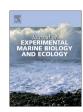
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Major – but rare – spring blooms in 2014 in San Francisco Bay Delta, California, a result of the long-term drought, increased residence time, and altered nutrient loads and forms



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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 NH₄ levels > 70 μM-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 μ 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 NH₄⁺ ~ 2 μ M-N), very low chlorophyll a levels (~3 μ 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 μ M-N), sufficient PO $_3^{4-}$ (>3 μ M-P), and reduced NH $_4^+$ levels (as low as 6 μM-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.

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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 µg 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;

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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 NH₄⁺ 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 μ M-N) when the plant came on line in the early 1980s to >20 mg L⁻¹ (= > 1400 μ M-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 NH₄, originating from sewage discharge, has led to concentrations of NH₄ 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 NH₄⁺, the phytoplankton community composition that develops under high NH₄⁺ concentrations differs from that under proportionately higher NO₃ 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 NH₄⁺ inhibition of NO₃ 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 NH₄ enrichment compared to those exposed to NO₃ enrichment (Donald et al., 2013; Parker, 2004). Chlorophyll yield per N assimilated for phytoplankton growing on NO₃ is as much as 2-fold higher than for phytoplankton growing on NH₄ (Glibert et al., 2014b). The inhibition of NO₃ uptake by NH₄ 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 NH₄⁺ 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, PO₄³⁻, and NH₄⁺ 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 μ m. 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

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