Major – but rare – spring blooms in 2014 in San Francisco Bay Delta, California, a result of the long-term drought, increased residence time, and altered nutrient loads and forms

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ABSTRACT

Rare spring blooms, $>20~\mu g~l^{-1}$ chlorophyll a, were observed in the San Francisco Bay Delta during the drought year of 2014 in both the upper Sacramento River and in Suisun Bay. The upper Sacramento River bloom was dominated by chlorophytes, but biomass and photosynthetic efficiency (based on variable fluorescence, Fv/Fm) precipitously declined downstream when cells were exposed to sewage effluent and NH_4^+ levels $> 70~\mu M$-N. Further downriver, substantial rates of nitrification occurred, based on increasing levels of NO_3^- and NO_2^- in proportion to decreasing NH_4^+ concentrations, reducing NH_4^+ levels to $<10~\mu M$-N. The other major tributary, the San Joaquin River, had extremely high nutrient levels ($NO_3^- > 400~\mu M$-N, $PO_4^{3-} > 13~\mu M$-P, but $NH_4^+ \sim 2~\mu M$-N), very low chlorophyll a levels ($\sim 3~\mu g~L^{-1}$) and low Fv/Fm values, but elevated bacterial production, suggesting presence of an algal inhibitor, possibly an herbicide. Both rivers converge above Suisun Bay, where elevated NO_3^- ($>50~\mu M$-N), sufficient PO_4^{3-} ($>3~\mu M$-P), and reduced NH_4^+ levels (as low as $6~\mu M$-N), and reduced flow created conditions conducive to a spatially large and physiologically healthy (elevated Fv/Fm) diatom bloom dominated by the species $Entomoneis$ sp. We conceptualize this bloom as a "window of opportunity" response by these diatoms to multiple factors promoted by the drought, including longer residence time for cell growth and biomass accumulation, and longer time for in-river nitrification to occur, reducing sewage-derived NH_4^+ to a level where diatoms could access NO_3^- for uptake and growth. We suggest that management practices that favor higher rates of flow may narrow the "window of opportunity" for phytoplankton growth, potentially leading to low productivity and food limitation for fish. Under high flow, a condition of "washout" may develop where both chlorophyll and unassimilated nutrients are transported out of the bay, and the phytoplankton that do develop are less favorable in terms of community composition for supporting the upper food web.

1. Introduction

The San Francisco Bay Delta has, for decades, been considered an estuary of exceptionally low productivity compared to many other estuaries worldwide (Boynton et al., 1982; Cloern et al., 2013). Spring blooms in most of the San Francisco Bay Delta, including Suisun Bay, have been a rarity in recent years. Consistent annual spring (March to May) blooms with chlorophyll a (chl a) levels $>20~\mu g~L^{-1}$ occurred during the last prolonged drought in the mid 1970s (Alpine and Cloern, 1992; Ball and Arthur, 1979; Jassby, 2008; Kimmerer, 2004), and only sporadic blooms have been reported since (Dugdale et al., 2012, 2013; Glibert et al., 2014b; Wilkerson et al., 2006). Suisun Bay more commonly has chl a levels that are $<5~\mu g~l^{-1}$ (Kimmerer et al., 2012), leading to a condition that is thought to be food limiting for major fish species.

Historically, nutrients have been dismissed as a major regulatory factor in phytoplankton production in Suisun Bay largely because most nutrients have been assumed to be at levels that saturate (maximize) phytoplankton growth; as a result of the seeming abundance of ambient nutrients in contrast to the chl a levels accumulated, this system is characteristic of a High Nutrient Low Growth or Low Chlorophyll (HNLG or HNLC) region (Dugdale et al., 2007; Sharp, 2001; Yoshiyama and Sharp, 2006). Phytoplankton growth has instead been considered to be regulated primarily by light limitation (Alpine and Cloern, 1992;

Cloern and Dufford, 2005; Cole and Cloern, 1984), while phytoplankton biomass accumulation has been thought be controlled largely by grazing (e.g., Kimmerer, 2004; Kimmerer and Thompson, 2014).

However, over the past decades there have been large changes in phytoplankton community composition and the role of nutrients in these changes has received increasing scrutiny because nutrient loads are high and increasing (e.g., Dugdale et al., 2007, 2013; Glibert, 2010; Glibert et al., 2011, 2013; Parker et al., 2012b; Van Nieuwenhuyse, 2007; Wilkerson et al., 2006). A major source of nutrients to the Bay Delta is sewage effluent (Jassby, 2008; Van Nieuwenhuyse, 2007), with one of the largest wastewater treatment plants (WWTP) on the upper Sacramento River discharging nitrogen (N) primarily as NH_4^+ at the rate of 14–15 tons day^{-1}, and at concentrations at the point of discharge that have increased from ~10 mg L^{-1} (=714 μM-N) when the plant came on line in the early 1980s to >20 mg L^{-1} (= > 1400 μM-N) in the 2000s (Glibert, 2010; Glibert et al., 2011). Under average flow conditions, approximately 90% of the total N in northern San Francisco Estuary originates from this single point source (Jassby, 2008).

In attempting to understand the factors that regulate phytoplankton growth and community composition and their changes over time, we have been studying how nutrient forms and ratios affect phytoplankton in the Bay Delta. Our working hypothesis has been that increased NH_4^+, originating from sewage discharge, has led to concentrations of NH_4^+ that, rather than stimulate phytoplankton growth, have actually been inhibiting or repressing phytoplankton growth (Dortch, 1990; Dugdale et al., 2007, 2012, 2013), and that phytoplankton community composition also changes in response to availability of both nitrogen (N) and phosphorus (P) and their proportions (e.g., Glibert, 2012; Glibert et al., 2011). While phytoplankton productivity throughout most of the year is indeed supported by NH_4^+, the phytoplankton community composition that develops under high NH_4^+ concentrations differs from that under proportionately higher NO_3^- concentrations and rates of productivity are reduced as well (Dugdale et al., 2007; Parker et al., 2012b). The reduction in N productivity is a function of NH_4^+ inhibition of NO_3^- uptake on the short time scale (minutes to hours), followed by differential growth of different phytoplankton taxa on a longer time scale (days to weeks), leading to an altered algal community composition and one that has a lower efficiency for N assimilation. Experimental evidence both from the Bay Delta (Glibert et al., 2014b; Parker et al., 2012a) and elsewhere are supportive of reduced rates of N-based productivity when phytoplankton are exposed to NH_4^+ enrichment compared to those exposed to NO_3^- enrichment (Donald et al., 2013; Parker, 2004). Chlorophyll yield per N assimilated for phytoplankton growing on NO_3^- is as much as 2-fold higher than for phytoplankton growing on NH_4^+ (Glibert et al., 2014b). The inhibition of NO_3^- uptake by NH_4^+ and urea has been widely reported in both field studies and laboratory cultures (e.g., Dortch, 1990; Dugdale et al., 2007; Flynn, 1999; Lipschultz, 1995; Lomas and Glibert, 1999a,b; Xu et al., 2012). In fact, the pattern of low rates of productivity in the presence of elevated NH_4^+ conditions in the Sacramento River and Suisun Bay is comparable to observations in other river, estuarine, and coastal ecosystems impacted by wastewater effluent (MacIsaac et al., 1979; Waiser et al., 2011; Xu et al., 2012; Yoshiyama and Sharp, 2006).

In an adaptive management approach, water flow through the estuary is rigorously managed through engineering of the isohaline where salinity is equal to 2; locally referred to as X2, this isohaline is defined as the distance from the Golden Gate Bridge up the axis of the estuary to where the tidally averaged, near-bottom salinity is 2 (Jassby et al., 1995; Kimmerer, 2004). Thus, X2 moves inland when flow is low and seaward when flow is high and is generally located in eastern Suisun Bay during the summer and autumn. The rationale for managing X2 is that the abundances or survival indices of many fish species, including those that are listed as threatened or endangered such as delta and longfin smelt, have been shown to be correlated with the position of X2, with the abundance of these and other fish species trending higher when X2 is lower or more seaward (Feyrer et al., 2010; Jassby et al., 1995; Kimmerer, 2002; Kimmerer et al., 2009). In recent years, increases in flow in order to move X2 seaward have been mandated through federal court decisions because of declines in abundance of these smelts (Wanger, 2007a,b). Although the underlying mechanisms for the relationships between X2 and fish abundance are not well characterized, it is hypothesized that the X2 position essentially defines an entrapment zone for fish, or a turbidity maximum region in the low salinity zone (estuary with salinity <6, usually located in the northern estuary and typically including Suisun Bay; Jassby et al., 1995). However, in recent years relationships between fish abundance and X2 have changed, and it is also of note that X2 is directly related to the long-term trends in availability of total phosphorus, PO_4^{3-}, and NH_4^+ that are also directly or indirectly related to fish abundance via alterations in the overall food web (Glibert et al., 2011). Thus it is possible, and in keeping with our nutrient hypothesis, that these fish are tracking availability and quality of food controlled by nutrient availability and its forms rather than habitat defined by salinity only; the low salinity zone has not been a site of suitable food production in recent decades.

In March 2014 we observed major phytoplankton blooms in the upper Sacramento River and in Suisun Bay. This study was undertaken as part of a multi-year study of the nutrient loads and forms and their effect on phytoplankton growth in the Sacramento River, San Joaquin River and Suisun Bay. Of particular interest is the fact that a previous large spring bloom in Suisun Bay, 1976/1977, occurred in similar climatic conditions; 2013/2014 is the first major drought in northern California since the 1970s. Our goal here is to describe the bloom, the nutrient conditions that supported it, and the physiological state of the algal and bacterial cells. We asked the questions: what was the source or sources of nutrients supporting this bloom, and was this bloom related to abiotic conditions associated with intense drought?

2. Methods

2.1. Site description

The northern San Francisco Bay Estuary, or Bay Delta, consists of Central Bay, San Pablo Bay, Suisun Bay and the Sacramento-San Joaquin Bay Delta, a complex of rivers, channels, wetlands, and floodplains (Fig. 1; Atwater et al., 1979; Nichols et al., 1986; Mueller-Solger et al., 2002). The Sacramento and San Joaquin Rivers converge at the confluence of the delta, then flow into Suisun Bay. With exception of the deeper Central Bay, the mean depths of the various sub-embayments in the estuary range from 3.3 to 5.7 m (Kimmerer, 2004). On a long-term basis, the Sacramento River contributes >80% of river inflow to the Bay Delta, while the San Joaquin delivers ~ 12%, the remainder coming from minor sources flowing into the Delta from the east (Jassby, 2008).

2.2. Sample collection

Samples were collected from the R/V Questuary on March 24, 2014. Samples were collected along a transect from the upper Sacramento River to Suisun Bay (Fig. 1). At each station, a Secchi disk was used to estimate water clarity and a Seabird Electronics SB-32 rosette mounted with 6, 3-L Niskin bottles and fitted with a Seabird SBE-19 plus CTD was deployed to collect both vertical profiles of temperature and salinity and near-surface water samples. At each site, samples were immediately filtered on board though Whatman GF/F filters (nominally 0.7 μm; precombusted 2 h 450 °C) for the collection of total chl *a*, and through Nuclepore membrane filters for the collection of the chl *a* fraction that was >5 μm. All chl *a* measurements were replicated. The GF/F filtrate was stored on ice, returned to the laboratory for subsequent analysis of NH_4^+, NO_3^-, NO_2^-, PO_4^{3-} and $Si(OH)_4$. On the same day as the cruise, samples were also collected from shore access from the San Joaquin River (Site C6; Fig. 2) and returned to the laboratory for similar processing. In addition, at sites Garcia Bend (GRC, Sacramento River), USGS4 (Suisun Bay), and C6 (upper San Joaquin River), bulk collections of
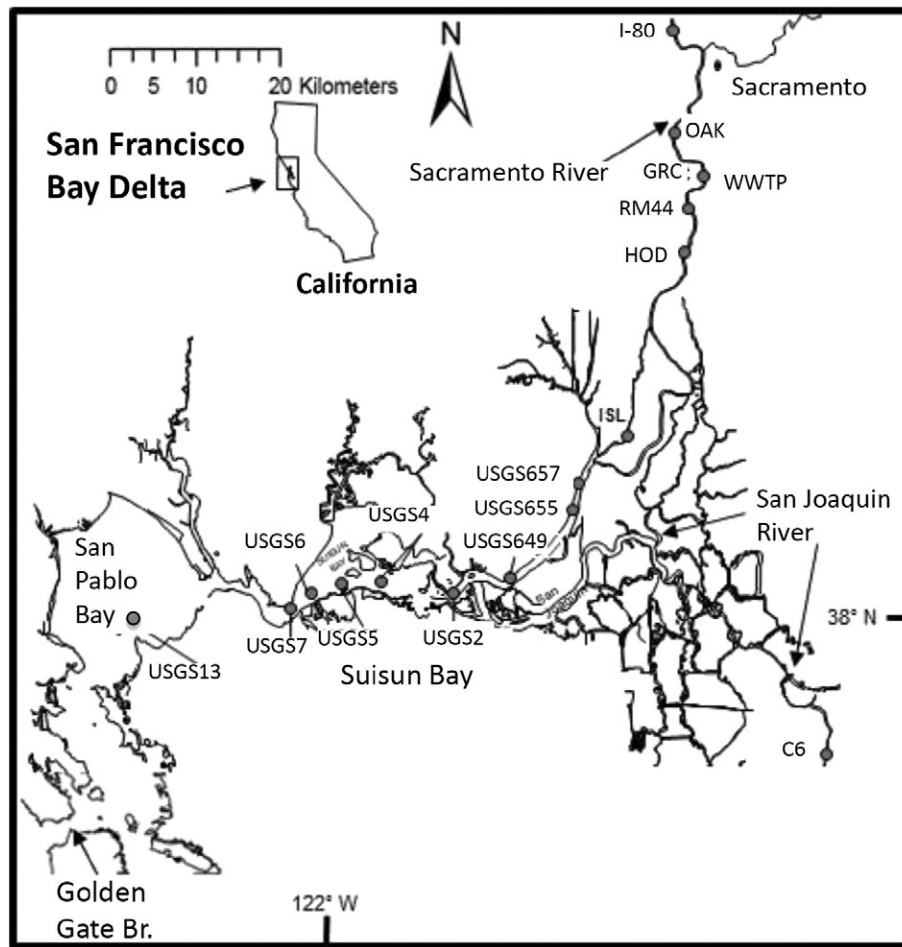
Fig. 1. Map of the Sacramento–San Joaquin Bay Delta indicating stations sampled on March 24, 2014.

water (150–300 L; filtered through 150 μm screening to remove large grazers) were made for nutrient enrichment experiments as described below.

At each site, measurements were also initiated of bacterial production by inoculating replicate 1.7 mL aliquots of sample water with 75 nM tritiated leucine (Kirchman et al., 1985). Samples were incubated for 40 min–1 h in the dark at ambient water temperatures. Incubations were terminated by addition of 100% (w/v) ice-cold trichloroacetic acid, and processed using the microcentrifuge method of Kirchman (2001). Samples were assayed using a PerkinElmer Winspectral Guardian LSC liquid scintillation counter.

2.3. Enrichment experiments

Nutrient enrichment experiments were designed to assess whether phytoplankton from the upper Sacramento River (GRC), Suisun Bay (USGS4) and upper San Joaquin River (C6) would be affected by a pulsed addition of NH_4^+. These experiments were designed as a direct test of the NH_4^+ inhibition hypothesis. An addition of 40 μM-N was made, equivalent to concentrations of NH_4^+ typically measured near the WWTP in the Sacramento River in previous studies. For comparison, a similar pulsed addition of NO_3^- was made to samples from the upper Sacramento River only (the other sites had ambient concentrations of NO_3^- exceeding this amount). Additionally, to test whether there was potential light limitation, the experiments on water from the upper Sacramento River and San Joaquin sites were conducted at high (60% natural irradiance) and low (15% natural irradiance) light. Samples and controls (no N additions) were incubated for 48 h under screening

(1 layer of screening for 60% irradiance experiments and 3 layers of screening for 15% irradiance experiments) in ambient light.

2.4. Analytical protocols

Ambient nutrients were analyzed using manual colorimetric assays (NH_4^+) and Autoanalyzer techniques (NO_3^-, NO_2^-, PO_4^{3-}, $Si(OH)_4$). Concentrations of NH_4^+ were analyzed according to Solórzano (1969). Concentrations of $NO_3^- + NO_2^-$ and NO_2^- were analyzed according to Whitledge et al. (1981) and Bran and Luebbe (1999a) Method G-172-96, PO_4^{3-} following Bran and Luebbe (1999b) Method G-175-96 and $Si(OH)_4$ following Bran and Luebbe (1999c) Method G-177-96. Samples had been stored frozen for a period of 2 days and then carefully thawed at room temperature for 24 h to reduce $Si(OH)_4$ polymerization at high concentrations (MacDonald et al., 1986). Samples for chl *a* were analyzed using a Turner Designs Model 10-AU fluorometer following a 24 h 90% acetone extraction at 4 °C (Arar and Collins, 1992), and 10% hydrochloric acid was added to estimate phaeophytin. The fluorometer was calibrated with commercially available chl *a* (Turner Designs).

Phytoplankton composition was assessed and enumerated microscopically from the samples collected in the upper Sacramento River (I-80) and Suisun Bay (USGS2 and USGS4). Both live samples and samples preserved in acid Lugol's solution were counted using a Sedgewick Rafter cell. These sites were selected for analysis based on preliminary chl *a* evidence that indicated where phytoplankton blooms appeared to be occurring. Finally, phytoplankton physiological state for samples from each site along the transect was assessed using a Turner Designs PhytoFlash variable fluorometer. Samples were held in the dark from
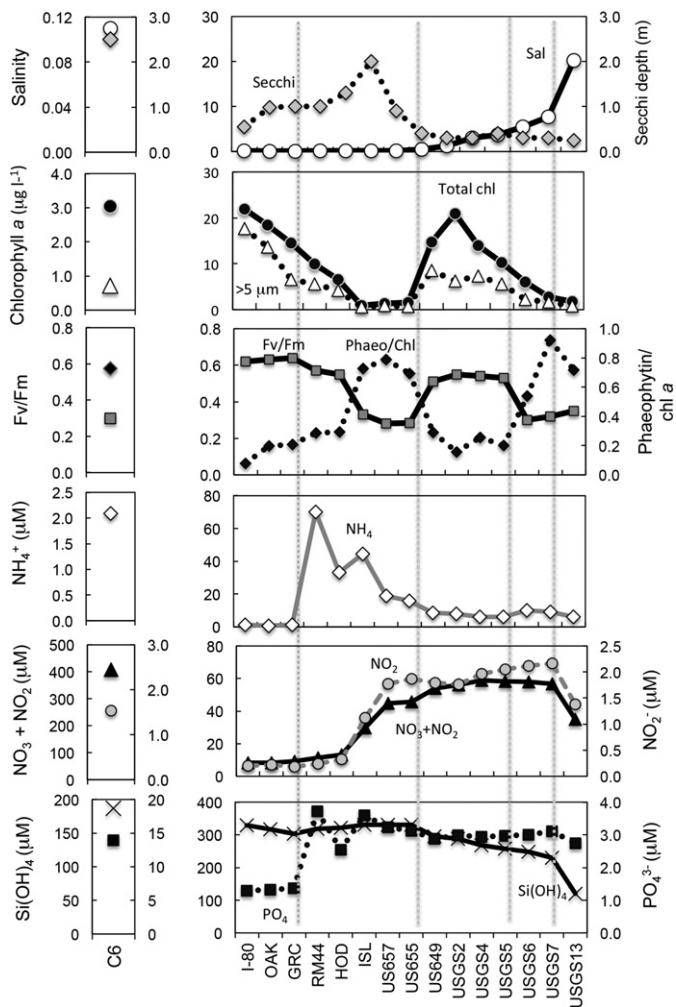
Fig. 2. Measured parameters along a transect of the Sacramento–San Joaquin Bay Delta on March 24, 2014. Spatial changes in abiotic and biotic parameters measured in the San Joaquin River (site C6, small panels) and along a transect from the upper Sacramento River to San Pablo Bay (sites I-80 to USGS13) on March 24, 2014. Vertical dashed lines delineate the various segments discussed in text. Note the change in scales from the small panels depicting data for C6 and the larger panels depicting data for the other stations. The relative standard error of replicate chlorophyll a determinations was 2.5%.

the period of collection until return to the laboratory and measurements of variable fluorescence, Fv/Fm, were all assessed at the same time of day. Reduced Fv/Fm is a measure of stress on photosystem II.

3. Results

3.1. Ambient conditions

Temperatures at all sites ranged from 16.2 to 18.8 °C; the two warmest sites were C6 in the San Joaquin River and HOD in the Sacramento River. Other ambient conditions varied regionally in the Bay Delta. Six distinct regions could be identified based on both abiotic and biotic parameters (Fig. 2) and these corresponded well with those previously described by Parker et al. (2012b). These regions were upper San Joaquin River, upper Sacramento River, mid Sacramento River, lower Sacramento River to upper Suisun Bay, lower Suisun Bay, and the more seaward San Pablo Bay. The isohaline of 2 (based here on surface salinity measurements, not tidally averaged values) was located between sites USGS2 and USGS4.

The upper San Joaquin (site C6) was characterized by very low salinity, a Secchi depth of >2 m, and low chlorophyll, 3 μg L^{-1}, less than a third of which was in the >5 μm size fraction (Fig. 2). The phytoplankton had high

phaeophytin/chl a ratios, as well as very low photosynthetic efficiency, 0.30, as measured by variable fluorescence, Fv/Fm, suggestive of cell stress. In contrast to the low chl a values, concentrations of $NO_3^- + NO_2^-$ at this site were extremely elevated, exceeding 400 μM-N, but concentrations of NH_4^+ were ~2 μM-N. Concentrations of PO_4^{3-} were also very elevated, exceeding 12 μM-P, and $Si(OH)_4$ concentrations also were high, approaching 200 μM-Si.

The upper Sacramento River (sites I-80 to GRC) was characterized by low salinity and Secchi depths of ~1 m (Fig. 2). A phytoplankton bloom was occurring, with total chl a values at the upper most site exceeding 20 μg L^{-1}, and although most of the chl a was in the >5 μm size fraction microscope examination suggested these were mostly small cells but some were clumped. This bloom was dominated by chlorophytes (Table 1). These phytoplankton had a high photosynthetic efficiency, with values of Fv/Fm > 0.6, and low (≲0.2) values of phaeophytin/chl a suggesting physiologically healthy cells. Nitrogen concentrations were moderate by comparison to the other regions; $NO_3^- + NO_2^-$ averaged < 10 μM-N, NO_2^- averaged 0.2 μM-N, and NH_4^+ concentrations were <2 μM-N. Concentrations of $Si(OH)_4$ were >300 μM-Si, and PO_4^{3-} values were ~1 μM-P.

The mid reach of the Sacramento River (sites GRC to USGS655) was considerably different from the upper river in both abiotic and biotic parameters (Fig. 2). While still fresh in terms of salinity, the river was more transparent (Secchi values up to 2 m). Chlorophyll a values declined precipitously, from 14.5 μg L^{-1} at GRC to 1.6 μg L^{-1} at USGS655, photosynthetic efficiency was depressed relative to values in the upper Sacramento, with Fv/Fm ranging from 0.3 to 0.6, and phaeophytin/chl a values reaching 0.79, indicative of significant cell stress. In fact, chl a concentrations actually began declining from the most up-river station, I-80. Beginning at the RM44 site, concentrations of NH_4^+ increased substantially, exceeding 70 μM-N near the discharge site of the WWTP. Concentrations of $NO_3^- + NO_2^-$ and NO_2^- increased downstream, reaching >40 μm-N, and 1.8 μm-N respectively, strongly suggestive of enhanced nitrification rates. An increase in concentrations of PO_4^{3-} were also observed likely also resulting from sewage discharge, averaging 3 μM-P, while $Si(OH)_4$ values were similar to the upper river site.

The region from the lower Sacramento River to the upper Suisun Bay (sites USGS649 to USGS5) was the second region where significant phytoplankton biomass was observed. Salinities remained low, and chl a exceeded 20 μg L^{-1} at USGS2 (Fig. 2). About 30% of this biomass was in the size fraction >5 μm and the phytoplankton community was dominated by the pennate diatom Entomoneis sp. (Table 1). At USGS4 where water was collected for the enrichment experiment, chl a was 14 μg L^{-1} and, in addition to Entomoneis sp., the diatoms Skeletonema costatum and Cylindrotheca closterium were also observed (Table 1). Characterized by high values of Fv/Fm and low phaeophytin/chl a, these cells appeared in healthy physiological status. Concentrations of NH_4^+ had

Table 1
Cell counts of the dominant phytoplankton in samples collected in Suisun Bay on March 24, 2014.

Station	Species	Cell abundance cells mL^{-1}
I-80	Chlorella spp.	33,113
	Cyclotella spp.	26
	Melosira varians	17
	Assorted other greens (Oocystis, Scenedesmus)	2–4
	Assorted pennate diatoms, (Synedra, Cylindrotheca closterium, Nitzschia)	4–6
USGS2	Entomoneis sp.	908
	Cylindrotheca closterium	2
USGS4	Entomoneis sp.	2296
	Cylindrotheca closterium	58
	Skeletonema costatum	23

declined to <10 μM-N, but concentrations of $NO_3^- + NO_2^-$ remained high, about 50 μM-N. Concentrations of both PO_4^{3-} and $Si(OH)_4$ were not substantially different from those observed in mid river.

In the lower Suisun (sites USGS5 to USGS7) salinity increased from 3 to 7, and chl *a* sharply declined and again showed evidence of physiological stress as based on low Fv/Fm and high phaeophytin/chl *a* (Fig. 2). Concentrations of nutrients in this part of Suisun Bay were not substantially different from those in upper Suisun Bay. Finally, into San Pablo Bay (USGS7 to USGS13), salinity rose sharply to >20 and there was a decrease in $NO_3^- + NO_2^-$ and in $Si(OH)_4$, as well as a decline in the phaeophytin/chl *a* ratio, although there was no corresponding increase in chl *a*.

3.2. Bacterial production rates

Highest bacterial production rates were observed in the upper Sacramento River at site I-80, exceeding 700 pmol C L^{-1} h^{-1} (Fig. 3). From stations OAK to HOD along the upper Sacramento River, rates of bacterial production were about half those observed at I-80, and rates further declined by another factor of 2 or more in the lower Sacramento River and Suisun Bay to values <150 pmol C L^{-1} h^{-1}. Station C6, from the San Joaquin River, however, also had elevated bacterial rates, >400 pmol C L^{-1} h^{-1}, but still less than found in the upper Sacramento River.

3.3. Experimental responses of chlorophyll a

Incubation experiments were conducted with samples collected from the blooms in the upper Sacramento River (GRC), the upper Suisun Bay (USGS4) as well as from the low-biomass San Joaquin site (C6). No evidence of light limitation was observed for the phytoplankton from the upper Sacramento River when growth was followed in varying light conditions for 48 h (Fig. 4A,B). In fact, overall highest chl *a* values were attained for the treatment enriched with NO_3^- and incubated under reduced irradiance; this growth was in the <5 μm size fraction. Growth was observed when treatments were enriched with NH_4^+, but these rates for the upper Sacramento River water were indistinguishable for growth of the controls at 24 h. Growth on NO_3^- was poor under high light. For Suisun Bay water, no difference was observed between the samples enriched with NH_4^+ and the controls and most of the growth was in the >5 μm size fraction (Fig. 4C). Virtually no growth was observed in any of the San Joaquin samples (Fig. 4D,E) and the abundance of >5 μm cells declined.

4. Discussion

The 2014 spring bloom in Suisun Bay was unusual; consistent and sustained spring chl *a* values had not been observed to exceed 10 μg L^{-1} in the past 4 decades except on rare and fleeting occasions, although

several spatially or temporally small spring blooms have been noted in the past few years. Since the mid 1980s, it has been thought that an important reason for lack of a spring bloom is aggressive grazing by the invasive clam, *Potamocorbula amurensis* (e.g., Kimmerer, 2004; *P. amurensis* = *Corbula amurensis*, Huber, 2010). This clam is generally abundant in brackish to saline water in this system (Thompson, 2005). However, recent mass balance estimates for Suisun Bay for the years 2006–2007 indicate that while total grazing by both bivalves and micro- and mesozooplankton combined generally equaled or exceeded phytoplankton growth at all times in channels, it did not equal phytoplankton growth during April– June or July over shoals where clams are more common (Kimmerer and Thompson, 2014). As the *P. amurensis* biomass and growth is dependent on phytoplankton for food, it is entirely possible that its biomass is merely a function of available food, and that other factors controlling phytoplankton biomass would also be a control on clam and/or zooplankton abundance (e.g., Glibert et al., 2011). In fact, York et al. (2014) showed, in experiments involving Suisun Bay zooplankton that the current food web was not highly efficient and that in ~30% of their experiments increasing copepod biomass led to greater growth of phytoplankton presumably due to release of grazing pressure from microzooplankton. Consequently, while grazing control is important, factors other than lack of grazing control were more likely promotive of the blooms of this drought year.

We conceptualize the phytoplankton dynamics in March 2014 in the Bay Delta as a "window of opportunity" response to multiple factors (Fig. 5). We hypothesize that the factors promoting the blooms in the upper Sacramento River and in Suisun Bay vary, as well as the factors limiting their spatial extent. Although we have defined these regions spatially here in this data set, we suggest that the regional influence of different promoters or inhibitors of blooms will fluctuate spatially dependent on flow conditions. All regions had temperatures that were favorable for diatom growth and NO_3^- uptake (e.g., Lomas and Glibert, 1999a). The upper Sacramento bloom, dominated by chlorophytes, was likely promoted in part by longer residence time from the drought. The upper Sacramento River had ample nutrients to support this bloom, and N forms were dominated by NO_3^-. High bacterial production rates were also found at this site, likely supported by phytoplankton dissolved organic matter release (Parker, 2005). However, the strength of this phytoplankton bloom rapidly declined downriver, declining from >20 μg L^{-1} at I-80 to <1 μg L^{-1} at the ISL site, and the physiological condition of these cells declined as well (reduced Fv/Fm, elevated phaeophytin/chl *a*). Such a decline in both biomass and physiological health is consistent with the NH_4^+ inhibition hypothesis (Dugdale et al., 2007). Declining chl *a* concentrations downriver from RM44 were ascribed in a previous study as well to the lack of both NO_3^- and NH_4^+ uptake by phytoplankton below the WWTP (Parker et al., 2012b). Note that elevated NH_4^+ concentrations resulting from sewage effluent discharge can at times be found upriver of the WWTP especially under low flow conditions. The drought was also an indirect contributor to the high NH_4^+ concentrations in the river; these concentrations were about double the concentrations observed in previous spring sampling (e.g. Glibert et al., 2014b; Parker et al., 2012a,b). Lower flow would be related to less dilution of the wastewater effluent. Also under the present low flow conditions the WWTP is required to hold back effluent at times due to the lack of sufficient dilution for discharge. Elevated concentrations of NH_4^+ will occur when held-back effluent is discharged into the river.

Consistent with the NH_4^+ inhibition hypothesis (e.g., Dugdale et al., 2007), when all chl *a* data are plotted as a function of NH_4^+ concentration, it can be seen that virtually all of the high biomass observations were found when NH_4^+ concentrations were reduced to <10 μM-N and this was the case also for cells that were >5 μm in size (Fig. 6A, B). These larger cells, which predominantly accumulated, and were presumably growing, at the lower NH_4^+ concentration levels were physiologically healthy, as evidenced by their high Fv/Fm (Fig. 6C). The one
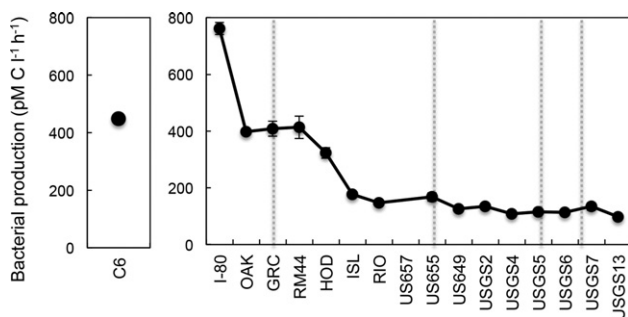

Fig. 3. Bacterial production along a transect of the Sacramento–San Joaquin Bay Delta on March 24, 2014. Where error bars are not shown, they are smaller than the size of the symbol. Vertical dashed lines delineate the various segments discussed in text.
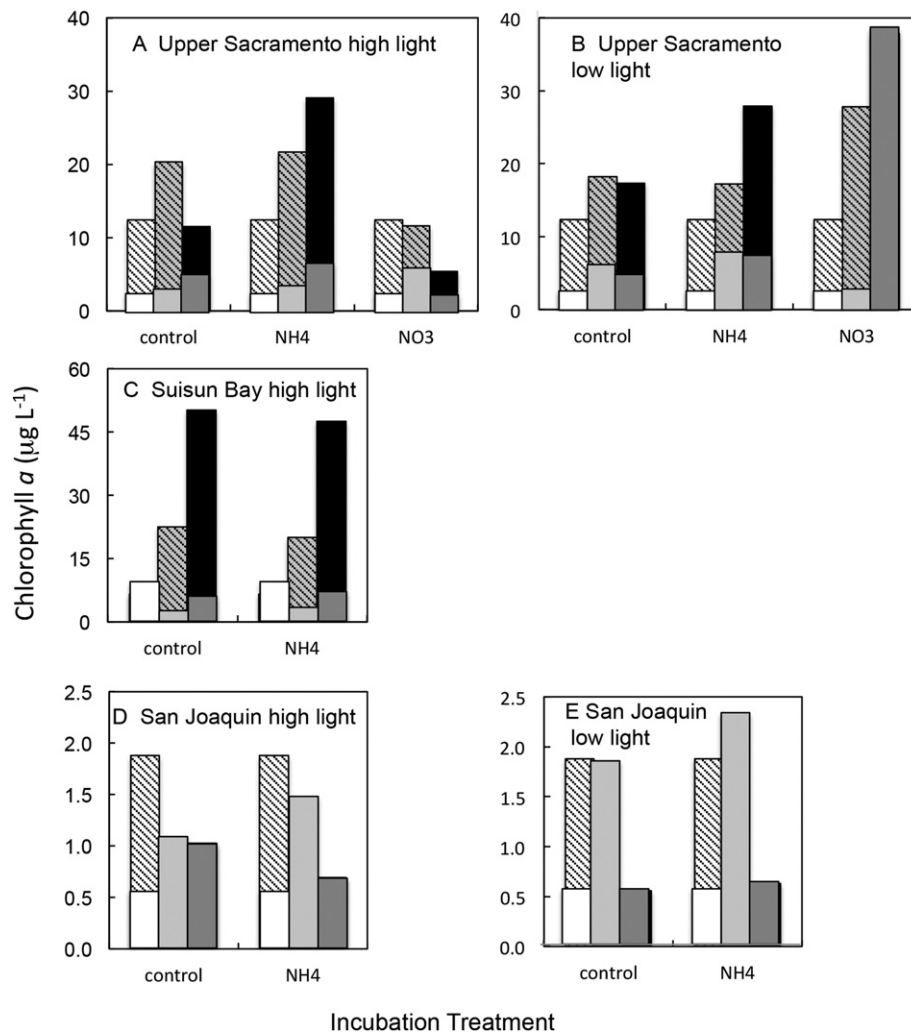
Fig. 4. Experimental responses of chlorophyll a of the samples variably enriched with different substrates and incubated for 48 h. Responses are shown. Each set of bars for each experimental treatment represent time 0, time 24 h and time 48 h. The hatched and black bars represent the size fraction >5.0 µm, the solid gray bars represent the size fraction 0.7–5.0 µm. If only one bar is shown (solid gray), then virtually all the chlorophyll a was in the smaller size fraction. The relative standard error of replicate chlorophyll a determinations was 2.5%. Note that there was no low light treatment for Suisun Bay and that NO_3^- enrichments were only made at the upper Sacramento site because the ambient NO_3^- was so high at the other sites.

observation of 10 µg L^{-1} chl a at a concentration of 70 µM-N NH_4^+ was from RM44, right at the discharge site and likely reflects transport of cells from upriver (Fig. 6A). Previously it has been suggested that a concentration of NH_4^+ of 4 µM-N was the threshold for biomass to accumulate (Dugdale et al., 2007). However, as many studies have shown, the extent and threshold concentrations of inhibition by NH_4^+ have been shown to depend on the species present, their physiological status (Dortch and Conway, 1984; Dortch et al., 1991; Maguer et al., 2007) and the environmental conditions to which they have been exposed (e.g. Bates, 1976; Harrison et al., 1996; L'Helguen et al., 2008; Lomas and Glibert, 1999a,b; Yin et al., 1998). In the current study, the inhibition threshold appears to be about twice the value previously reported for inhibition in Suisun Bay (Dugdale et al., 2007). A somewhat higher NH_4^+ threshold may be tolerated by the Suisun Bay phytoplankton community because of the relatively high concentrations of NO_3^- (>50 µM). Threshold for NH_4^+ inhibition was apparent for cells >5 µm in size (Fig. 6B). While the experimental treatments from Suisun Bay that were enriched with NH_4^+ would suggest that these NH_4^+ additions supported growth (Fig. 4C), in fact, the responses were no different than the controls and growth was, in fact, supported by NO_3^-.

The middle reach of the Sacramento River appeared to sustain very high rates of nitrification. Both NO_2^- and NO_3^- rapidly increased from sites RM44 to USGS2, and an inverse relationship between the

concentrations of NH_4^+ and NO_3^- can be seen for the data from these stations (Fig. 6D). Relatively high pelagic nitrification rates in the Sacramento River have previously been inferred from water column changes in NH_4^+ and NO_3^- (Parker et al., 2012b). However, while bacterial production rates overall were low in this part of the river (Fig. 3), nitrifying archaea may be more important than bacteria for pelagic nitrification (J. Damashek and C. Francis, pers. comm.) and the role of heterotrophic nitrifiers (Ward, 2008) in this system is completely unknown. Nitrifiers may also be exported to the river from the WWTP when the effluent is discharged. Previous direct measurements of nitrification from sediments collected at sites closer to the confluence of the rivers suggest that the contribution of the sediment to these fluxes is small (Cornwell et al., 2014). In measurements made on sediments in March 2011 at sites closer to the confluence of the two rivers, fluxes of $NO_3 + NO_2$ were generally directed into the sediments rather than out of the sediments and rates were overall much lower than observed during the warmer months later in the summer (Cornwell et al., 2014).

In contrast to the upper Sacramento River, in the upper San Joaquin River while there were extremely high nutrient values (NO_3^- > 400 µM-N, PO_4^{3-} > 15 µM-P, but NH_4^+ ~ 2 µM-N), there was very little chl a accumulation (~3 µg L^{-1}). Furthermore, these samples demonstrated extremely poor physiological condition based on variable fluorescence. We hypothesize that an unidentified inhibitor was
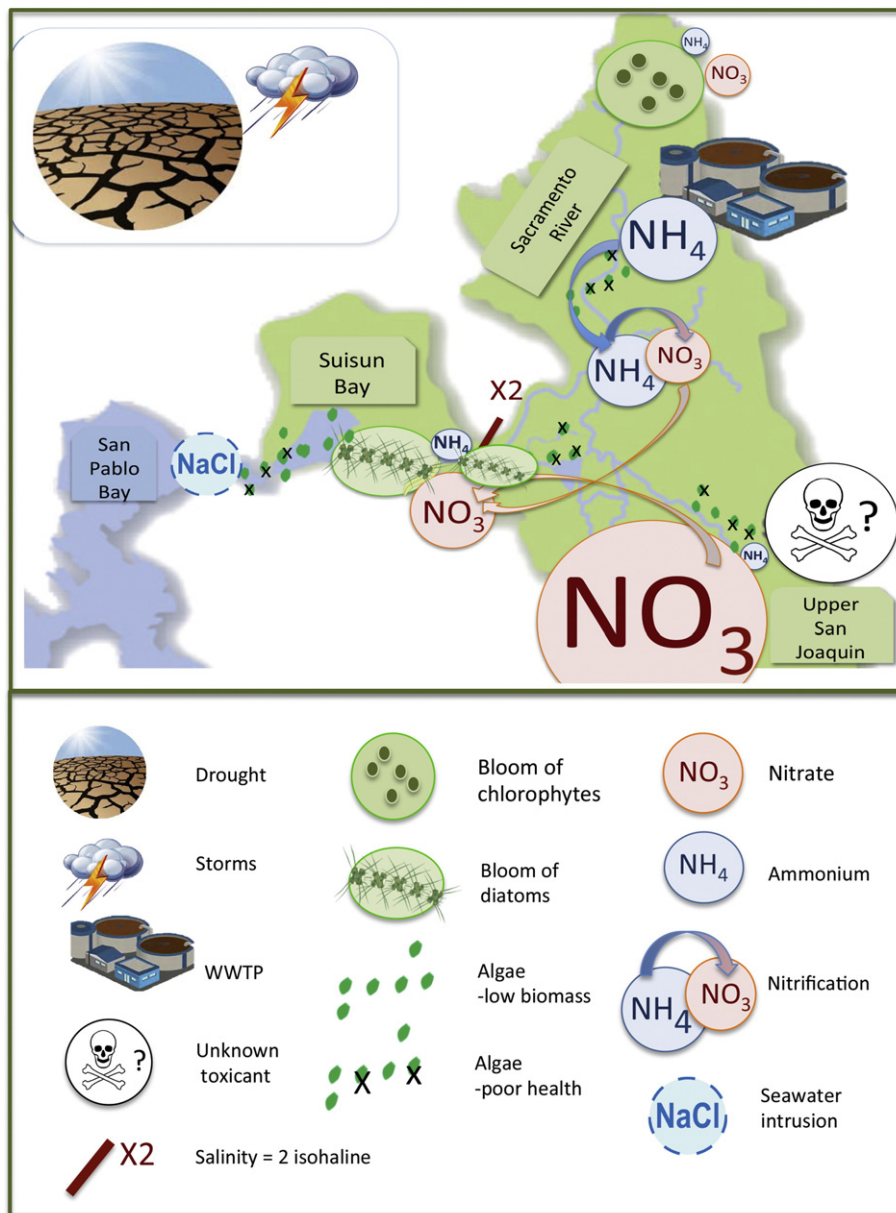
Fig. 5. Conceptual summary of the factors regulating the 2014 spring blooms in the Bay Delta. Note that for nutrients only the major N forms are shown; levels of both PO_4^{3-} and $Si(OH)_4$ are not depicted on the diagram.

depressing growth in this region. There were ample nutrients to support growth, and concentrations of NH_4^+ were less than typically taken to be inhibiting. It is suggested that not only is the early spring period a time of fertilizer application in the agricultural region, but it is also a time of herbicide application. It is possible that high nutrients resulted from runoff from the intense but short rains that had occurred in the prior weeks (a "pineapple express" rainstorm occurred a few weeks prior to our sampling), and that herbicides – or other contaminants – also were present in runoff, and they prevented phytoplankton growth in this reach of the river. It has previously been documented that herbicides such as diuron are used agriculturally and most commonly are applied in the months of January to March (Miller et al., 2002; Jassby et al., 2003) and that they do inhibit phytoplankton production in the Bay Delta (Blaser et al., 2011). The observed high bacterial production (Fig. 3) without algal growth would be consistent with an herbicide or photosynthetic inhibitor, as would the lack of growth in the experimental treatments from this station (Fig. 4D,E).

If phytoplankton were not taking up the nutrients (NO_3^- and PO_4^{3-}) directly in the San Joaquin, these nutrients would have been exported downriver, and would have reached the confluence with Sacramento River and may have been transported further downstream. In fact, assuming the San Joaquin supplied 10–12% of the water in Suisun Bay, on average, and assuming no uptake during transit, concentrations of NO_3^- and PO_4^{3-} in Suisun would be 49 and 1.47 μM, values that are slightly less than the measured concentrations of 59 and 2.9 μM, respectively, with the difference coming from the Sacramento River or from other new sources of nutrient input along the San Joaquin River, including other WWTP effluent discharges. The Suisun Bay diatom bloom thus occurred where NH_4^+ concentrations were sufficiently low, and NO_3^- and PO_4^{3-} concentrations sufficiently high, with no other inhibiting substances restricting growth.

Moving further down-bay towards San Pablo Bay, the collapse of the bloom downstream of Suisun Bay is suggested to be a function of salinity intolerance (e.g., Quinlan and Phlips, 2007; Muylaert et al., 2009). The correlation between chl *a* and salinity for samples from sites
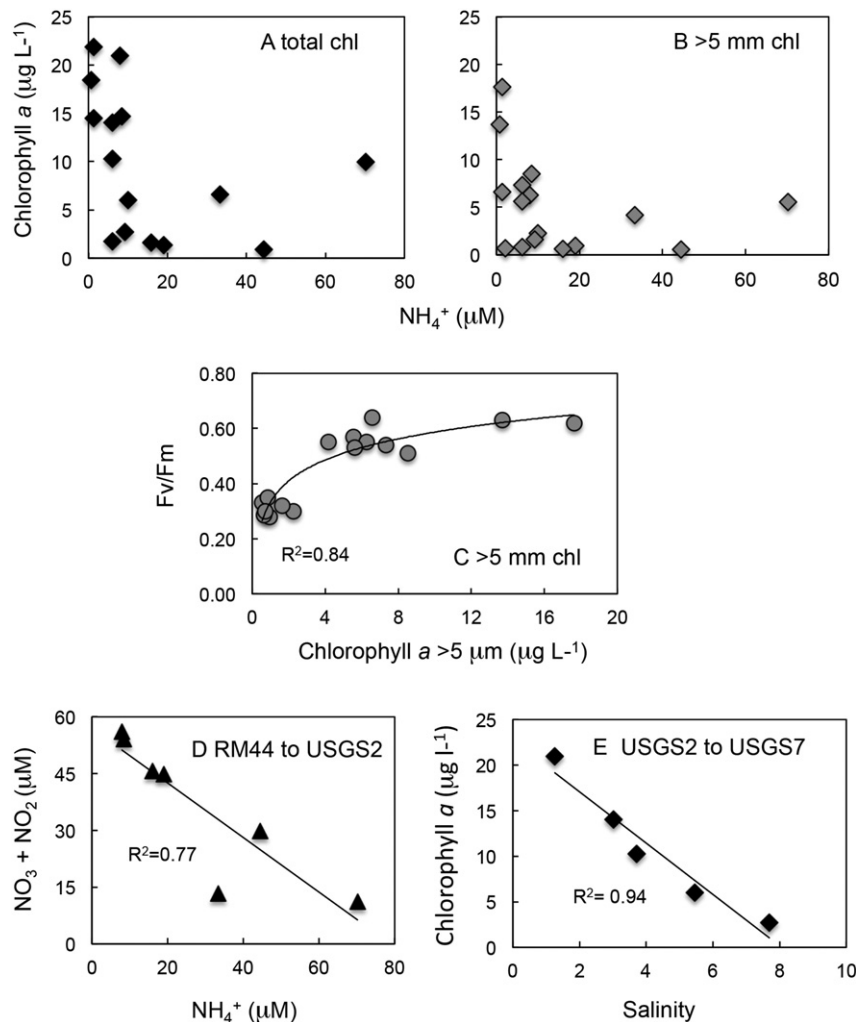
Fig. 6. Property–property plots for several parameters in the Bay Delta in March 2014. A—Total chlorophyll a as a function of NH_4^+ concentrations for all stations samples. B—Chlorophyll a in the >5 μm size fraction as a function of NH_4^+ concentration for all stations sampled. C—Measurements of photosynthesis efficiency (Fv/Fm) as a function of chlorophyll a > 5 μm for all stations. D—$NO_3^- + NO_2^-$ concentrations in relation to NH_4^+ concentrations for stations in the lower Sacramento River to Suisun Bay, RM44 to USGS2. E—Relationship between chlorophyll a (total fraction) and salinity from stations below Suisun Bay, USGS2 to USGS7.

USGS4 to USGS7 is strongly negative ($R^2 = 0.94$; Fig. 6C). There is a suggestion of some recovery of cell physiological status by the San Pablo station, along with some nutrient removal, but no increase in chl a was observed.

Numerous other studies suggest that large or long-chained diatoms frequently are the main phytoplankton in regions where salinity increases in estuaries, and further seaward it is suggested that increased production by diatoms (although a different community composition) may well be expected. This has been shown, for example, in the Suwanee River Estuary (Bledsoe and Phlips, 2000; Quinlan and Phlips, 2007), in Tampa Bay (Badylak et al., 2007), and in Apalachicola Bay where pennate diatoms were also found to be the main contributors to phytoplankton >20 μm in size (Putland et al., 2014). In contrast, in lower salinity estuaries, as shown in the Neuse River Estuary (Gaulke et al., 2010), Thau Lagoon (Vaquer et al., 1996), Pensacola Bay (Murrell and Caffrey, 2005), among other systems, picoplankton are often dominant. Increased riverine discharge may therefore reduce total chl a accumulation and may contribute to a shift in phytoplankton community composition as well. Thus, a combination of maintenance of Suisun Bay as a low salinity zone, and the inhibiting effects of elevated NH_4^+ due to increasing amounts of wastewater discharge, contribute to conditions conducive to the observed shift in phytoplankton

community from large diatoms, which were common up to the mid 1970s, to smaller flagellates and cyanobacteria since the mid 1980s (Lehman, 1996; Lehman et al., 2005, 2008; Glibert, 2010; Brown, 2010; Glibert et al., 2011).

Changes in the phytoplankton community have many consequences for the food web. In oceanography it is generally well accepted that where the algal community is dominated by cyanobacteria, or other picoplankton, the system generally sustains a proportionately greater flow through the microbial loop and a less efficient food web (Azam et al., 1983; Legendre and Lefevre, 1995; Legendre and Rassoulzadegan, 1995). Production in Suisun Bay was historically dominated by diatoms (Ball and Arthur, 1979) and formed the base of a healthy fish community. While food quality is often characterized in terms of lipid and protein content (e.g., Putland and Iverson, 2007; Putland et al., 2014), it is now thought that altered nutrient stoichiometry, a result of both altered community composition (e.g., Finkel et al., 2010) and of variable stoichiometry within functional groups of primary producers can also have effects on secondary producers (e.g., Glibert et al., 2011; Jeyasingh and Weider, 2005, 2007; Laspoumaderes et al., 2010; Malzahn et al., 2010; Sterner and Elser, 2002). Thus, it will be interesting to assess how the spring bloom of Suisun Bay in 2014 alters zooplankton production and ultimately food

available for fish species of concern and whether higher chl *a* becomes the "new norm" with increasingly drier years.

Climate variability is, without question, changing many estuarine systems. Not only are some dry regions getting drier and some wet regions getting wetter, but large scale storm events are increasing in frequency in many regions. Episodic weather events, including hurricanes have been associated with both algal bloom events and longer-term changes in many other estuaries (Mallin and Corbett, 2006; Paerl et al., 2006; Burkholder et al., 2006; Briceño and Boyer, 2010; Voynova and Sharp, 2012; Glibert et al., 2014a). In the Maryland Coastal Bays, for example, large episodic storms have recently been hypothesized to have resulted in high water levels, overwash, and surface runoff especially in the northern segments, and, together with a change from long-term dry to long-term wet conditions have resulted in a shift in dominant phytoplankton, and an increase in conditions associated with a more eutrophic state (Glibert et al., 2014a). Episodic storms preceding the sampling here may have contributed to runoff and the high concentrations of nutrients (and potentially inhibitors of algal growth) observed especially in the upper San Joaquin River.

While the 2014 diatom bloom in Suisun Bay was a rare event in recent decades, *Entomoneis* sp., had been noted to dominate the phytoplankton in the low salinity zone (= Eastern Suisun Bay), albeit at low chl *a* (2 to 3 µg L^{-1}) in late summer 2006 and in spring and summer 2007, the latter also having been a dry year in northern California, but this species had not been mentioned in studies of phytoplankton community composition prior to 1992 (Kimmerer et al., 2012). *Entomoneis* sp. was also a dominant in the phytoplankton assemblage in Suisun Bay in early April 2010 (Dugdale et al., 2012) and a spatially restricted diatom bloom had also been recorded in March 2013 although its composition was not determined (Glibert et al., 2014b). Dugdale et al. (2012) developed a conceptual model that correctly predicted the development of two of these recent spring phytoplankton blooms in Suisun Bay based on only three criteria: the rate of NH$_4^+$ loading (based on present day sewage effluent loads), the water column concentration of NH$_4^+$, and river flow (analogous in steady-state chemostat

growth to "washout"). This conceptual model was further advanced in a one-dimensional, N-based model for coastal embayments such as Suisun Bay (Dugdale et al., 2013), which included terms for time-varying rates of maximum NO$_3^-$ uptake as a function of NO$_3^-$ concentration and for inhibition of NO$_3^-$ uptake by NH$_4^+$. The model predicts two steady states for particulate N (as a proxy for algal biomass) as a function of flow and NH$_4^+$ concentrations in the inflowing water to an embayment, e.g., Suisun Bay (Fig. 7). One steady state is a high-biomass, NO$_3^-$-based, high-productivity state that occurs at low flow and a large range in NH$_4^+$. This is analogous to the pre-1982, diatom-dominated era of the Bay Delta during which delta smelt were plentiful (Glibert, 2010; Glibert et al., 2011). The second steady state is a low-biomass, low-productivity state that occurs at higher flows with relatively high NH$_4^+$; this is analogous to the post-1982 cryptophyte/flagellate-dominated era that is related to the decline of smelt, threadfin shad, and young-of-the-year striped bass (Glibert, 2010; Glibert et al., 2011). The flow during this study was low, ca. 150 m^3 s^{-1} (average of Delta Outflow values for the week preceding the study date, 24 March 2014; http://www.water.ca.gov/dayflow/). When plotted on the modeled two states scenario of the N-based model, this 2014 Suisun Bay bloom fits well with the high biomass state (Fig. 7). It also compares favorably with pre-1982 conditions (see Fig. 13 in Dugdale et al., 2013).

The management implications of these findings of this study are significant. If indeed this unusual spring bloom is a consequence of drought conditions with associated longer residence times for growth and longer time for nitrification to reduce sewage-derived NH$_4^+$ loads, then any management practice using increased flow, e.g. managing X2 for an increased low salinity zone for fish, needs to be done with care to avoid the unintended consequence of reduced phytoplankton production. Increased flow and reduced residence times can tip the ecosystem into low biomass state and possibly washout, a condition where phytoplankton growth cannot keep pace with dilution, resulting in a condition of overall poor productivity. High flow also reduces the opportunity for in-river nitrification and therefore dilution/reduction of inhibiting NH$_4^+$ levels. In other words, by promoting higher rates of flow to increase the spatial extent of low salinity habitat for fish, a "squeeze play", rather than a "window of opportunity," for phytoplankton growth may be created in terms of both spatial and temporal suitable nutrient conditions. While high flow may dilute the upriver concentrations of NH$_4^+$, it extends its effects spatially into Suisun Bay because nitrification is less, thereby limiting the favorable habitat for phytoplankton growth. For phytoplankton growth that does occur under higher flow, lower salinity and consequently still elevated NH$_4^+$ conditions, smaller, non-diatom taxa are favored. Increased flow thus inhibits chl *a* accumulation and also results in transport of phytoplankton and unassimilated nutrients out of the Bay; the low salinity zone is maintained in a phytoplankton poor condition.

Should the 2014 bloom be sustained, it is hypothesized, based on historic food webs, that the summer and fall of 2014 may see an increase in delta smelt, and perhaps other fish of concerns, and one of their prey items, calanoid copepods. Calanoid copepods were comparatively more abundant in prior decades when diatoms were more common (Kimmerer, 2004; Glibert et al., 2011). Delta smelt is a species responsive to changes in the lower food web, including copepod abundance, due in part to its short (generally 1 year) life cycle (Bennett, 2005). Such an outcome would be consistent with relationships developed from long-term trends in various components of the food that suggest that prey density rather than habitat availability *per se* is the most important factor affecting the abundance of this and other fish species of concern (Glibert et al., 2011; Miller et al., 2012). Of note is the finding that larvae of delta smelt were observed in the river confluence region of the delta in 2013 and they reached a size of 20 mm earlier in the year than in other recent years (Damon, 2014), possibly a response, at least in part, to a similar (but spatially smaller) spring diatom bloom that was observed in Suisun Bay in March 2013 (Glibert et al., 2014b).
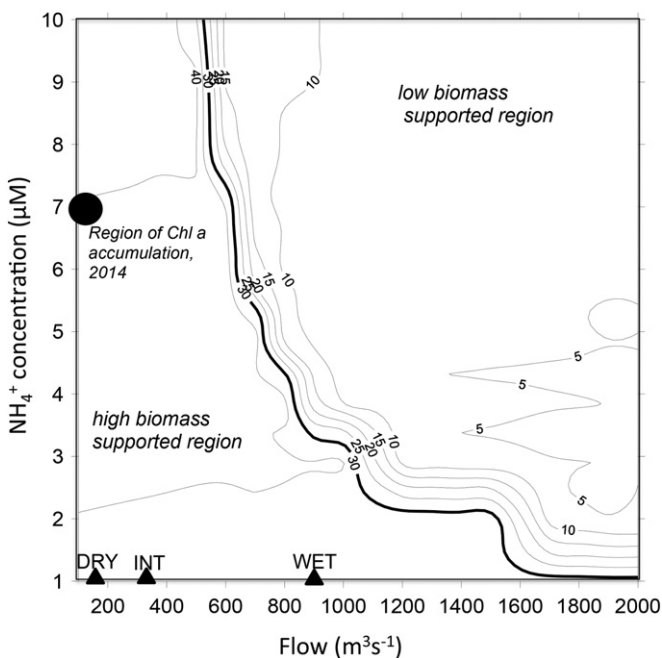

Fig. 7. Modeled effect of flow and initial NH$_4^+$ concentrations on biomass accumulation in Suisun Bay. The contours are particulate nitrogen concentrations (in µM-N) showing two steady states: low biomass and high biomass. The location of the 2014 Suisun Bay bloom in the high biomass region is overlaid in this flow and NH$_4^+$ space (symbol to the left). Arrows show flows in dry, intermediate and wet water years from Peterson et al. (1985).

The drought of 2014 has provided an unplanned ecosystem experiment on low flow effects in the Bay Delta. The spring bloom response may prove to be a positive event for the food web. While many estuaries experience the detrimental effects of eutrophication, including hypoxia, with large spring blooms resulting from land-derived nutrient inputs, the Bay Delta may benefit from modest spring blooms in that the food web may show much needed recovery. However, should future blooms be prolonged and of even greater magnitude, the negative effects of eutrophication may well be of concern. As noted by Kemp et al. (2005), in the analysis of eutrophication of the Chesapeake Bay, reinforcing feedbacks can both accelerate ecosystem degradation and eutrophication, but positive biogeochemical reinforcing feedbacks can also help to reinforce restoration once water quality improvements begin to take hold.

Acknowledgments

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