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NOTE

Strong differences characterize *Microcystis* blooms between successive severe drought years in the San Francisco Estuary, California, USA

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ABSTRACT: The frequency, intensity and duration of cyanobacterial harmful algal blooms are expected to increase with climate change. Here we tested the null hypothesis that successive severe drought years would not differ in the magnitude, community composition and controlling factors for *Microcystis* blooms during 2014 and 2015, the third and fourth most severe drought years on record in the San Francisco Estuary, California, USA. Identical sets of physical, chemical and biological data were collected every 2 wk at 10 stations between August and November for each year. Primary producer biomass, abundance, biovolume, community composition and toxin production were quantified. Contrary to expectation, the surface and subsurface *Microcystis* bloom in 2014 was at least an order of magnitude greater than in 2015, the drier and warmer year. In addition, the 2015 drought had a greater percentage of other cyanobacteria (non-*Microcystis*) and eukaryotic phytoplankton than 2014. Median water quality conditions were similar between years, but correlations among physical, chemical and biological variables often differed in magnitude and direction. PRIMER DISTLM (BEST) analysis identified water temperature, the landward extent of saltwater intrusion and outflow as variables that accounted for the most variation in *Microcystis* surface biovolume (R^2 = 0.48) or subsurface abundance (R^2 = 0.45). We conclude that the magnitude of *Microcystis* blooms may not always increase with drought severity or prolonged drought, and are dependent on within-year spatial and temporal variation.

KEY WORDS: *Microcystis* · Drought · Cyanobacteria · Bloom · Estuary · Water quality · CHAB

INTRODUCTION

The frequency, intensity and duration of harmful algal blooms of *Microcystis* spp. (MICI) are expected to increase with the predicted increase in drought conditions due to climate change (Harke et al. 2016). MICI is one of the most common freshwater cyanobacteria, and has increased with drought periods worldwide, including the Murray and Edward Rivers, Australia (Bowling et al. 2016), the Nakong River, South Korea (Ha et al. 1999), and the Guadiana River, Spain and Portugal (Moreno et al. 2004). However, little is known about how MICI varies with physical, chemical and biological factors between successive drought years.

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Toxic MICI blooms have occurred in the San Francisco Estuary (SFE) since 1999 (Lehman et al. 2017). MICI abundance and total microcystin concentration were greater during dry than wet years in SFE, and increased by at least an order of magnitude over previous years during the 2014 severe drought (Lehman et al. 2017). Elevated water temperature and reduced streamflow were associated with MICI biovolume and toxin concentration (Lehman et al. 2008a, 2017). Understanding the cause(s) of MICI blooms is important in SFE, where research suggests that total microcystin concentration can affect the health and survival of phytoplankton, zooplankton and fish (Ger et al. 2010, Lehman et al. 2010, Acuña et al. 2012, Kurobe et al. 2018).

The purpose of this research was to test the null hypothesis that the magnitude, primary producer community composition and controlling factors associated with the MICI bloom would not differ between successive severe drought years in SFE. These hypotheses were tested by comparing spatial and temporal variation in physical, chemical and biological variables during the bloom seasons in 2014 and 2015, the third and fourth driest years on record in SFE (http://cdec.water.ca.gov/cgi-progs/iodir/WSIHIST).

MATERIALS AND METHODS

Study site

SFE contains an inland delta (Delta) of 2990 km^2 with 1100 km of waterways, which receives water from the Sacramento and San Joaquin Rivers (Fig. 1). Water depth varies from a few meters in flooded islands to 13 m in river channels. Tides reach 2 m in height, velocities up to 30 cm s^{-1} and excursions of 10 km. Nutrients occur in excess, but do not lead to eutrophic conditions due to light limitation from suspended sediment (Jassby 2008).

Field sampling and analyses

Sampling was conducted every 2 wk between August and early November at 10 stations (n = 140) within the Sacramento and San Joaquin Rivers in 2014 and 2015 (Fig. 1). Physical conditions were measured by a YSI sonde. Surface MICI colonies were collected by hand towing a plankton net (75 µm mesh). Water samples for measurement of cyanotoxins (by ELISA), nutrients, pigment concentration, total and dissolved organic carbon and total and volatile suspended solid concentrations, as well as whole-water primary producer composition and abundance (by qPCR and microscopy) were collected by a van Dorn bottle at 0.3 m depth. Details of the laboratory analytical methods are described by Lehman et al. (2017). Streamflow data were obtained from the DAYFLOW database (www.water.ca.gov).

Statistical analyses

Multiple and single comparisons, ordination and multiple regression analysis were conducted using PRIMER v.7 software (Clarke & Gorley 2015) and SAS (SAS Institute 2013). Due to collinearity ($r > 0.95$), specific conductance (EC) was used to represent total dissolved solids and chloride. Deviations from the median were computed as median absolute deviation (MAD).

RESULTS

Environmental conditions

Median streamflow was similar ($p > 0.05$) at Rio Vista (RIO) on the Sacramento River in 2014 (93 ± 17 m^3 s^{-1}) and 2015 (87 ± 21 m^3 s^{-1}), but decreased from 10 ± 2 m^3 s^{-1} in 2014 to 7 ± 4 m^3 s^{-1} in 2015 on the San Joaquin River (SJR, $p < 0.01$, Fig. S1a,b in the Supplement at www.int-res.com/articles/suppl/a081p293_supp.pdf). The distance landward from the Pacific Ocean where the bottom salinity is 2 (X2) was also further upstream in 2014 (89 ± 2 km) than in 2015

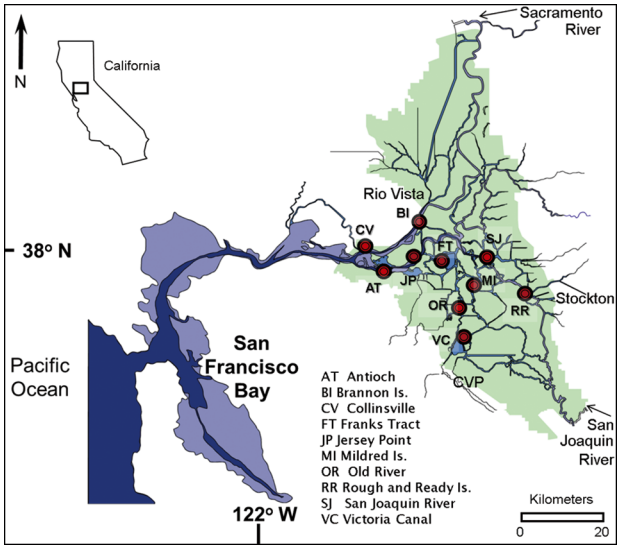

Fig. 1. Map of San Francisco Estuary showing the location of sampling stations

(86 ± 1 km, $p < 0.01$, Fig. S1c), particularly during the peak of the bloom in August and September. Similarly, total river outflow (OUT) was less for 2014 (99 ± 17 $m^3 s^{-1}$) than for 2015 (136 ± 21 $m^3 s^{-1}$) ($p < 0.01$) during the peak of the bloom (Fig. S1d).

Only soluble reactive phosphorus (SRP), silica (SiO_2), integrated euphotic zone light (LITE) and pH were greater in 2014 than 2015 over the bloom season (August through November; Table 1). August and September (summer) had higher SRP, SiO_2, dissolved oxygen and pH in 2014 than 2015. October and November (fall) had greater LITE and SiO_2 in 2014 than 2015, but greater total phosphorus (TP) in 2015 than 2014. Within years, summer had greater water temperature (WT), LITE, percent dissolved oxygen concentration and pH than the fall, while the fall had greater nitrate (NO_3), ammonium (NH_4), SRP and SiO_2 concentration than the summer (Table 1).

Primary producers and toxins

Surface chlorophyll *a* concentration (CHLA-S) and surface *Microcystis* biovolume (MICI-S), as well as subsurface *Microcystis* abundance (MICI-D) of potentially toxic and non-toxic cells determined by qPCR, and sub-surface total microcystin concentration (TMICN-D) were greater ($p < 0.01$) in 2014 than 2015 over the summer and bloom season (Table 1). CHLA-S and MICI-D were greater for both years in the central and south Delta along the SJR and Old River at Stns FT, JP, MI, OR, RR, SJ and VC (see Fig. 1) than near the confluence of the Sacramento River and SJR at Stns AT, BI and CV ($p < 0.05$; Fig. 2a,e). MICI-S and TMICN-D did not differ between stations due to high variability (Fig. 2c,g). Among months, peak CHLA-S, MICI-S and MICI-D occurred in summer for both years ($p < 0.05$; Fig. 2b,d,f). TMICN-D was greater for summer in 2014 ($p < 0.05$; Fig. 2h), but did not differ among months in 2015.

Median percent total subsurface cyanobacteria biovolume (MICI plus other cyanobacteria) in the >10 µm diameter size fraction (microscopy) was greater in 2014 (72 ± 27%) than 2015 (55 ± 26%; $p < 0.01$; Fig. S2a,b). MICI comprised over half of the total cyanobacteria biovolume in 2014 (60 ± 23%), but only a quarter of the biovolume (24 ± 26%; $p < 0.01$) in 2015. For eukaryotic phytoplankton, cryptophyte biovolume was greater in 2014, while diatom, green algae and chrysophyte biovolume was greater in 2015 ($p < 0.01$; Fig. S2a,b). Diatoms comprised the largest percentage of all eukaryotes, and increased from 12 ± 14% to 27 ± 19% of the total primary producer biovolume between 2014 and 2015. The percent dinoflagellate biovolume was low, and did not differ between years.

The relative abundance of cyanobacteria in all size fractions within subsurface samples (qPCR) also differed between 2014 and 2015. The percent MICI-D was greater in 2014 (14 ± 7%) than 2015 (4 ± 5%) by a factor of 3, while the percent of potentially toxic MICI-D cells was greater in 2014 (3 ± 3%) than 2015 (0.05 ± 0.07%) by over an order of magnitude ($p < 0.01$; Fig. S3a,b). The percent *Aphanizomenon* was also greater in 2014 (6 ± 4%) than 2015 (2 ± 3%; $p < 0.01$). In contrast, both *Dolichospermum* (0% and 0.01 ± 0.01%; $p < 0.05$) and other cyanobacteria (75 ± 11% and 92 ± 9%; $p < 0.01$) were greater in 2015 than 2014, respectively.

Correlations

Correlations among physical and chemical variables differed for 2014 and 2015. RIO and SJR were negatively correlated in 2015, but were not correlated in 2014 (Table S1a,b). WT was correlated with RIO in 2015, but not in 2014. In contrast, WT was correlated with X2 in 2014, but not 2015. Although WT and EC were negatively correlated for both years, the correlation was stronger in 2014 than 2015. Turbidity was more strongly correlated with EC and LITE in 2015 than 2014, while LITE was more strongly correlated with streamflow variables and EC in 2015 than 2014. TP and SJR were positively correlated in 2015 and negatively correlated in 2014. Ammonium concentration was negatively correlated with RIO in 2015, but not 2014.

The direction and magnitude of correlations between MICI-S and MICI-D, CHLA-S and environmental variables also differed between years. MICI-D, MICI-S and CHLA-S increased with WT and X2 in 2014, but not 2015 (Table S2). For 2015, MICI-D was less strongly correlated with WT and WEST, and more strongly correlated with nitrogen than in 2014. MICI-D and CHLA-S were also correlated with LITE or RIO and TP in 2015, but not 2014.

An ordination of all environmental variables demonstrated similar water quality conditions, but a large difference in bloom magnitude between the 2 years (Fig. 3). For log transformed values, Akaike's information criterion (AIC) and R^2 criteria indicated that a combination of WT and X2 explained the largest amount of variation (adj. $R^2 = 0.44$) in MICI-D for both years combined (PRIMER v.7 DISTLM [BEST]

Table 1. Median ± median absolute deviation (MAD) of physical, chemical and biological variables measured for the summer (August and September), fall (October and November) and entire bloom season (August through November) for 2014 and 2015. Differences are indicated as significantly greater than (>), less than (<) or non-significant (ns) at the 5% level or higher

Variable	Abbrev.	2014 summer	2014 fall	Summer vs. fall	2014 season	2015 summer	2015 fall	Summer vs. fall	2015 season	2014 versus 2015		
										Summer	Fall	Season
Surface chlorophyll ($\mu g\ l^{-1}$)	CHLA-S	1.65 ± 1.23	0.24 ± 0.24	s>f	0.83 ± 0.95	0.52 ± 0.35	0.22 ± 0.25	s>f	0.40 ± 0.39	2014 > 2015	ns	2014 > 2015
Surface phaeophytin ($\mu g\ l^{-1}$)	PHAE-S	0.05 ± 0.05	0.02 ± 0.01	s>f	0.03 ± 0.03	0.004 ± 0.006	0.007 ± 0.006	ns	0.006 ± 0.008	2014 > 2015	2014 > 2015	2014 > 2015
Log surface *Microcystis* biovolume ($\mu m^3\ l^{-1}$)	Log MICI-S biovolume	9.5 ± 0.3	8.7 ± 0.4	s>f	9.1 ± 0.5	8.4 ± 0.4	8.2 ± 0.6	s>f	8.2 ± 0.5	2014 > 2015	2014 > 2015	2014 > 2015
Log subsurface *Microcystis* (qPCR) (cells ml^{-1})	Log MICI-D	5.0 ± 0.3	4.3 ± 0.4	s>f	4.7 ± 0.6	3.9 ± 0.5	3.2 ± 0.6	s>f	3.6 ± 0.6	2014 > 2015	2014 > 2015	2014 > 2015
Total microcystins ($\mu g\ l^{-1}$)	TMICN-D	0.88 ± 0.42	0.12 ± 0.0	s>f	0.56 ± 0.61	0.17 ± 0.0	0.12 ± 0.0	ns	0.15 ± 0.0	2014 > 2015	ns	2014 > 2015
Integrated euphotic zone light ($\mu mol\ m^{-1}\ s^{-1}$)	LITE	1063 ± 383	973 ± 336	s>f	1051 ± 347	854 ± 376	710 ± 546	s>f	819 ± 402	ns	2014 > 2015	2014 > 2015
Soluble reactive phosphorus ($mg\ l^{-1}$)	SRP	0.09 ± 0.01	0.09 ± 0.01	f>s	0.09 ± 0.01	0.08 ± 0.02	0.09 ± 0.01	f>s	0.08 ± 0.01	2014 > 2015	ns	2014 > 2015
Total phosphate ($mg\ l^{-1}$)	TP	0.11 ± 0.01	0.10 ± 0.01	s>f	0.11 ± 0.01	0.11 ± 0.01	0.12 ± 0.01	f>s	0.11 ± 0.01	ns	2015 >2014	ns
Silicate ($mg\ l^{-1}$)	SiO_2	13.8 ± 1.33	16.3 ± 1.19	f>s	15.00 ± 2.08	11.75 ± 2.00	12.92 ± 1.94	f>s	12.00 ± 2.00	2014 > 2015	2014 > 2015	2014 > 2015
pH	pH	7.96 ± 0.21	7.66 ± 0.18	s>f	7.82 ± 0.27	7.81 ± 0.24	7.66 ± 0.22	s>f	7.73 ± 0.27	2014 > 2015	ns	2014 > 2015
Dissolved oxygen ($mg\ l^{-1}$)	DO	8.20 ± 0.47	8.46 ± 0.52	ns	8.35 ± 0.47	8.67 ± 0.78	8.28 ± 0.71	ns	8.44 ± 0.82	2015>2014	ns	ns
Percent dissolved oxygen	PCTDO	94.05 ± 5.48	89.80 ± 4.00	s>f	91.70 ± 5.93	98.9 ± 9.49	91.5 ± 2.82	s>f	93.50 ± 5.04	ns	ns	ns
Water temp. (°C)	WT	22.39 ± 1.88	18.28 ± 2.65	s>f	21.12 ± 3.28	22.68 ± 1.65	19.86 ± 2.44	s>f	21.57 ± 2.03	ns	ns	ns
Specific conductance ($\mu S\ cm^{-1}$)	EC	771 ± 752	949 ± 659	ns	880 ± 700	1299 ± 1018	1108 ± 851	ns	1262 ± 977	ns	ns	ns
Chloride ($mg\ l^{-1}$)	CL	210 ± 193	226 ± 193	ns	215 ± 193	288 ± 251	268 ± 242	ns	272 ± 240	ns	ns	ns
Ammonium ($mg\ l^{-1}$)	NH_4	0.02 ± 0.01	0.03 ± 0.01	f>s	0.02 ± 0.01	0.02 ± 0.01	0.04 ± 0.02	f>s	0.02 ± 0.01	ns	ns	ns
Nitrate ($mg\ l^{-1}$)	NO_3	0.21 ± 0.17	0.44 ± 0.17	f>s	0.32 ± 0.22	0.26 ± 0.16	0.43 ± 0.10	f>s	0.31 ± 0.18	ns	ns	ns
Dissolved organic nitrogen ($mg\ l^{-1}$)	DON	0.30 ± 0.15	0.20 ± 0.15	s>f	0.20 ± 0.15	0.26 ± 0.07	0.23 ± 0.06	ns	0.24 ± 0.06	ns	ns	ns
Dissolved organic carbon ($mg\ l^{-1}$)	DOC	2.95 ± 0.67	2.50 ± 0.74	ns	2.80 ± 0.74	2.7 ± 0.89	2.70 ± 0.89	ns	2.70 ± 0.89	ns	ns	ns
Total organic carbon ($mg\ l^{-1}$)	TOC	2.95 ± 0.74	2.60 ± 0.74	ns	2.80 ± 0.74	2.85 ± 0.82	2.70 ± 0.89	ns	2.80 ± 0.89	ns	ns	ns
Turbidity (NTU)	NTU	7.20 ± 7.04	4.90 ± 6.00	s>f	5.85 ± 6.67	6.15 ± 5.63	6.55 ± 6.89	ns	6.50 ± 6.38	ns	ns	ns
Volatile suspended solids ($mg\ l^{-1}$)	VSS	2.00 ± 1.48	1.00 ± 1.48	ns	2.00 ± 1.48	2.00 ± 1.48	2.00 ± 1.48	ns	2.00 ± 1.48	ns	ns	ns
Total dissolved solids ($mg\ l^{-1}$)	TDS	618 ± 496	582 ± 391	ns	582 ± 427	735 ± 583	621 ± 454	ns	705 ± 547	ns	ns	ns
Total suspended solids ($mg\ l^{-1}$)	TSS	6.00 ± 5.93	6.00 ± 5.93	ns	6.00 ± 5.93	6.50 ± 6.67	9.00 ± 8.89	ns	8.00 ± 8.61	ns	ns	ns
Wind ($km\ h^{-1}$)	WND	6.2 ± 1.0	4.8 ± 1.3	s>f	5.6 ± 1.8	6.2 ± 1.6	5.5 ± 1.8	s>f	5.9 ± 1.9	ns	ns	ns

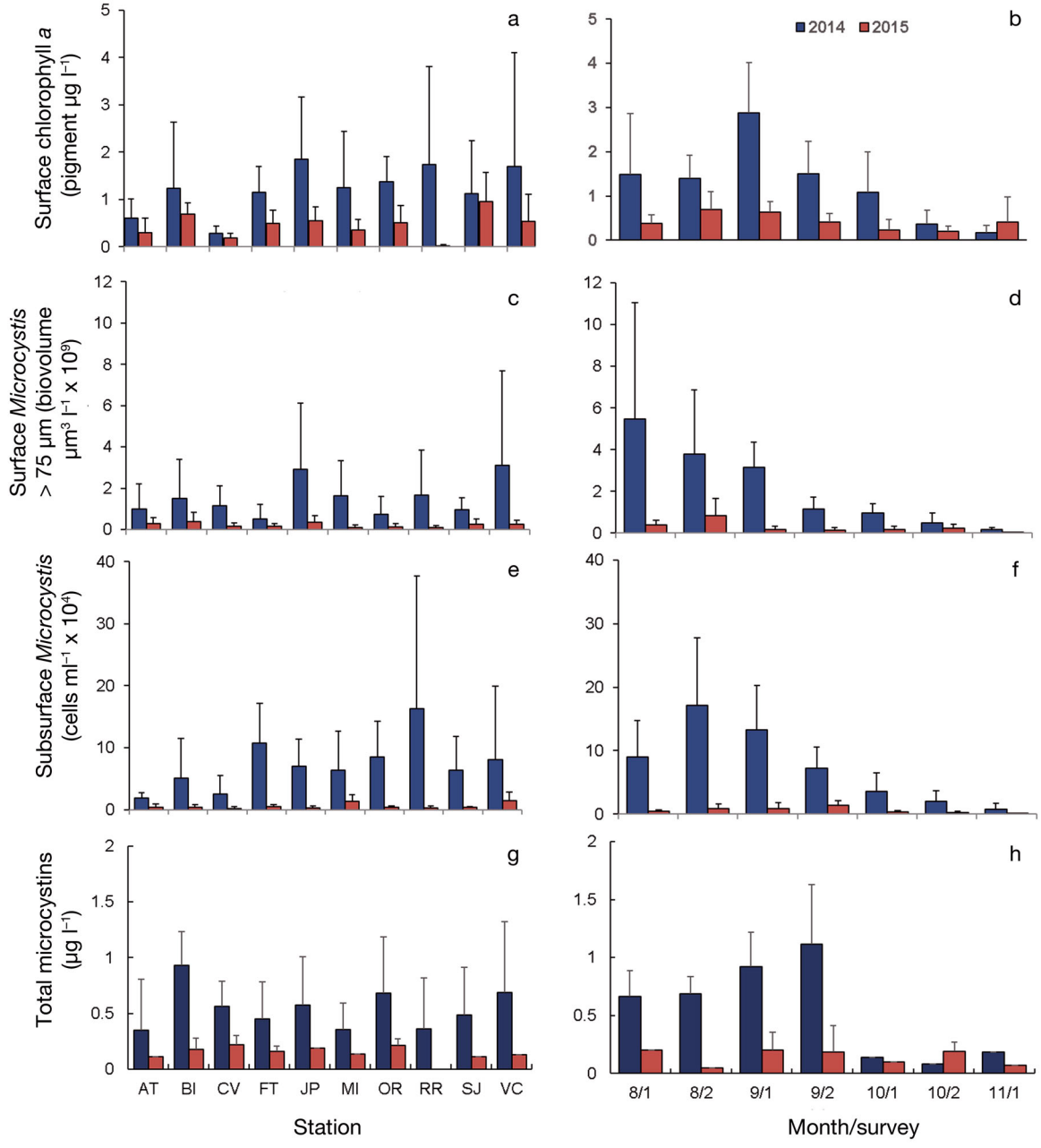

Fig. 2. Median and median absolute deviation (MAD, error bars) by station and month/survey (1 or 2) of (a,b) surface chlorophyll *a* concentration, (c,d) surface *Microcystis* biovolume (>75 µm size fraction, (e,f) subsurface *Microcystis* abundance and (g,h) total microcystins measured every 2 wk between August and November in 2014 and 2015 at 10 stations in the Sacramento San Joaquin Delta, California, USA (see Fig. 1 for abbreviations and locations)

analysis; Table 2). Similarly, WT and outflow explained the largest amount of variation (adj. R^2 = 0.47) in MICI-S for both years combined. A distance-based redundancy analysis (db-RDA ordination) containing only WT and X2 demonstrated a strong separation in MICI-D between years (Fig. S4). Even though median WT values were similar between years (Table 1), the percentage of values above 25°C (18%) was twice as high in 2014 than 2015 (8%) in summer. Maximum MICI-D occurred when WT was above 24°C and X2 was at 89 km in 2014.

DISCUSSION

We rejected the hypothesis that the MICI bloom would be greater in the climatically drier and warmer severe drought year 2015 compared with 2014. This

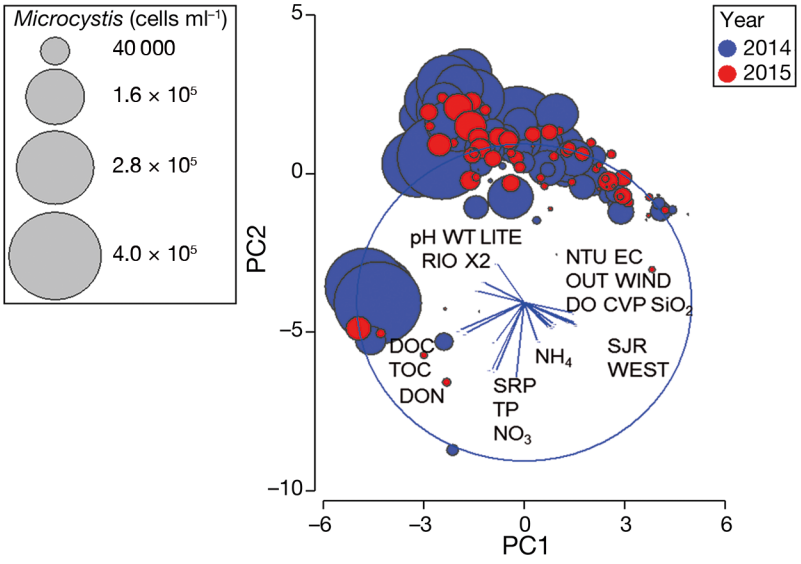

Fig. 3. Ordination of environmental variables overlaid with the abundance of subsurface *Microcystis* abundance measured every 2 wk between August and early November at 10 stations in 2014 and 2015. See abbreviations of variables in Table 1 plus total outflow (OUT) and the landward extent of salt water intrusion to bottom salinity of 2 (X2)

Table 2. Environmental variables that describe the variation in *Microcystis* subsurface abundance and surface biovolume determined using PRIMER v7. DISTLM (BEST) analysis for 2014 and 2015. All data were log transformed; in all cases, p = 0.001. X2: distance landward from the Pacific Ocean where the bottom salinity is 2

Dependent variable	Predictor variable	Adj. R^2
Subsurface *Microcystis* abundance	X2	0.32
	Water temp.	0.44
Surface *Microcystis* biovolume	Outflow	0.38
	Water temp.	0.47

finding seemed to contradict previous research indicating that the MICI bloom increased with warmer and drier conditions in SFE (Lehman et al. 2017). However, the higher frequency of warm WT during August and September probably favored the growth of more MICI in 2014 than 2015. MICI reaches the peak biomass-specific growth rate in August and September, so an increase in WT during these months would have a large impact on the population (Lehman et al. 2008a). MICI grows well at high WT, and the high relative importance of WT as a controlling factor for MICI growth among a suite of environmental conditions was confirmed in laboratory bioassays (Jiang et al. 2008, Lürling et al. 2017) and field research (Bowling et al. 2016).

Similarly, more frequent WT below 25°C during the bloom season in 2015 may partially explain the greater percentage of other cyanobacteria, *Dolichospermum* and diatoms in 2015 than 2014. *Aphanizomenon*, *Dolichospermum* and diatoms are common below 25°C worldwide (Carey et al. 2012), and were more common during the unseasonably low WT in the summer of 2011 in SFE (Kurobe et al. 2013).

Due to their impact on colony retention, outflow and X2 were also key factors influencing the magnitude of the MICI blooms in 2014 and 2015. Lower outflow in 2014 than 2015 reduced the movement of colonies seaward near the surface, where the flow is high. Higher X2 in 2014 than 2015 also facilitated accumulation of subsurface colonies by increasing water retention time in the SJR (Jassby et al. 1995). Because MICI has a slow growth rate compared with most primary producers, its abundance is often due more to accumulation than growth (Reynolds 2006). For SFE, maximum biomass-specific growth rate of MICI was less than half of that for non-MICI primary producers (Lehman et al. 2008a,b). MICI blooms commonly develop as a result of low streamflow in rivers or tidal estuaries, including the Murray River, Australia (Bowling et al. 2016), and the Nakong River, South Korea (Ha et al. 1999).

Differences in physical, chemical and biological correlations and the primary producer community suggest there was a shift in the structure and function of the estuary between the 2014 and 2015 droughts. A shift in the primary producer community could have been influenced by MICI, because cyanobacteria can release peptides and alkaloids that are allelopathic to phytoplankton (Paerl & Paul 2012). In SFE, low abundance of diatoms and green algae coincided with high MICI abundance between 2004 and 2008 (Lehman et al. 2010). The increased diversity of the cyanobacterial community in 2015 may also reflect a change in the overall bacterial community within the SJR (Otten et al. 2017).

Large differences in the bloom magnitude, and correlations among physical, chemical and biological variables for these 2 successive severe drought years, suggest that understanding the cause of cyanobacterial blooms during prolonged severe drought requires knowledge of the variation in environmental and biological variables at multiple spatial and temporal scales.

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