditions were also characterized by greater ammonium concentrations due to reduced dilution of waste water treatment discharge in the Sacramento River (Jassby, 2005). Elevated ammonium concentrations can favor *Microcystis* which

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outcompetes other primary producers for ammonium (Takamura et al., 1987; Jassby, 2005; Yoshida et al., 2007).

The increased *Microcystis* abundance in dry years was accompanied by an expansion of the spatial distribution seaward. This expanded distribution may reflect the presence of more favorable physical and chemical water quality conditions for *Microcystis* growth throughout the delta in dry years. It may also reflect decreased streamflows and increased water residence time that enable *Microcystis* colonies to accumulate throughout the delta instead of being flushed downstream. Because *Microcystis* maximum potential growth rate is slow compared with other primary producers, blooms can reflect accumulation of colonies more than elevated growth rate (Wang et al., 2010; Elliott, 2012). Previous measurements of growth rate in 24 h dissolved oxygen light and dark bottle incubation studies confirmed the average maximum specific growth rate of *Microcystis* and associated communities in surface waters of the delta ranged from 1.15 to 2.38 mg C (mg chl $a)^{-1}$ h^{-1} (Lehman et al., 2008). This is lower than the minimum 3.6–4.4 mg C (mg chl $a)^{-1}$ h^{-1} measured by similar dissolved oxygen incubation techniques for other primary producers in floodplain and riverine habitats within the delta (Lehman et al., 2008).

Microcystis may have increased in the dry years 2007 and 2008 partly because it has become better adapted to conditions in the delta over time. *Microcystis* blooms in SFE and northern California contain multiple genotypes that would allow them to adapt to environmental conditions (Moisander et al., 2009; Bozarth et al., 2010). For example, a separate genotype in the western delta suggested that *Microcystis* may have evolved to tolerate the elevated salt in this region of SFE where salinity reaches 18 (Moisander et al., 2009). It is unknown if *Microcystis* colonies grow or merely tolerate these brackish water conditions because growth is thought to stop at salinity greater than 10–12.6 (Tonk et al., 2007; Black et al., 2011). However, strains within each genotype could rapidly adjust to local environmental conditions. Quantitative PCR analysis indicated that toxic strains varied both spatially and temporally on a biweekly basis across the delta in 2007 (Baxa et al., 2010). The presence of different strains was further suggested by the presence of at least 11 different types of microcystins within *Microcystis* blooms in 2004 and 2005 (Lehman et al., 2005, 2008). Such variability is common within *Microcystis* blooms; for example, 14 different types of microcystins occurred throughout the bloom season in German lakes (Fastner et al., 1999).

The increase in toxic total microcystins concentration and dissolved organic carbon concentration in *Microcystis* blooms and within mesozooplankton tissue over time was probably due to the increase in *Microcystis* abundance and not an increase in cellular toxicity or extracellular release of dissolved organic carbon. Total microcystins concentration and *Microcystis* biomass are often poorly correlated because not all cells within *Microcystis* blooms contain microcystins (Davis et al., 2009). However in SFE, because most of the *Microcystis* tissue samples contained toxic microcystins, there was a strong correlation between total microcystins concentration and *Microcystis* cell abundance. Further, because dissolved organic carbon concentration decreased with streamflow, the increased concentration in dry years may have been due to increased *Microcystis* abundance. These relationships may change in future blooms. Toxic and non-toxic varieties of *Microcystis* respond differently to nutrient and temperature changes (Davis et al., 2009) and as the abundance increases during blooms, toxic strains are sometimes replaced by non-toxic strains with different physiological characteristics and vice versa (Briand et al., 2008, Rinta-Kanto et al., 2009). PCR analyses conducted for the 2007 bloom identified both toxic and non-toxic strains in the delta (Baxa et al., 2010).

Environmental factors

Threshold conditions

Both threshold and maintenance conditions control the seasonal initiation, persistence, and decline of *Microcystis* blooms in SFE. A threshold response for water temperature characterized the initial phase of the *Microcystis* bloom in the early summer when water temperature reached 19°C and probably initiated vertical migration of *Microcystis* vegetative cells that have been shown in other systems to remain at the bottom of the water column over the winter (Verspagen et al., 2005). A higher water temperature threshold of 20°C was reported for 2005, but this probably reflects the later start of the sampling

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program that year (Lehman et al., 2008). An initial water temperature threshold of 7–18.8°C has been measured for *Microcystis* growth in laboratory and field studies worldwide (Latour et al., 2004; Jiang et al., 2008). *Microcystis* can grow at water temperatures as high as 29–32°C, but optimum growth often occurs around 25–30°C (Robarts & Zohary, 1987; Davis et al., 2009). Because maximum water temperature in the delta is commonly 25–30°C, the bloom is probably not inhibited by an upper water temperature threshold.

The initiation of the bloom was also facilitated by a light threshold of surface irradiance in the visible range above 100 W m^{-2}, turbidity less than 50 NTU, and average integrated PAR_{pz} of over 50 μmol photons m^{-2} s^{-1}. The surface irradiance threshold is reached 3 months earlier than the water temperature threshold, making water temperature the variable that is most likely to restrict the bloom to June through September. Light is also thought to trigger the initial vertical migration of vegetative over-wintering colonies from bottom sediments to the surface in the summer and the bottom in the fall (Sigee, 2005). After initiation of the bloom, light is thought to be adequate because *Microcystis* colonies can migrate to the surface of the water column where light is available. A high-effective quantum yield allows *Microcystis* colonies to outcompete other primary producers at the high surface irradiance levels near the surface that would inhibit most other planktonic primary producers (Wu et al., 2011).

However, the strong negative correlation between *Microcystis* abundance and turbidity in this study suggested light or one of its correlates was an important environmental factor needed to maintain daily growth in SFE. Low turbidity may directly facilitate *Microcystis* growth in SFE where high turbidity creates light-limited growth for most primary producers (Jassby, 2005). Light was also found to be an important factor controlling the duration and onset time of *Microcystis* blooms in Lake Taihu, China (Zhang et al., 2012). Turbidity may also be a proxy for water residence time in the delta because turbidity decreases at low streamflow due to sedimentation of particulate matter and reduced transport of sediment from upstream in this very turbid estuary (Lehman, 2004; Wright & Schoellhamer, 2004). Turbidity could also be a proxy for vertical mixing which increases at elevated streamflow and would negatively impact *Microcystis* growth by limiting the time colonies remain in the surface layer during the day where light is elevated and transport is maximized. Vertical mixing of deep riverine channels has been associated with reduced net primary productivity in the Delta where the photic zone is shallow due to heavy sediment (Cloern, 1987). In addition, vertical mixing is physically detrimental to *Microcystis* colonies because it disaggregates large buoyant colonies into small, less buoyant ones (O'Brien et al., 2004).

Nutrients

The maintenance of *Microcystis* blooms requires the availability of the macronutrients nitrogen and phosphorus, but there was no suggestion that these nutrients or their ratio controlled the seasonal or inter-annual variation in the bloom. The nitrate concentration greater than 0.2 mg N l^{-1} and SRP concentration greater than 0.003 mg l^{-1} needed to support *Microcystis* growth in laboratory cultures (Jiang et al., 2008) was well below the average ambient nitrate and SRP concentrations in SFE of 0.32 ± 0.14 mg l^{-1} and 0.07 ± 0.04 mg l^{-1}. However, both nitrate and SRP concentrations in SFE were far lower than the 8.7 mg N l^{-1} nitrate and 0.22 mg l^{-1} SRP measured for maximum growth yield at Laguna de Bay in the Philippines or the 1.4 mg l^{-1} total nitrogen concentration needed to efficiently metabolize carbohydrate and maintain buoyancy in laboratory cultures (Brookes & Ganf, 2001; Baldia et al., 2007). This suggests that increased nutrient concentrations could increase the magnitude of the bloom in SFE.

It is also possible that nitrate may be of lesser importance as a source of nitrogen for *Microcystis* growth in SFE because of the availability of ammonium. *Microcystis* has a strong affinity for ammonium which gives it a competitive advantage over other primary producers even at low concentrations (Takamura et al., 1987). An ammonium concentration of 0.025 mg N l^{-1} was sufficient to support a *Microcystis* bloom in Lake Erie, USA while an ammonium concentration of only 0.007 mg N l^{-1} was sufficient to support a *Microcystis* bloom in Steilacoom Lake, WA (Jacoby et al., 2000; Chaffin et al., 2011). The summer time ammonium concentration of 0.04 ± 0.02 mg N l^{-1} was therefore probably sufficient to support the *Microcystis* bloom in SFE. Recent stable

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isotope analyses of the $\delta^{15}N$ in particulate organic matter for 2007 and 2008 by Lehman confirmed that ammonium was the sole nitrogen source during *Microcystis* blooms in all but a few samples. The preference of ammonium and not nitrate as the primary nitrogen source for primary producers was also supported by nitrogen uptake studies in the Sacramento River (Parker et al., 2012). The often exclusive uptake of ammonium casts doubt on the importance of Redfield level DIN:DIP molar ratios on *Microcystis* growth as well (Glibert et al., 2011). Median DIN:DIP molar ratios of 11.4 (range 5.8–17.7) in SFE during the peak of the bloom in August and September were usually near or a little lower than the Redfield ratio of 16 needed for optimum phytoplankton growth but drop precipitously to a median of 1.31 (range 0.2–3.2) when ammonium is the only nitrogen source used. DIN:DIP molar ratios in SFE were also similar to those in Steilacoom Lake where peak *Microcystis* biomass occurred at DIN:DIP molar ratios less than 15 (Jacoby et al., 2000). Nitrogen and phosphorus concentrations or their ratio were also not correlated with *Microcystis* blooms in Lake Taihu, China (Zhang et al., 2012).

While the SRP concentration in SFE was not categorized as limiting for growth, it may have influenced the structure and function of the bloom. Phosphorus may be important for regulating vertical migration in SFE. The average ambient SRP concentration in SFE of 0.07 ± 0.04 mg l^{-1} was below the 0.2 mg l^{-1} upper threshold that facilitates growth of wide diameter colonies (Shen & Song, 2007). Wide diameter colonies, like those in SFE, are more buoyant and have lower half saturation constants for phosphorus uptake than small diameter colonies which make them more competitive for nutrients. Slow growth of wide diameter colonies also reduces nutrient depletion while limiting the growth of food resources that support predator populations (Raikow et al., 2004; Shen & Song, 2007).

Streamflow

Streamflow was probably the most important maintenance factor for the bloom. Low streamflows were needed to provide sufficiently long water residence time for the slow growing *Microcystis* colonies to accumulate into blooms (Reynolds, 1997). *Microcystis* blooms were associated with streamflows less than 13–15 m^3 s^{-1} in the Swan River and Neuse River estuaries (Christian et al., 1986; Robson & Hamilton, 2003). Previous research in SFE suggested that *Microcystis* blooms occur when streamflow is low at 28–35 m^3 s^{-1} in the San Joaquin River (Lehman et al., 2008). In this study we refined these streamflow levels to negative 240 to positive 50 m^3 s^{-1} for the QWEST index and 100–450 m^3 s^{-1} for QRIO. A comparatively high streamflow may be needed initially to move colonies from the upper San Joaquin River into the central delta where high residence time associated with low advective and dispersive streamflow would retain colonies in the delta. Flushing along with salinity was similarly found to be the primary driver of *Microcystis* blooms in the Volkerak Estuary, the Netherlands (Verspagen et al., 2006). Streamflow was also correlated with all of the environmental variables, particularly turbidity which was the variable most closely associated with *Microcystis* abundance, chlorophyll *a* concentration and total microcystins concentration. Importantly, it affected both water temperature and light which were key variables in the seasonal initiation and decline of the bloom.

Climate change

The increase in water temperature, light intensity, and nutrient concentration associated with future climate change will likely increase the intensity and duration of *Microcystis* blooms in SFE. *Microcystis* first appeared about 2000 when both the minimum and maximum average water temperature between 1984 and 2007 increased by 1–2°C at three continuous monitoring stations in the Delta (Brooks et al., 2012). *Microcystis* blooms could intensify as water temperature increases because *Microcystis* outcompetes other primary producers at elevated water temperature (Paerl & Huisman, 2008; Paerl & Paul, 2012). Modeling studies also suggest that increased water temperature in the spring could lead to earlier timing and duration of cyanobacteria blooms (Elliott, 2012). This would apply to *Microcystis* blooms in the Delta as well where earlier occurrence of the 19°C water temperature threshold, coupled with the already adequate surface irradiance, could extend the bloom by as much as 3 months into the spring. In fact, water temperature has already increased during the spring by at least 0.5–1°C since 1985 (Lehman, 2004). Increased maximum, minimum, and mean water temperature as

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well as light intensity were also important in extending the duration of *Microcystis* blooms in Lake Taihu, China (Zhang et al., 2012).

Increase in the frequency, intensity, and duration of both high precipitation and drought events with climate change in California (Cloern et al., 2011) could also increase *Microcystis* blooms in SFE. High precipitation would benefit *Microcystis* by increasing the availability of nutrients, particularly ammonium, from runoff and if coupled with subsequent low flow conditions, would restrict flushing and further increase bloom intensity (Paerl & Paul, 2012; Reichwaldt & Ghadouani, 2012). Conversely, the expected increased frequency and intensity of droughts could facilitate *Microcystis* blooms in SFE by reducing the flushing of *Microcystis* colonies out of the Delta and increasing light in the water column by facilitating sedimentation of particulate matter (Elliott, 2012; Reichwaldt & Ghadouani, 2012). Greater salinity and pH during droughts would also favor *Microcystis* blooms that survive over a wide range of freshwater to brackish water conditions and pH in SFE (Lehman et al., 2005). Lastly, biological feedback mechanisms could facilitate the increase in *Microcystis* bloom intensity during droughts because reduced vertical mixing would likely increase aggregation of cells into wide diameter colonies with increased buoyancy near the surface and reduce exposure to limiting light and carbon concentration within the water column (Paerl & Paul, 2012).

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