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Nutrient Dynamics of the Delta: Effects on Primary Producers

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ABSTRACT

Increasing clarity of Delta waters, the emergence of harmful algal blooms, the proliferation of aquatic water weeds, and the altered food web of the Delta have brought nutrient dynamics to the forefront. This paper focuses on the sources of nutrients, the transformation and uptake of nutrients, and the links of nutrients to primary producers. The largest loads of nutrients to the Delta come from the Sacramento River with the San Joaquin River seasonally important, especially in the summer. Nutrient concentrations reflect riverine inputs in winter and internal biological processes during periods of lower flow with internal nitrogen losses within the Delta estimated at approximately 30% annually. Light regime, grazing pressure, and nutrient availability influence rates of primary production at different times and locations within the Delta. The roles of the chemical form of dissolved inorganic nitrogen in growth rates of primary producers in the Delta and the structure of the open-water algal community are currently topics of much interest and considerable debate. Harmful algal blooms have been noted since the late 1990s, and the extent of invasive aquatic macrophytes (both submerged and free-floating forms) has increased especially during years of drought. Elevated nutrient loads must be considered in terms of their ability to support this excess biomass. Modern sensor technology and networks are now deployed that make high-frequency measurements of nitrate, ammonium, and phosphate. Data from such instruments allow a much more detailed assessment of the spatial and temporal dynamics of nutrients. Four fruitful directions for future research include utilizing continuous sensor data to estimate rates of primary production and ecosystem respiration, linking hydrodynamic models of the Delta with the transport and fate of dissolved nutrients, studying nutrient dynamics in various habitat types, and exploring the use of stable isotopes to trace the movement and fate of effluent-derived nutrients.

KEY WORDS

Sacramento–San Joaquin Delta, nutrients, primary production, ammonium, nitrate, *Microcystis*, macrophytes, nutrient sensors

INTRODUCTION

The paradigm concerning nutrients in California's Sacramento–San Joaquin River Delta (Delta), developed over several decades of research, is that nutrient levels are high, nutrient limitation is rare, and factors other than nutrients regulate the rates of primary production (Jassby et al. 2002). Annual rates of phytoplankton primary production varied 5-fold between 1975 and 1995. Jassby et al. (2002) explained the strong annual variability as resulting from at least four processes: (1) the effects of invasive clams on phytoplankton biomass; (2) a long-term decrease in total suspended sediments that affect the light regime; (3) changes in river inflows to the Delta that reflect climate variability; and (4) an additional unknown pathway. The *State of Bay–Delta Science 2008* (Healey et al. 2008) did not contain a chapter on nutrients because of this ruling paradigm, and there was little mention of nutrients in chapters on water quality and aquatic ecosystems.

Thoughts about the roles of nutrients in the Delta have changed considerably over the past decade. The emergence of blooms of the toxic cyanobacteria, *Microcystis aeruginosa* (*Microcystis*), starting about 1999, has generated questions about the sources of nutrients needed to sustain these blooms (Lehman et al. 2015). The proliferation of invasive aquatic macrophytes within the Delta, especially *Egeria densa* (Brazilian waterweed) and *Eichhornia crassipes* (water hyacinth), has also raised questions about the sources of nutrients that support summertime coverage of up to 15% of the Delta's waterways by submerged and floating aquatic vegetation (Santos et al. 2009). The growing water clarity in the Delta (Schoellhamer et al. 2013; Hestir et al. 2013) contributes to the increasing role for primary producers in Delta food webs, and the interactions among primary producers, light, nutrients, and hydrodynamics are emerging as critical Delta research topics (Schoellhamer et al. 2016). The chemical forms and concentrations of inorganic nitrogen (i.e., ammonium and nitrate) and the stoichiometry of nitrogen and phosphorus (N:P ratios) are also hypothesized to affect rates of primary production, the composition of the primary producer communities, and the structure of the aquatic food web (Dugdale et al. 2007; Parker et al. 2012a; Glibert et al. 2016). Nutrients and their multiple roles in the Delta landscape have emerged as important topics for monitoring and research in a changing Delta.

This paper addresses the following topics relating to nutrients within the Delta:

- nutrient inputs into the Delta from tributary rivers and the San Francisco Bay,
- nutrient inputs, transport, and fate within the Delta,
- rates and controls on phytoplankton primary production and nutrient uptake,
- changing Delta clarity and the effects of this change on primary production and nutrient uptake,
- whether the form of inorganic nitrogen potentially affects the productivity of phytoplankton, and if the elemental stoichiometry of nitrogen and phosphorus affects algal community composition,
- interactions between nutrients and harmful algal blooms such as *Microcystis*,
- nutrients and invasive aquatic vegetation like *Eichhornia crassipes* (water hyacinth) and *Egeria densa* (Brazilian waterweed) in the Delta,
- technological advances that allow continuous measurement of certain soluble nutrients in Delta waters, and
- thoughts on research needs and directions for future studies regarding nutrients in the Delta.

This paper focuses on nitrogen, the better-studied nutrient within the Delta, and also considers phosphorus. Nutrient concentration and nutrient cycling pathways within the Delta are changing. An upgrade to the Stockton Regional Wastewater Control Facility (SRWCF) in 2007 changed the dominant form of effluent nitrogen from ammonium to nitrate, and a major plant upgrade of the Sacramento Regional County Sanitation District (Regional San) in 2021 will change both the load and form of nutrients discharged into the Delta. An overview of current knowledge about nutrient dynamics within the Delta is timely and relevant.

NUTRIENT INPUTS INTO THE DELTA FROM TRIBUTARY RIVERS AND THE BAY

The Sacramento and San Joaquin rivers deliver the largest loads of nutrients to the Delta, with municipal and agricultural discharge contributing the bulk of these loads (Kratzer et al. 2011). Agricultural discharges include both irrigation return flows that transport fertilizer and soil-derived nutrients and discharge from dairies and feedlots. Although the Sacramento River delivers the largest nutrient loads to the Delta, loading from the San Joaquin River is particularly large, given its size. This is most evident in summer, when the San Joaquin contributes almost half the total nitrogen load to the Delta despite flows less than 20% of the Sacramento (Kratzer et al. 2011). However, water exports from the south Delta divert much of the San Joaquin River water, reducing the effect of these nutrients on the greater Delta (Schlegel and Domagalski 2015). Although San Francisco Bay and the ocean can contribute a small fraction of water to the western Delta, their contribution to the Delta nutrient supply is negligible (Novick et al. 2015). The Sacramento River, therefore, plays the largest role in supplying nutrients to the Delta.

Municipal discharge is also a significant nutrient source to the Delta. Publicly Owned Treatment Works (POTWs) are estimated to supply approximately 25% of the total nitrogen (TN) and 20% of the total phosphorus (TP) loads to the Delta, combining all upstream and in-Delta sources (Domagalski and Saleh 2015; Saleh and Domagalski 2015). The Sacramento Regional Wastewater Treatment Plant (SRWTP) contributes about 90% of the annual total ammonia load to the Delta with effluent discharge occurring in the Sacramento River at Freeport in the north Delta (Jassby 2008).

Concentrations and Trends

Trends in nutrient inputs to the Delta via the Sacramento and San Joaquin rivers have been assessed (Kratzer and Shelton 1998; Cloern 2001; Kratzer et al. 2004; Kratzer et al. 2011; Schlegel and Domagalski 2015). It is important to note that these compilations use as their furthest-downstream reporting station Freeport on the Sacramento River, and Vernalis on the San Joaquin River, which are upstream of the major wastewater treatment plants that serve the Sacramento region and Stockton, respectively.

In the Sacramento River, the annual mean nitrate concentration declined 20% from values near 10 μM between 1980 and 2000, to values below 8 μM in 2013 (Schlegel and Domagalski 2015). The flow-normalized trend in annual loading to the Delta, however, remained relatively constant. The annual mean concentration and mean loading of ammonium from rivers that enter the Delta were reduced by a factor greater than five in the 1970s, and both values have continued to decline modestly since (excluding the SRWTP). The annual mean concentrations of TP were almost halved from values above 3.5 μM in the 1970s to values near 2.0 μM in 2013, with somewhat lower ongoing declines in total annual loads (Schlegel and Domagalski 2015).

Unlike the concentrations in the Sacramento River, the annual mean nitrate concentrations in the San Joaquin River show no decline from the 1970s to 2013, maintaining a concentration near 80 μM, with similarly little change in annual loads. Ammonium concentrations in the San Joaquin River over the same period, however, did show a monotonic decline from values above 14 μM to less than 3.5 μM in 2013, with similar declines in total annual loads. The annual mean TP concentration at Vernalis also declined from highs of over 8 μM in the 1970s, 1980s, and 1990s to values near 5 μM in 2013, with little appreciable change in annual loading to the Delta (Van Nieuwenhuyse 2007; Schlagel and Domagalski 2015).

Schlagel and Domagalski (2015) also noted a strong, discharge-dependent seasonality in nitrate and TP in both the Sacramento and San Joaquin rivers. The highest concentrations in nitrate were observed in the Sacramento River during high discharge in winter months. Although the highest concentrations also occurred in the San Joaquin River during winter, they were greatest at intermediate discharge values. Presumably, the nitrate is diluted in the San Joaquin River at high flows, but this effect is not observed in the Sacramento River, where landscape yields of nitrate can keep pace with increased discharge. In contrast, Schoellhamer et al. (2012) observed TP concentrations to be highest on average in the fall, for both the Sacramento and San Joaquin rivers,

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coincident with elevated sediment flux. Average values declined in the winter months, particularly at low flows.

Landscape Yields

Saleh and Domagalski (2015) studied nitrogen sources and transport in the rivers and streams of California, including the major inputs to the Delta, using the SPAtially Referenced Regressions On Watershed (SPARROW) attributes modeling framework. They found that agricultural lands comprised the largest source (47%) of TN to the Delta in the Sacramento River drainage, with point sources (chiefly POTWs) accounting for 32%. In the San Joaquin River drainage, agricultural lands contributed a greater fraction of TN loading to the Delta (62%), with point sources concomitantly lower (19%). TP loading to the Delta was also investigated using the same modeling approach (Domagalski and Saleh 2015), and this study suggested that agricultural lands contributed 65% and 58% of the total loading from the Sacramento River and San Joaquin River drainages, respectively. Point sources respectively accounted for 21% and 15% of TP loadings for these two drainages. The SPARROW model results also showed evidence of nitrogen retention within the aquatic system in small and medium-sized streams (Mulholland et al. 2008), but little retention in rivers. Retention for both P and N in reservoirs was also found to be small, largely because the reservoirs are located above most cultivated lands (Domagalski and Saleh 2015; Saleh and Domagalski 2015).

NUTRIENT INPUTS, TRANSPORT AND LOSSES WITHIN THE DELTA

Spatial and temporal variation of nutrient concentrations within the Delta are driven by multiple influences: long-term changes in climatic conditions and anthropogenic inputs, and seasonal and climatic variation in flow and temperature as well as in internal biological processes (Novick et al. 2015). Over shorter time-scales, nutrient concentrations within the Delta can vary markedly because of source-related, tidal or biological processes (Pellerin et al. 2009).

Nutrient Sources within the Delta

Although nutrient loading to the Delta is large and responds to long-term and seasonal changes, nutrient loading *within* the Delta is thought to be relatively small and relatively constant, comprising loadings from the internal municipal sources (included above) and nutrients introduced through island drainage, which are thought to be balanced between water withdrawal and island discharge (Novick et al. 2015).

Nitrification—the biological transformation of ammonium into nitrate—plays an important role in the Delta because it represents an internal source of nitrate to the Delta even though it does not change TN (Damashek et al. 2016; Foe et al. 2010). As the ammonium the SRWTP discharges is transported down the distributary channels of the Sacramento River into the central Delta, the north Delta, and into the lower Sacramento River, the ammonium concentrations are observed to decline, accompanied by a concomitant increase in nitrate (Foe et al. 2010; Novick et al. 2015; Parker et al. 2012b), with wastewater ultimately being the major source of nitrate in the central Delta (Novick et al. 2015). The finding that nitrification of wastewater-derived ammonium is significant in determining Delta nitrate concentrations is supported by much available N isotope data (Novick et al. 2015), but it clearly is not the sole determinant.

Nutrient Concentration Trends and Seasonality in the Delta

Trends in nutrient concentrations in the Delta generally have been flat or downward since 1998, with nitrate declining in the Western Delta but little trend elsewhere (Novick et al. 2015). Novick et al. (2015) observed declines in ammonium concentration in the north, central and western Delta. They attributed the observed declines to management source control efforts because the declines run counter to the increasing population density and agricultural intensity of the Central Valley. During this period, phosphate generally remained flat or declined, following the longer-term declines Jassby (2008) reported, which are attributable to declines in POTW discharge of phosphate (Kratzer et al. 2011).

Substantial seasonal and spatial variability in nutrient concentrations is observed in the Delta, driven by a combination of the location of the various inputs as well as internal processes (Figure 1). Concentrations of TN, dissolved inorganic nitrogen (DIN), nitrate, and ammonium are all generally higher in winter months, with lower values in summer—an expression of the multiple controls on concentration. As noted above, the loads of nitrate and phosphate delivered to the Delta are highest during periods of high runoff, and decline during lower flows (Kratzer et al. 2011). These inflows both positively and negatively regulate initial concentration values; winter concentrations in the Delta largely resemble river inputs and spatial variation is muted.

During lower-flow periods in the spring and summer, internal processes become more dominant in determining nutrient distributions. During this period, a characteristic feature of the spatial distribution of nutrients in the Delta is that concentrations of both nitrate and ammonium decline appreciably, particularly in the central and western Delta (Novick et al. 2015). This effect is unrelated to the source of water or initial concentration, and persists into Suisun Bay. The reason for this drawdown of N during transit through the Delta is discussed in the next section.

In-Delta Losses

As is commonly observed in river, delta, and estuarine systems globally, river-borne nitrogen is appreciably attenuated in the Delta (Seitzinger et al. 2006; Wollheim et al. 2008). This effect is generally attributed to changes in water residence time as systems become tidal, uptake into biomass, and denitrification (Seitzinger et al. 2006). Novick et al. (2015) have quantified this effect in the Delta using a simple box model as well as a one-dimensional

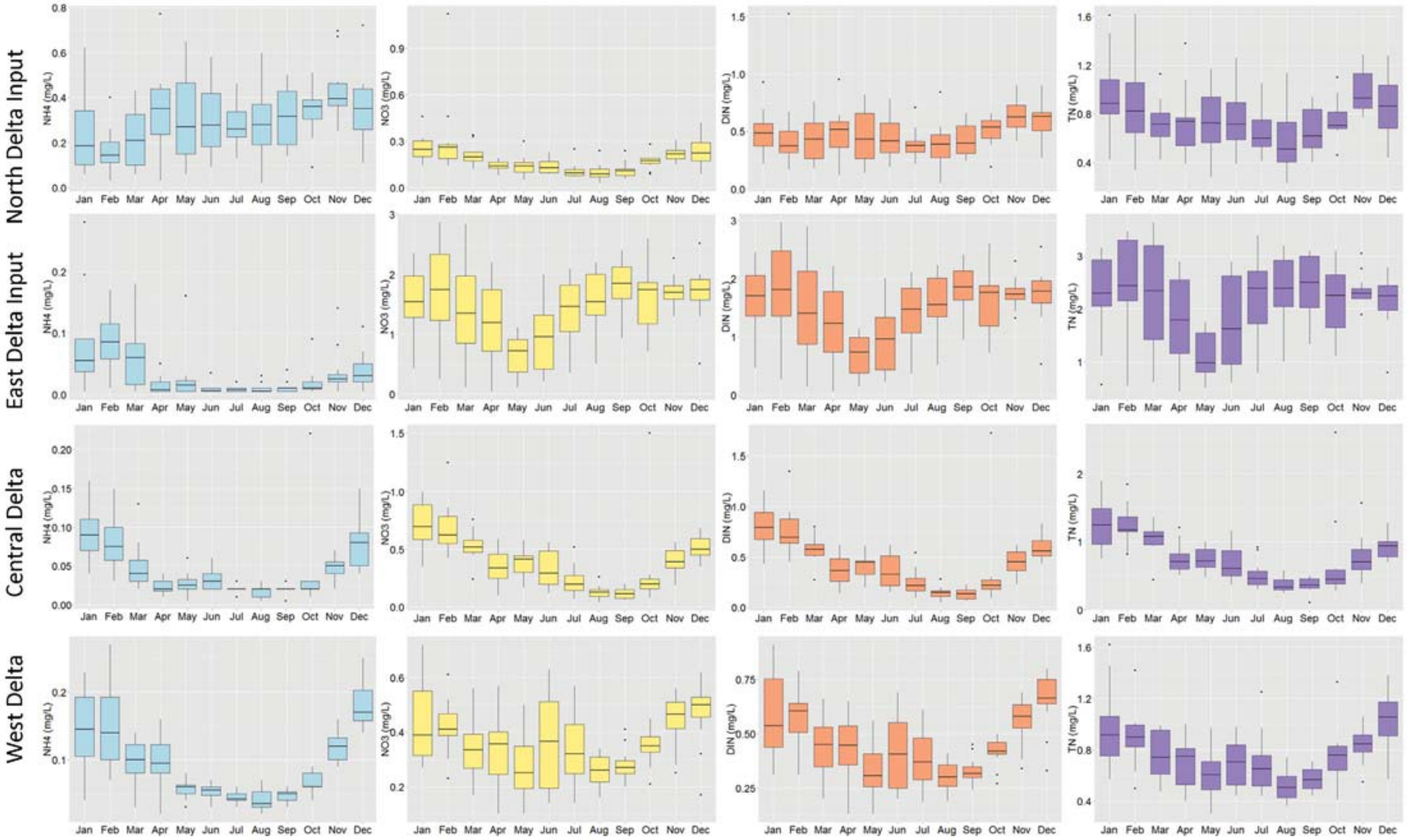

Figure 1 Boxplots of NH_4, NO_3, DIN, and TN concentrations at a subset of CDWR–IEP stations for the period 2000–2011. The boxes show median concentration and 25th/75th percentiles, and the whiskers extend to 1.5x the interquartile range. Anything beyond that are considered outliers and shown with dots. Note the varying y–axis scales. Source: figure from Novick et al. (2015).

hydrodynamic model (DSM2) to characterize losses. They estimated internal N losses to be near 30%, with significant spatial variation in the extent of loss across the Delta. Losses were greatest in summer and fall, during periods of high temperature, lower flows, and increased residence time. Further, they found that losses were greatest in the north, south, and central Delta, attributing this effect to the presence of flooded islands, wetlands, and higher mean residence times. Phosphate has not been similarly analyzed.

Higher residence time leads to higher loss because it provides greater opportunity for uptake into aquatic organisms as well as microbial transformation through denitrification—the conversion and subsequent loss to the atmosphere of nitrate to N_2 gas. Denitrification requires an environment depleted in oxygen, such as those found in sediments and wetlands (Seitzinger et al. 2006). Cornwell et al. (2014) measured denitrification rates in Delta sediments and established that they fell within the range found in estuaries around the world. Scaling these results to the area of Delta sediments, Novick et al. (2015) found that denitrification could account for 25% to 30% of the estimated nitrogen loss in the Delta. In a similar fashion, they estimated that uptake into biomass could account for half of the nitrogen loss in the Delta.

However, these heuristic estimates of the drawdown of nitrogen in the Delta do not account for the effects of wetlands; wetlands can be “hot spots” for denitrification and biomass uptake, as well as efficient traps for phosphate (Harrison et al. 2012; Wollheim et al. 2014). Changes in the type, location, and density of wetlands has the potential to significantly alter the attenuation of nitrogen that passes through the Delta, and, perhaps more importantly, where and when the drawdown occurs (Smyth et al. 2013). A study in Elkhorn Slough, California, found that restoration resulted in 50% to 70% reductions in nitrate, ammonium, and phosphate, with the effects most prominent near the restoration project (Gee et al. 2010). Understanding nutrient uptake into Delta wetlands is a significant gap in our knowledge, given the plans for large-scale wetland restoration.

RATES AND CONTROLS ON PRIMARY PRODUCTION AND NUTRIENT UPTAKE

The potential role of inorganic nutrients as a control on phytoplankton primary production within the San Francisco Estuary (estuary) and Delta has been the subject of substantial debate since *The State of Bay–Delta Science 2008* was published (SBDS 2008, Healey et al. 2008). The issue is critical for ecosystem management because phytoplankton carbon biomass likely plays a disproportionate role over terrestrially derived carbon, supplying much of the organic matter to the estuarine pelagic food web through photosynthesis (Sobczak et al. 2005).

Before the 1980s, Suisun Bay supported persistent, large diatom blooms in late summer that were accompanied by complete exhaustion of inorganic nitrogen (NO_3 and NH_4) (Di Toro et al. 1977; Ball and Arthur 1979; Dugdale et al. 2013). That condition changed dramatically with the invasion of the Asian overbite clam, *Potamocorbula amurensis* in the mid-1980s. Today, despite generally abundant nutrients, there has been persistently low phytoplankton biomass throughout the northern estuary and Delta (Cloern 1996), and measurements of primary production in Suisun Bay (Kimmerer et al. 2012; Parker et al. 2012c; Wilkerson et al. 2015) are among the lowest of estuarine–coastal ecosystems in the world (Cloern et al. 2014). The northern estuary and Delta have been characterized as “high-nutrient, low-growth” environments (HNLG, Wilkerson et al. 2015; Sharp 2001).

Light and Grazing as Primary Controls on Phytoplankton Production and Standing Stock

High suspended-sediment concentrations and the resulting turbidity that characterize the estuary serve as the primary control on phytoplankton production by reducing the availability of light needed to drive photosynthesis (Cloern 1999). This is evidenced by the successful application of a simple productivity model that relates rates of primary production to the availability of light for photosynthesis and phytoplankton biomass (Harding et al. 2002). The model requires calibration for individual systems to derive a “light utilization efficiency” term (Ψ), which has been shown to be robust, and can be used in other light-limited estuarine systems (Cole and Cloern 1987; Parker et al. 2012c). Much of our understanding of productivity is based upon this model and, as developed, the model output is best viewed as an index of the relationship between light availability and phytoplankton biomass through time (Jassby 2008). Changes in Ψ may signal alterations in phytoplankton community composition, altered grazing pressure, or nutrient effects. This suggests that continued direct measurements of phytoplankton production and application of the light-productivity model with regular calibrations are not only necessary but could serve as an indicator of secondary controls on phytoplankton production.

The light-limited conditions that characterize much of the estuary provide a certain resilience against the common effects of high nutrient loads and concentrations, such as accumulations of phytoplankton biomass as "blooms" (Cloern 2001). Delta-wide, phytoplankton biomass is inversely related to freshwater discharge through control of water residence time (Jassby 2008). The intense benthic grazing pressure by *P. amurensis* in the brackish and marine reaches of the estuary and by *Corbicula fluminea* in freshwater reaches, along with grazing pressures from copepods and microzooplankton (Kimmerer and Thompson 2014), appear to keep phytoplankton biomass low. However, given that light availability serves as a primary control of phytoplankton production, increasing water column transparency in the Delta should result in higher primary productivity that supports accumulation of phytoplankton biomass and the potential for phytoplankton blooms, should grazing pressure fail to keep pace with phytoplankton supply. Small but significant increases in Delta chlorophyll have been documented in recent decades, along with declines in diatoms and increases in green algae, cyanobacteria, and flagellates (Jassby 2008; Lehman 1996), although the quality of some of the phytoplankton enumeration data collected has recently been called into question (Cloern et al. 2014). Ephemeral blooms in excess of $30\,\mu g\,\text{Chl-}a\,L^{-1}$ have been routinely detected in Suisun Bay with more temporally intensive sampling (e.g., Wilkerson et al. 2006, 2015; Dugdale et al. 2012), and a persistent bloom, rivaling pre-1980 blooms ($\sim 70\,\mu g\,\text{Chl-}a\,L^{-1}$) was observed in the lower Sacramento River in the spring of 2016. Elevated nutrients create at least the potential for phytoplankton to reach nuisance levels of biomass and production (Jassby 2008).

Recent Measurements of Phytoplankton Primary Production in the Delta

Over the past decade, several investigators have measured primary production directly in Suisun Bay and the Sacramento and San Joaquin rivers using incubation techniques, including the use of C isotope tracers or changes in dissolved oxygen concentrations—with some interesting patterns revealed.

Suisun Bay. Primary production has been measured in two comprehensive studies in Suisun Bay (Kimmerer et al. 2012; Wilkerson et al. 2015). Kimmerer et al. (2012) made temporally intensive measurements of phytoplankton biomass and production during spring and summer in the low salinity zone (generally Suisun Bay) over 2 years (Figure 2). The authors found little variation in biomass or primary production seasonally or inter-annually despite large differences in freshwater flow between years. Periodic phytoplankton blooms do occur in Suisun Bay (Wilkerson et al. 2006, 2015; Dugdale et al. 2012). Wilkerson et al. (2015) examined primary production during spring over 2 years (2011 and 2012) and found lower rates during high freshwater discharge in 2011. Spatially, primary production was lowest in mid-Suisun Bay and substantially higher (7- to 10-fold) at a shoal station in Grizzly Bay, when compared to the deeper channel in Suisun Bay. The depth-integrated production measurements varied considerably from $112\,mg\,C\,m^{-2}\,d^{-1}$ to $>490\,mg\,C\,m^{-2}\,d^{-1}$. The timing of highest net production was earlier in upstream locations compared to downstream locations (Jassby and Cloern 2000).

Sacramento River. Primary production has been directly measured in the Sacramento River (Lehman 2007; Kress 2012; Parker et al. 2012b) and in the Yolo Bypass (Lehman 2007), where substantially higher rates of primary production were observed and were attributed to improved light conditions. Differences in phytoplankton community composition were also noted, with diatoms and green algae characterizing the Yolo Bypass while cryptophytes were dominant in the Sacramento River. Transects of the Sacramento River

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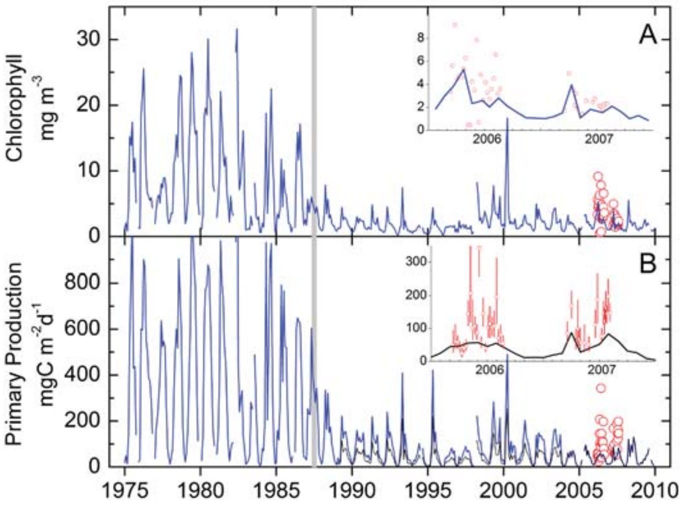

Figure 2 Chlorophyll–*a* (**A**) and estimated primary production (**B**) in the Delta from 1975 to 2010. Insets show data from intensive sampling in the low salinity zone (S from 0.5–5 ppt) during 2006 and 2007. Primary production estimates (**B**) are based on the empirical light utilization model of Cole and Cloern (1984) and two values of Ψ. Source: Kimmerer et al. (2012).

from above the confluence of the American River in Sacramento to the confluence with Suisun Bay have revealed what has been described as a "U-shaped" pattern in phytoplankton biomass and primary production (Foe et al. 2010; Parker et al. 2012b; Kress et al. 2012; Glibert et al. 2014). The lowest rates of primary production were observed between Hood and Rio Vista. Kraus et al. (forthcoming) have attributed this pattern to top-down controls that include grazing and the sinking of diatoms. Kress et al. (2012) noted a dominance of flagellates in the Sacramento River, except for during an "extreme" freshwater flow event during the spring of 2011, when the Sacramento River was dominated by diatoms and supported elevated phytoplankton biomass (Kress 2012).

San Joaquin River. Declines in phytoplankton biomass and primary production in the San Joaquin River were documented downstream of Stockton before the SRWCF was upgraded (Lehman 2007). The lower primary production was associated with higher biomass-specific C uptake, indicating that the changes were mostly from declines in phytoplankton biomass. Based on these results, it was speculated that less turbid, slower moving water or ammonium concentrations may have led to shifts in the phytoplankton community from diatoms to flagellates. After the 2007 upgrade to advanced secondary treatment at the SRWCF that included reductions in ammonium, Kress (2012) also observed declines in phytoplankton biomass in the vicinity of the area of effluent discharge, with the phytoplankton community primarily made up of diatoms and chlorophytes. The Stockton Deep Water Ship Channel, one of the few regions of the Delta where bottom water hypoxia commonly occurred, was also linked to ammonium load from the SRWCF with the low dissolved oxygen attributed to a combination of nitrogen-fueled increases in phytoplankton biomass and to biochemical oxygen demand (Jassby and Van Nieuwenhuyse 2005).

Measurements of Phytoplankton Nutrient Uptake in the Delta

Unlike the decades-long history of primary carbon production studies in the Delta, we are not aware of direct measurements of phytoplankton nitrogen uptake in the estuary or Delta before 1999. Over the past decade several studies have reported rates of nitrate and ammonium uptake, providing insight into the interactions of varying forms of inorganic nitrogen and their relations with primary production.

The Northern Estuary and Suisun Bay. Weekly to monthly measurements of chlorophyll, nitrate uptake, and ammonium concentration between 1999 and 2003 (Figure 3; Wilkerson et al. 2006) revealed seasonal inorganic nitrogen uptake rates that were similar between spring and summer with nitrate contributing roughly a third to inorganic nitrogen uptake during spring but only ~15% in all other seasons. Phytoplankton blooms appeared to be associated with periods when phytoplankton were assimilating the much larger pool of inorganic nitrogen in the form of nitrate at rates that were substantially higher than rates observed for ammonium uptake. The results have been interpreted to suggest that one condition necessary for bloom formation was phytoplankton use of nitrate. Similar patterns have been described for phytoplankton blooms between 2010 and 2013 (Dugdale et al. 2012; Wilkerson et al. 2015).

Sacramento River. Transects completed in the Sacramento River showed nitrate uptake to have occurred only in the reach above the SRWTP at

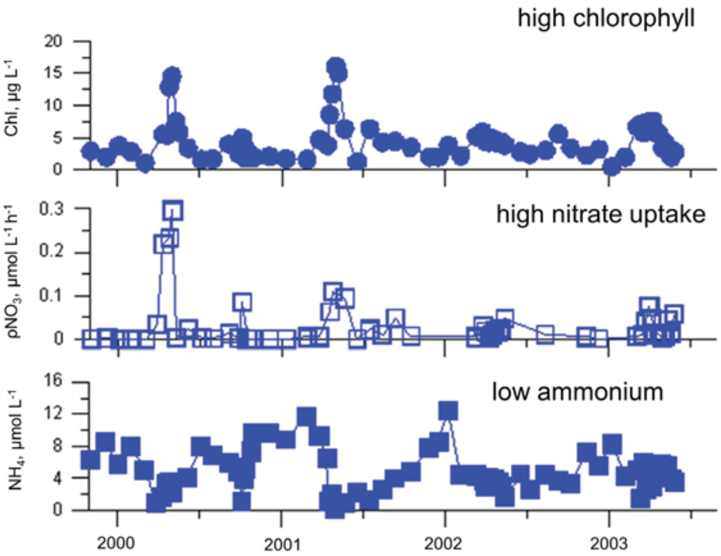

Figure 3 Times series (1999–2003) of chlorophyll–*a*, nitrate uptake and ammonium concentrations in the northern estuary. Associations between elevated chlorophyll–*a* ($>10\ \mu g\ L^{-1}$), high nitrate uptake and low ammonium concentrations were observed in all three sub-embayments of the northern estuary (San Pablo Bay shown; from Wilkerson et al. [2006]).

Freeport (Parker et al. 2012b). In the upper reach nitrate uptake represented ~80% of phytoplankton inorganic nitrogen assimilation, because ammonium concentrations were often quite low (<1 μM). Similar to observations made for primary production, phytoplankton nitrogen uptake rates declined in the middle reaches of the Sacramento River between Hood and Rio Vista, and phytoplankton relied on ammonium as their primary inorganic nitrogen source. Nitrogen uptake often rebounded south of Rio Vista, and phytoplankton used both ammonium and nitrate to meet cellular N demand.

Currently, few published results explore the influence of irradiance on the assimilation of nitrogen in the Delta, and this remains an area for future scientific effort. The broader oceanographic and estuarine literature suggests that phytoplankton N uptake is light-dependent and displays Michaelis–Menten (hyperbolic) kinetics in response to irradiance that varies by the form of inorganic N being used (MacIsaac and Dugdale 1972). Specifically, the uptake of nitrate by phytoplankton appears strongly light-dependent, whereas ammonium uptake in the dark frequently occurs at rates between 30% and 95% of uptake in the light (MacIsaac and Dugdale 1972; Pennock 1987; Boyer et al. 1994). In central San Francisco Bay, hyperbolic N uptake versus irradiance curves indicate that both nitrate and ammonium uptake were light-saturated at relatively low irradiances (>15% of surface values), with lower light intensities required for phytoplankton to begin assimilating ammonium (Dugdale et al. 2016). Using water collected from the Sacramento River upstream of Freeport, Glibert et al. (2014) performed N amendment experiments at both high and low light, and suggested that river diatoms may be favored in conditions with high nitrate and low light.

To our knowledge, there are no measured rates of phytoplankton phosphorus (P) uptake in the Delta; clearly, this is a data gap for nutrient management in the Delta. Van Nieuwenhuyse (2007) analyzed trends in P in the lower San Joaquin River between 1975 and 2005, and noted a steep decline in P loading during the mid-1990s associated with mandated bans of P-based detergents. The rapid decline in P coincided with similar declines in chlorophyll-*a* concentrations, indicating a potential role for P in regulating phytoplankton. The author could not associate the decline of chlorophyll-*a* to documented changes in zooplankton or clam grazing, but ruled out light limitation as a cause by noting that the decline occurred at the same time the photic zone depth increased. N:P ratios were low (generally <10), suggesting a greater likelihood for N rather than P limitation. The author suggested that either the assumed N:P ratio of the algal cells was wrong or the bioavailability of the inorganic N and P pools were not the same as overall inorganic N:P ratios.

NUTRIENT EFFECTS ON PHYTOPLANKTON PRODUCTION

Although the paradigm in estuarine management is that anthropogenic nutrient loading will increase the probability of cultural eutrophication and associated declines in estuarine water quality, the reality is that estuaries exhibit a broad spectrum of responses to nutrient enrichment (Glibert et al. 2010). Given the diversity of habitats that occur in the estuary and Delta, it is likely that a range of nutrient-related responses may be observed (Figure 4). Phytoplankton-nutrient processes in the estuary represent a largely unexplored research area. However, monitoring and

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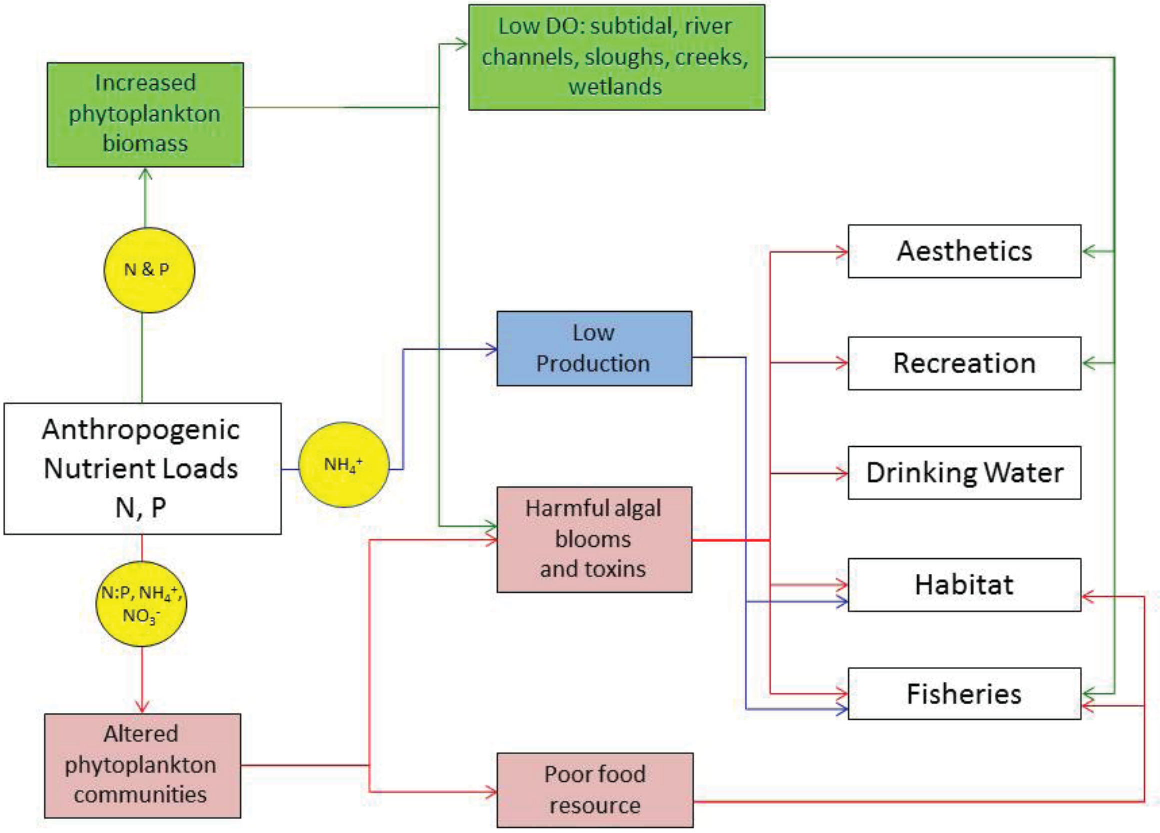

Figure 4 Conceptual model of potential pathways for nutrient-mediated ecosystem disruptions via phytoplankton processes in the high nutrient Delta (modified from Senn and Novick [2014a]). Green boxes represent pathways leading to the "classical" cultural eutrophication response. The blue box highlights the pathway described by the Ammonium Paradox (Dugdale et al. 2007), and red boxes highlight the pathways described by ecological stoichiometry theory (Glibert et al. 2011).

management frameworks for nutrients are currently under development for the bay (Senn and Novick 2014a) and the Delta (CVRWQCB 2014).

At present much of the published research on nutrients in the Delta addresses one set of related conceptual models: the Ammonium Paradox/Ecological Stoichiometry. These conceptual models have linked elevated ammonium concentrations to the estuarine food web through multiple pathways (Brown et al. 2016). The section that follows describes the published research on the "Ammonium Paradox" and points to extensive challenges to the proponent's interpretations. Senn and Novick (2014b) provide a nice synthesis of arguments for and against the ammonium paradox for Suisun Bay, and the reader is directed there for more detailed discussion. Perhaps because of the level of scientific uncertainty and the resulting controversy, the Ammonium Paradox has dominated nutrient research in the Delta at the expense of a broader discussion of potential nutrient-related effects on phytoplankton in the Delta. Studies that more completely consider the continuum of estuarine responses to elevated nutrients are still needed.

The Ammonium Paradox

One observed response to elevated nutrients in estuaries runs counter to the conventional wisdom of cultural eutrophication. This is the observations of *lower* phytoplankton growth with *higher* levels of nutrients (e.g., Yoshiyama and Sharp 2006). Borrowing from oceanography, these systems are referred to as "high-nutrient low-chlorophyll" (HNLC; Cloern 2001) or HNLG (Sharp 2001). Dugdale et al. (2007), and several publications that followed have promoted the HNLG paradigm for the estuary and have suggested that estuarine managers must separately consider the impacts of anthropogenic nitrate and ammonium on estuarine production in the estuary. The hypothesis that lower production results from ammonium enrichment has come to be known as the "Ammonium Hypothesis" (Dugdale et al. 2007; Wilkerson et al. 2015) or the "Ammonium Paradox" (Dugdale et al. 2012; Wilkerson and Dugdale 2016). The paradox is that ammonium is necessary for phytoplankton growth, but ammonium can also reduce growth relative to phytoplankton with access to the generally larger pool of DIN that is in the form of nitrate. The Ammonium Paradox was briefly mentioned in the SBDS 2008 as an area of emerging research (Kimmerer et al. 2008), and the proposed mechanisms behind these hypotheses have been more completely described since that time.

Acknowledging that light serves as the primary control of estuarine production, Dugdale et al. (2007) conceptualized "productivity windows": situations in which the light field becomes favorable for blooms during which anthropogenic increases in nutrients—specifically ammonium—could result in declines in estuarine primary production by cutting off phytoplankton access to nitrate. It is debated that not all inorganic nitrogen is equal with respect to phytoplankton physiology; some phytoplankton (i.e., diatoms) are nitrate opportunists that can accelerate or "shift up" nitrate transport and assimilation based upon the external supply of nitrate (Dugdale et al. 2006). Dugdale et al. (2007) also hypothesize that in the estuary, as well as in other estuaries that receive large anthropogenic ammonium loads, ammonium concentrations are sufficient to inhibit phytoplankton access to nitrate, resulting in a lower probability of phytoplankton blooms. When light conditions are favorable for phytoplankton blooms, dissolved inorganic nitrogen concentration represents the potential fuel for primary production. However, when ammonium inputs are sufficient to maintain concentrations that inhibit nitrate uptake, primary production is supported only by ammonium and the nitrate, along with potential additional primary production, is exported to the coastal ocean through the Golden Gate. Therefore, under most conditions, nitrate is for all practical purposes a conservative property in the estuary.

The Ammonium Paradox is based upon three underlying hypotheses with each receiving scrutiny and challenge. The first hypothesis is that elevated ammonium concentrations inhibit nitrate uptake. It is well established from phytoplankton studies (for reviews see Dortch 1990; Glibert et al. 2016) that phytoplankton will take up ammonium before nitrate. The interaction of ammonium and nitrate is sometimes described as "preference" because the energetic cost to phytoplankton cells to assimilate ammonium into protein is less than that required for nitrate (Syrett 1981). However, the presence of ammonium has been shown to inhibit the transport of nitrate into phytoplankton cells (e.g., He et al. 2004; Song and Ward 2007) as well as inhibiting the manufacture of the enzymes necessary for nitrate assimilation (Eppley et al. 1969; Vergera et al. 1998), and so the terms "inhibition" or "repression" have also been used to describe the phenomenon. In locations where it has been tested ([1] the three embayments of the northern estuary, Wilkerson et al. 2006; Dugdale et al. 2007; [2] the Sacramento River, Parker et al. 2012b, and [3]the San Joaquin River, Lehman et al. 2015; Parker, unpublished; Figure 5), results suggest that ammonium inhibition of nitrate is a universal feature of the estuary and Delta. A review of ammonium in Suisun Bay (Senn and Novick 2014b) concludes that there is "strong support" that ammonium inhibition of nitrate uptake does occur in the estuary.

A second hypothesis embedded in the Ammonium Paradox is that nitrogen uptake is higher when phytoplankton use nitrate rather than ammonium. This higher uptake is attributed to differences in algal communities that occur in response to the supply of nitrate and ammonium, even at nitrogen concentrations considered saturating for algal growth (Glibert et al. 2016 and references therein). Studies have suggested that diatoms thrive in nitrate-rich systems, whereas chlorophytes and cyanobacteria are often associated with ammonium-rich systems (e.g., Blomqvist et al. 1994; Hyenstrand et al. 1998; Glibert and Berg 2009; McCarthy et al. 2009; Domingues et al. 2011). Experimental manipulations conducted using algae and water from the Delta reproduced these observations (Glibert et al. 2014). Diatoms, when supplied with high concentrations of nitrate in upwelling systems, can rapidly assimilate this form of nitrogen and produce large phytoplankton blooms. Called "shift up," diatoms appear to up-regulate the cellular machinery necessary to assimilate

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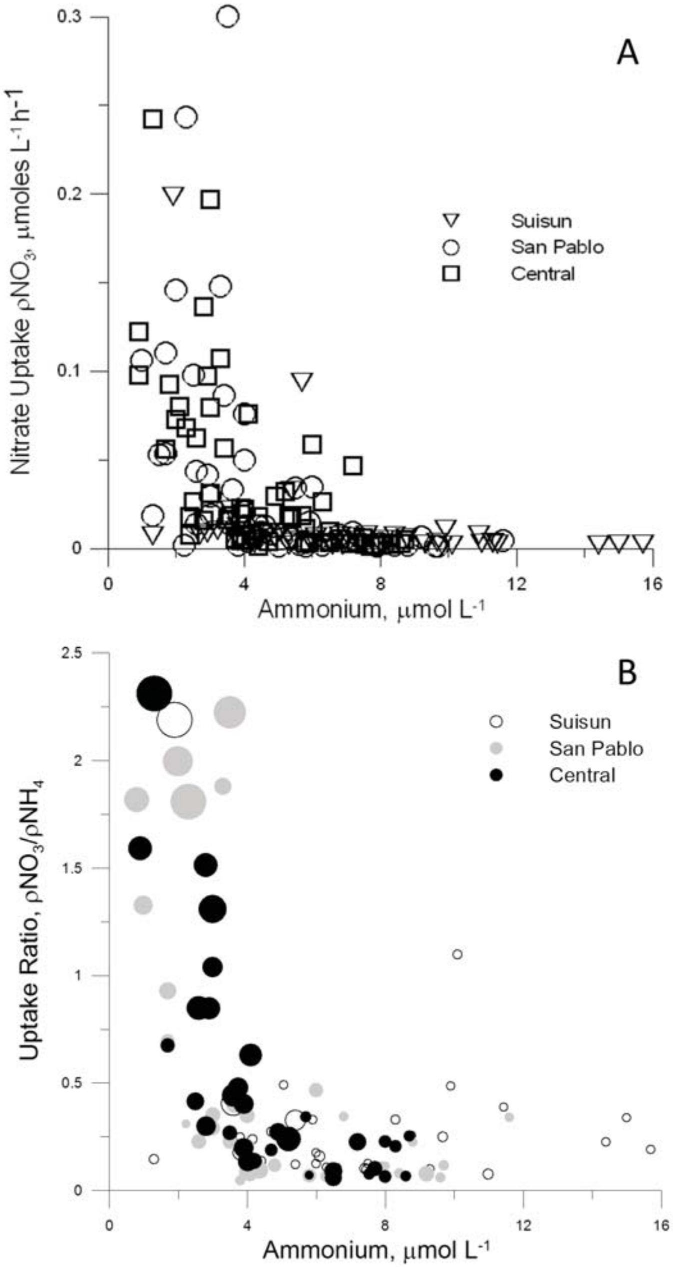

Figure 5 (**A**) Nitrate uptake versus ammonium concentration in the three sub-embayments of the northern estuary. Nearly compete inhibition of nitrate uptake occurs at ammonium >4 µmol L^{-1}. (**B**) Ratio of nitrate to ammonium uptake versus ammonium concentration. Bubble size is proportional to the concentration of chlorophyll-*a*. Nitrate/ammonium uptake occurs at ammonium <4 µmol L^{-1}; elevated chlorophyll-a concentrations occur at high nitrate: ammonium uptake. Source: Dugdale et al. (2007).

nitrate (Smith et al. 1992; Lomas 2004; Allen et al. 2006) in response to increasing concentrations of nitrate (Dugdale et al. 1981; MacIsaac et al. 1985; Wilkerson and Dugdale 1987). No such shift up has been demonstrated for ammonium (Glibert et al. 2016). Here, too, there is skepticism about whether the observed differences in nitrogen uptake rates for nitrate versus ammonium have been sufficiently demonstrated or rather reflect experimental artifacts (Senn and Novick 2014b; Reed et al. 2014).

Finally, the third hypothesis to the Ammonium Paradox requires that phytoplankton primary production is lower when phytoplankton use ammonium rather than nitrate. Surveys conducted in the urban Delaware River (Figure 6), the Hong Kong Harbor, and the Sacramento River provide support for the hypothesis that elevated ammonium may inhibit C and ammonium uptake (Yoshiyama and Sharp 2006; Xu et al. 2012; Parker et al. 2012b). However, a recent study (Kraus et al., forthcoming) found no evidence of ammonium inhibition of primary production when

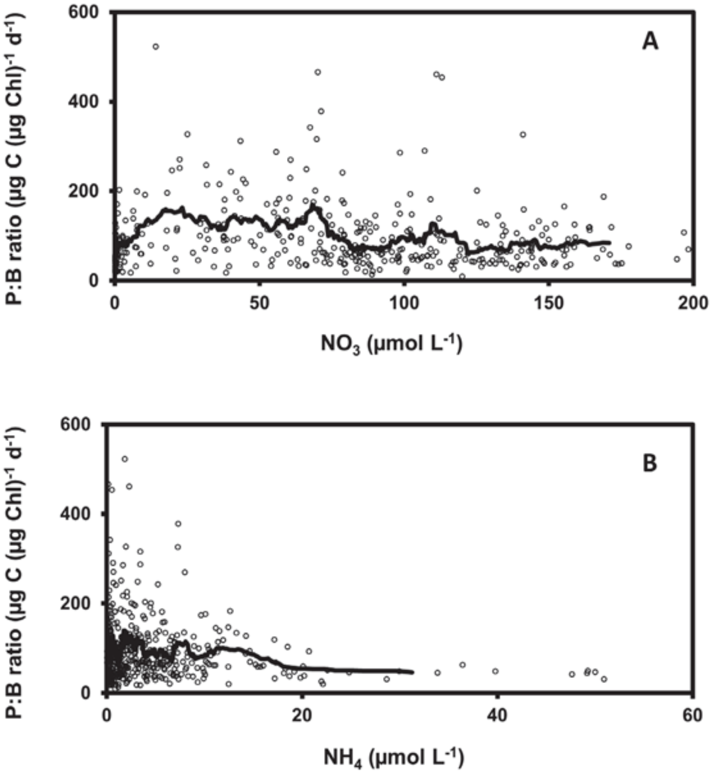

Figure 6 Evidence of ammonium inhibition of estuarine primary production during summer from the Delaware Estuary. Maximum volumetric primary production per unit Chl-*a* (P : B ratio) versus (**A**) nitrate and (**B**) ammonium. Source: Yoshiyama and Sharp (2006).

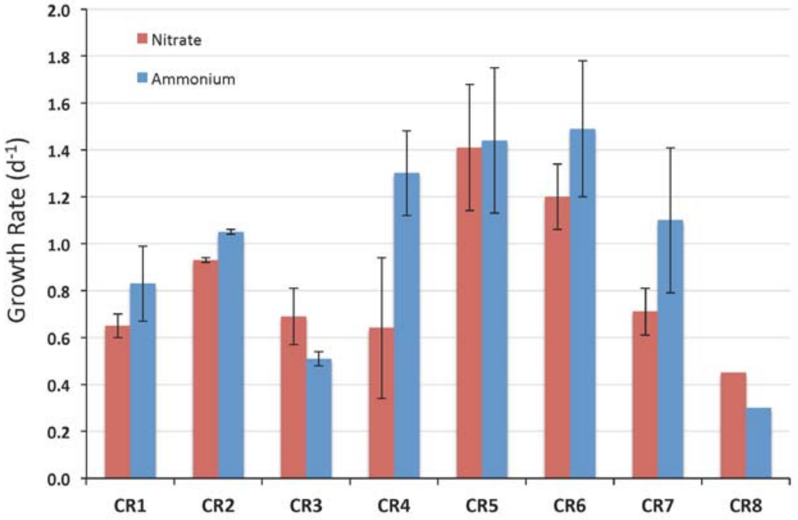

Figure 7 Difference in growth rates of *Cylindrospermopsin raciborskii* when grown on nitrate (red bars) versus ammonium (blue bars) for eight different strains. Source: Data from Saker and Neilan (2001) and Sucken et al. (2014), as presented by Berg and Sutula (2015).

tracking phytoplankton growth in the Sacramento River in the presence and absence of SRWTP effluent. The water parcel absent of this effluent was created by diverting wastewater into storage basins. Controlled laboratory culture studies suggest that phytoplankton, including cyanobacteria and diatoms, grow as well on ammonium as on nitrate (Collos and Harrison 2014; Berg and Sutula 2015; Figure 7). In one field study, Esperaza et al. (2014) were able to produce a diatom bloom that was supported by ammonium during a wastewater hold in a slough adjacent to Suisun Bay. Dugdale et al. (2012, 2013), however, argued that these observations did not consider the interaction between river flow and nutrient concentration. Further complicating this picture is that unknown contaminants could serve as an anthropogenic stressor for phytoplankton C, and N uptake may co-occur with the ammonium loads in anthropogenic settings such as the Delta. This is because much of the ammonium load comes from municipal wastewater. Under this scenario, ammonium serves as a “tracer” of the effect of unidentified contaminants rather than as the direct cause. The studies from Suisun Bay and the Delta (Parker et al. 2012a, 2012c) and the Delaware River (Yoshiyama and Sharp 2006) have raised this possibility.

Cloern et al. (2014) used long-term monitoring program data from Suisun Bay to look for ecosystem-scale evidence for the Ammonium Paradox or nutrient stoichiometry as drivers of phytoplankton declines, especially for diatoms. Based on annual mean data from two stations, the authors concluded that there was no correspondence between increasing ammonium concentrations and declining chlorophyll-*a* or diatoms. This result may be from the coarse temporal scale used as a result of annual data aggregation, which might have obscured the processes described to initiate phytoplankton blooms in the Ammonium Paradox. Still, Cloern et al. (2014) raised an important challenge to the Ammonium Paradox, namely to place the declines in primary production attributed to anthropogenic ammonium within the context of the demonstrated phytoplankton losses resulting from grazing by clams. They conclude that though sewage inputs may play a role in declining production, it is overwhelmed by other processes. The management implications articulated in Cloern et al. (2014) are important for both sides of the controversy. Controls on phytoplankton processes are likely regulated by many factors, including light availability, grazing, freshwater flow, and nutrients; and the relative importance of these drivers likely vary temporally and spatially across the diverse hydrographic landscapes of the estuary and Delta. Efforts to manage a single “master variable” (e.g., light, grazing, flow, or nutrients) are unlikely to improve ecosystem conditions for phytoplankton throughout the Delta. Continued studies of potential phytoplankton responses (Figure 4) to the Delta's high nutrient conditions are still needed, and management of nutrient loading remains an important goal for the estuary (Jassby 2008).

MICROCYSTIS AND CYANOBACTERIAL HARMFUL ALGAL BLOOMS

Overview

Growth of cyanobacteria has become increasingly prevalent in waters around the world, including the Delta, in the past 2 decades. These harmful algal blooms (cyanoHABs) are linked to anthropogenic nutrient enrichment that originates from agricultural, industrial, and urban development (Heisler et al. 2008; Li et al. 2014; Paerl and Huisman 2008). CyanoHABs are associated with a number of adverse consequences to aquatic ecosystems and human wellbeing. Blooms reduce water clarity, ultimately to the detriment of aquatic habitat (Paerl and Otten 2013). As blooms die, bacterial decomposition can cause hypoxia or anoxia and potentially fish kills (Paerl and Otten 2013). CyanoHABs also produce toxins that can lead to mortality and sublethal effects on wildlife and which require expensive treatment of drinking water supply in order to prevent negative effects on humans (Berg and Sutula 2015). Blooms are expensive to mitigate and can reduce tourism near affected water bodies, thus affecting local economies.

Several major factors affect cyanobacterial blooms, including salinity, irradiance, stratification, temperature, water residence time, and nutrient availability (Berg and Sutula 2015; Lehman et al. 2013). Salinity gradients do not control the geographic distribution of cyanoHABs; common cyanobacteria have a broad range of salinity tolerance and can survive in brackish waters (Berg and Sutula 2015). Cyanobacteria have a photo-protective function that allows them to thrive in high light levels, and their positive buoyancy helps to ensure that they have adequate irradiance (Berg and Sutula 2015). At elevated temperatures (25°C and higher), cyanobacteria grow well and outcompete diatoms and green algae (Jöhnk et al. 2008; Paerl and Huisman 2008; Reynolds 2006), and toxic strains of *Microcystis* dominate over nontoxic strains (Davis et al. 2009; Paerl and Otten 2013).

Long residence times and strong vertical stratification can lead to persistent blooms in nutrient-enriched waters (Berg and Sutula 2015; Paerl and Otten 2013), although high flushing rates, vertical mixing, and turbulence negate some of the competitive advantages for cyanoHABs. The effects of stratification, (e.g., warmer temperatures, higher irradiance, and diminished loss rates) likely promote cyanoHABs, rather than the stability of the water column itself (Berg and Sutula 2015; Elliott 2010). When a period of high flow, providing a large influx of nutrients, is followed by a period of low flow, leading to higher residence times, bodies of water are prone to cyanoHABs (Paerl and Otten 2013). Additional factors that affect cyanoHABS include dissolved inorganic C cycling, zooplankton grazing, iron availability, turbidity, pH, sediment-water column exchange of stored nutrients (Paerl and Otten 2013), nutrient recycling by heterotrophic bacteria, viral lysis, exposure to herbicides and pesticides, and dissolved silica (Paerl and Otten 2013; Spier et al. 2013).

Finally, an ample supply of nutrients (N and P) is important. Although algal blooms persist with reduced N and P (Paerl and Otten 2013), the blooms will eventually die back without adequate nutrient availability. Elevated concentrations of dissolved macronutrients favor the growth of the toxigenic ecotypes of *Microcystis* (Downing et al. 2005; Paerl and Otten 2013). In addition, Harris et al. (2016) recently found that microcystin-producing cyanobacteria were favored, as was toxin production at low N:P ratios, in midwestern U.S. reservoirs. Some cyanobacteria are capable of nitrogen fixation, though most of their demand is met through fixed N: ammonium, nitrate, nitrite, urea, amino acids, and cyanate (Berg and Sutula 2015).

Stable isotope analysis suggests ammonium as the primary source of nitrogen for cyanoHABs in the Delta (Lehman et al. 2015), though many different forms of inorganic and organic N are bioavailable (Lee et al. 2015). *Microcystis* abundance appears to be more tied to absolute amounts of N and P than the N:P ratio (Lehman et al. 2005). Relatively high nitrate concentrations in the Delta dominate the N:P molar ratio, and this evidence further supports that nitrate concentrations have little influence on *Microcystis* blooms.

The Delta

CyanoHABs in the Delta were first observed in 1999 and have become commonplace since, though not necessarily present every year (Berg and Sutula 2015). Blooms generally begin in the central Delta and extend seaward (Lehman et al. 2005, 2008, 2010, 2013) with an increasing geographic range (Figure 8; Berg and Sutula 2015; Lehman et al. 2005). Although a number of cyanobacteria that form harmful blooms have been observed in the Delta (Cloern and Dufford 2005; Kurobe et al. 2013), *Microcystis* is most common (Berg and Sutula 2015). Lehman et al. (2013, 2015) found that Delta *Microcystis* originates in the Old River and the San Joaquin River. Compared with other regions known for prevalent cyanoHABs, the coverage and biomass of *Microcystis* during a bloom in the central Delta is low (Berg and Sutula 2015; Mioni et al. 2012). Guidelines for cyanotoxin levels in California are not yet determined, but microcystin concentrations in the Delta are within the range of potential harm to aquatic health according to the California Office of Environmental Health Hazard Assessment (Berg and Sutula 2015; OEHHA 2009).

Blooms in the Delta have been associated with high irradiance, warm water temperatures, timing of flows, and high nutrient concentrations (Lehman et al. 2005; Paerl and Otten 2013; Spier et al. 2013). Because nutrient ratios do not differ before and during the bloom, it is inferred that neither N nor P limits *Microcystis* growth (Lehman et al. 2013). It is possible that the Delta is occasionally at sub-saturated levels for N, so an increase in N enrichment, especially ammonium, could lead to increased N uptake in *Microcystis* communities (Lee et al. 2015). Overall, nutrient levels are non-limiting, and nutrient concentrations do not correlate well with cyanobacterial cell abundance. Therefore, it is unlikely that nutrients play a major role in seasonal or inter-annual variability in cyanoHABs (Lehman et al. 2008, 2013). Lehman et al. (2013) observed increasing *Microcystis* abundance and toxin concentration between 2004 and 2008, with elevated occurrences during dry years. These observations

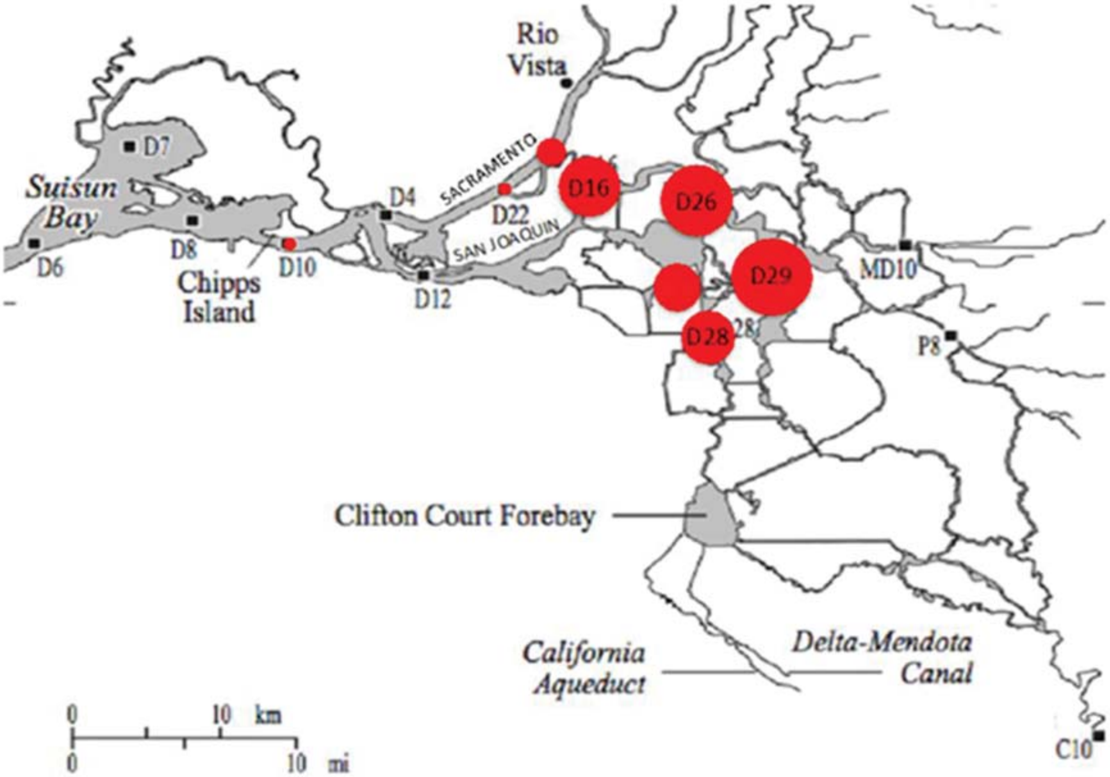

Figure 8 The Sacramento–San Joaquin Delta region. Red bubbles mark locations with greatest *Microcystis* associated surface Chl-*a* concentrations (largest bubble = 554 µg Chl-*a* L^{-1}). Sources: figure from Berg and Sutula (2015); data from Lehman et al. (2005).

are especially well correlated with lower streamflow, suspended solids, higher water temperature, and nutrient levels. Dry years have elevated ammonium concentrations because less water dilutes effluent in the Sacramento River (Jassby 2005), and the ammonium concentration of the effluent increases.

Although nutrients may play a critical role in the magnitude and extent of cyanoHABs, the factors that likely promote the proliferation of *Microcystis* in the Delta are increased water temperatures (Paerl and Paul 2012) and water column clarity (Lehman et al. 2013). If these two factors occur early in the cyanoHAB season (June to November), algal blooms could initiate earlier and grow for a longer period of time (Berg and Sutula 2015; Peeters et al. 2007). The effects of vertical mixing (ultimately reducing the availability of light) can temper these conditions. In fact, artificial mixing is a technique used to address blooms in some systems (Burford and O'Donohue 2006; Reynolds et al. 1983), and natural mixing that occurs in the Delta may help restrict cyanoHABs (Berg and Sutula 2015).

Because cyanobacteria are not routinely monitored in the Delta (though many indicator variables are, including salinity, turbidity, temperature, chlorophyll-*a*, and phytoplankton species composition), status and trends are difficult to determine and the relative importance of nutrients remains unclear (Berg and Sutula 2015). In spite of these uncertainties, nutrient management could be considered as a potential method for cyanoHAB management. Increasing flushing rates could effectively control cyanoHABs, if the incoming water has low nutrient concentrations (Paerl et al. 2011; Paerl and Otten 2013); however, this solution may be politically infeasible in the Delta, where water is a precious resource and the region is regularly affected by drought. One practical method of cyanoHAB control may be reducing nutrient inputs through wastewater treatment facility upgrades, or reducing nutrient loading through removal strategies such as wetland restoration (Paerl and Otten 2013).There has been a call for more research concerning cyanobacteria community composition, population dynamics, and nutrient biogeochemistry both in general and in the Delta specifically. The SRWTP upgrade presents a valuable research opportunity in the Delta because ammonium levels and N loads will decrease in the next decade, which may reduce the growth rate of *Microcystis* and decrease the frequency and intensity of blooms (Lee et al. 2015). Phytoplankton biomass and primary productivity are often low compared to available nutrients in the Delta, so the effect of this "large-scale ecosystem experiment" on *Microcystis* is an important standing question.

INVASIVE AQUATIC VEGETATION

Dramatic increases in coverage of invasive aquatic vegetation have occurred across the Delta over the last decade, particularly for two species: *Egeria densa* (Brazilian waterweed) and *Eichhornia crassipes* (water hyacinth, Figure 9). Coverage of *E. densa*, now the dominant submerged aquatic plant species in the Delta (Santos et al. 2011), increased 50% from 2000 hectares in 2007 to 2900 ha in 2014, while coverage of *E. crassipes* increased 4-fold from ~200 hectares on average from 2004 to 2007 to ~800 hectares in 2014 (reviewed in Boyer and Sutula 2015). A growing threat is being recognized in a suite of related species in the genus *Ludwigia* (water primrose, Figure 9), which have now attained coverage approximately equal to that of *E. crassipes* despite being relatively unknown a decade ago.

Globally, *E. densa* and *E. crassipes* are recognized as nuisance species throughout much of the temperate world (Bini and Thomaz 2005; OTA 1993). These species are especially problematic to human activities in the Delta because they impede navigation for commercial or recreational purposes, but they are also implicated in altering habitat and negatively affecting native species. These invasive macrophytes are considered ecosystem engineers (Yarrow et al. 2009; Wright and Jones 2006; Jones et al. 1994), because their presence in an environment affects the availability of resources for other species through alteration of biotic or abiotic materials. Importantly, these species often create conditions that are more favorable to their own growth in a positive feedback loop. For example *E. densa* has been shown to reduce turbidity and water velocity—conditions that facilitate growth and range expansion (Hestir et al. 2015). As such, much attention has been placed on understanding factors that drive the growth and distribution of these species worldwide (e.g., nutrients, light, temperature, salinity).

Figure 9 Invasive aquatic macrophyte species in the Delta. Top: *Ludwigia* (water primrose) at Big Break Visitor Center, Oakley, California; photo by Maggie Christman. Middle: the submerged *Egeria densa* (Brazilian waterweed); photo by the California Department of Boating and Waterways. Bottom: the floating species *Eichhornia crassipes* (water hyacinth); photo by Maggie Christman.

Nutrients and Macrophyte Growth

Two recent studies document the importance of salinity (Borgnis and Boyer 2016) and turbidity and depth (Durand et al. 2016) on the growth of invasive vegetation in the Delta, but the relative importance of nutrients in driving the growth and expansion of these species remains largely unknown. For example, no local studies have assessed the effects of nutrients on macrophyte growth under various scenarios of light or temperature. Generally, increasing nutrient concentrations result in increased biomass of *E. densa* or *E. crassipes* (Feijoó et al. 1996, 2002; You et al. 2014), though at least some studies have found no such response, possibly because they were conducted at relatively high nutrient concentrations (at or above $\sim 360\,\mu M$ N–NO_3^- or N–NH_4^+). The magnitude of the effect of elevated nutrients on *E. crassipes* biomass depends on various factors including the N : P ratio and temperature (You et al. 2014). Concentrations of nutrients used in all of these studies are typically much higher than those reported for the Delta (on the order of $36\,\mu M$ DIN and $2\,\mu M$ DIP; Foe et al. 2010), so extrapolation of results must be done with caution.

Aquatic macrophytes can generally obtain nutrients from either the water column or sediments, though the proportion of nutrient uptake by source has been debated for different species and nutrients (Chambers et al. 1989). Truly free-floating vegetation like *E. crassipes* primarily obtain nutrients from the water column. For submerged or emergent species rooted in the sediment, such as *E. densa* and *Ludwigia* spp., the primary source of nutrients is often the upper layer of the sediment (Barko and Smart 1981). However, at least one study has found that *E. densa* shoots can be the primary tissue for nutrient uptake (Feijoo et al. 2002). To date, no studies have investigated these processes in the Delta. Understanding which tissues primarily absorb nutrients is essential to understanding if and how nutrient management could affect macrophyte growth in the Delta. For example, management of water column nutrients may have a more straightforward effect in floating species such as *E. crassipes* compared to species rooted in the sediment, where sediment nutrient cycling would still need to be considered.

Both N and P, the primary nutrients that control plant growth worldwide, are available in Delta waters at concentrations well above levels likely to be limiting (Cloern 2001). In the Delta, ammonium concentrations and N:P ratios increased over a 30-year period that ended in 2006 (Glibert 2010). However, in the decade that has followed—the period of dramatic expansion of these macrophytes—those trends are no longer evident (Larry Walker Associates 2015). TN and TP also show no clear trends over this time period. Regardless of Delta-wide trends, no studies have directly assessed trends in species growth or coverage against nutrient concentrations at specific sites.

Changing forms and proportions of nutrients are an important stressor in aquatic systems throughout the world, including the Sacramento–San Joaquin Delta (Glibert 2012). Wilson et al. (2005) estimated that N becomes limiting for *E. crassipes* at inorganic N:P ratios less than 7. Because the N:P ratio of Delta waters averages above 8 (Foe et al. 2010; Glibert 2010), *E. crassipes* is not likely to be limited by N. *Egeria densa* is believed to grow well even under high water column N:P ratios because of its ability to tolerate high levels of N, particularly when in the form of ammonium, and because it can acquire P from sediments as well as the water column (Feijoo et al. 2002). Dense submerged macrophyte beds also can produce low dissolved oxygen and high pH conditions, which can stimulate P release from sediment (Barko and Smart 1980; Cornwell et al. 2014; Glibert 2012) and promote growth in a positive feedback loop. Phosphate also appears to be more readily absorbed in *E. densa* than either ammonium or nitrate (Feijoo et al. 2002).

The ratio of available N forms has been shown to affect phytoplankton blooms (Wilkerson et al. 2006), but any similar relationship for aquatic macrophytes has not been studied in the Delta. *E. crassipes* readily absorbs added N regardless of form (Carignan and Neiff 1992; Heard and Winterton 2000; Moran 2006), though at least one study has found the species to be more efficient at taking up ammonium than nitrate when both were supplied in equal proportions (Reddy and Tucker 1983). Similarly, *E. densa* has been shown to take up ammonium more readily than nitrate in studies occurring in Brazil (Feijoo et al. 2002) and in Florida (Reddy et al. 1987). However, there was no significant effect of N source on biomass in any of these studies.

Nutrient Cycling

E. densa and *E. crassipes* are both known for their abilities to take up and store nutrients (Gopal 1987; Reddy et al. 1987). In fact, *E. crassipes* has been employed in water treatment projects to remove nutrients from water bodies around the world (Malik 2007). *E. crassipes* is capable of higher N and P removal than other co-occurring species, including *E. densa* (Reddy and DeBusk 1985). Despite these species' large capacities for nutrient uptake, their effects on water column nutrient concentrations is hypothesized to be low because of the relatively low total coverage of these species Delta-wide (Hestir et al. 2008; Boyer and Sutula 2015; 3% for *E. crassipes*, 11% for *E. densa* in 2014, Khanna and Ustin, as cited in Boyer and Sutula 2015).

Decomposition of large mats of *E. crassipes* could have a large effect on nutrient cycling. In the Delta, only one study has investigated decomposition's effect on nutrient cycling. Greenfield et al. (2007) assessed the effects of mechanical shredding on water column nutrient concentrations and found elevated TP, organic P, and TN. Flow conditions influenced the duration of the effect; under low flow, the elevated nutrients lasted for several weeks. Seasonal die-back of *E. crassipes* might produce a similar effect. *E. densa* does not die back seasonally in the Delta (Boyer et al. 2013; Santos et al. 2011), but die-back of dense submerged vegetation beds after chemical control treatments could lead to similar spikes in nutrient concentrations. To fully characterize the roles of these species on nutrient cycling in the Delta would require information on productivity rates, nutrient sequestration, and nutrient cycling among plant tissues, the water column, and sediments (Boyer and Sutula 2015).

Can nutrient management reduce the distribution and coverage of aquatic macrophytes in the Delta? A major limitation to understanding the mechanisms that underlie the expansion of invasive macrophytes in the Delta is that Delta-wide surveys of vegetation occur only sporadically. There has never been a consistent monitoring program to assess Delta-wide trends in spatial coverage of invasive aquatic macrophytes. In addition, Boyer and Sutula (2015) cite the need to develop a biogeochemical model focused on nutrient and organic C fate and transport, and the need to better understand the relative importance for each species of nutrient acquisition from the water column versus sediment.

CONTINUOUS SENSING OF NUTRIENTS WITHIN THE DELTA

New Developments in Sensor Technology

Recent technological advances now permit collection of nutrient data—nitrate, phosphate and ammonium—*in situ*, and frequently enough to resolve processes on diurnal, tidal, and individual-event time-scales, dramatically improving our understanding of processes that shape aquatic systems (Johnson et al. 2010; Kirchner et al. 2004; Pellerin et al. 2016). Collection of nutrient data at frequent intervals in aquatic systems has in almost all cases revealed much higher temporal variability than was evident in less frequent discrete sample collection (Bende–Michl et al. 2013; Pellerin et al. 2009, 2011, 2014; Wild–Allen and Rayner 2014). These data also revealed patterns in nutrient dynamics that occur at yearly, seasonal, diurnal, tidal, and individual-event time-scales, which are difficult if not impossible to detect using lower-resolution data (Bende–Michl et al. 2013; Bowes et al. 2009; Cohen et al. 2012, 2013; Pellerin et al. 2009, 2011, 2014; Wild–Allen and Rayner 2014).

One fundamental consequence of finding higher-than-expected variability is that it calls into question classical techniques for calculating loads as a function of intermittent concentration data and continuous discharge data. Comparison of nutrient fluxes and loads calculated using less-frequent grab sample data to that calculated from high-frequency data has demonstrated that data collection at more frequent intervals improves accuracy, even in large rivers that are assumed to be buffered from short-term nutrient pulses (Carey et al. 2014; Cassidy and Jordan 2011; Pellerin et al. 2014). Assessments of these types of nutrient data do not yet exist for the Delta.

Although improved load estimates are important, the highlight of high-frequency data is that it provides novel insights into nutrient sources and cycling, and improves the ability to quantify these processes. There are many excellent recent examples in the literature (Bowes et al. 2015; Cohen et al. 2012; Collins et al. 2013; King et al. 2014; Voynova et al. 2015). One such example from the Delta is for quantifying nitrification rates in the Sacramento River (O'Donnell 2014). O'Donnell (2014) used data from the USGS monitoring stations located at Freeport and Walnut Grove on the Sacramento River to estimate nitrification rates by determining the change in nitrate concentration between stations (Figure 10). To account for exogenous inputs and in-river uptake of nitrate, the nitrate change was also determined during the times the SRWTP effluent was diverted into storage basins for maintenance or testing. The difference between the calculated nitrate change in the presence and absence of wastewater effluent was taken to be nitrification of wastewater-derived ammonium. As expected from the differences in temperature, estimated nitrification rates were 70% greater in the summer than in the winter, and within the range of published rates from other aquatic ecosystems (O'Donnell 2014). Results indicate that if the measured rates are representative, it would take between 11 and 17 days to convert the entire ammonium pool to nitrate, similar to transit times from the Sacramento River to the estuary, demonstrating why improving our understanding of nitrification rates is warranted.

Additional Nutrient Sensors

Although most high-frequency nutrient studies to date involve nitrate sensors, adoption of commercially available in situ analyzers for phosphate and prototype sensors for ammonium is growing (Rozemeijer et al. 2010; Cassidy and Jordan 2011; Bende–Michl et al. 2013; Cohen et al. 2013; Gilbert et al. 2013; Outram et al. 2014; Bowes et al. 2015). We are aware of few studies that report results from *in situ* high-frequency ammonium analyzers, and—not surprisingly—these studies found that ammonium, nitrate, and phosphate variability are not necessarily linked (Bende–Michl et al. 2013; Gilbert et al. 2013). Although there are no published studies from the Delta using *in situ* measurements of ammonium and phosphate, data collected by the USGS on the Sacramento River at Walnut Grove demonstrates their variability and the complex relationship they share with nitrate (Figure 11).

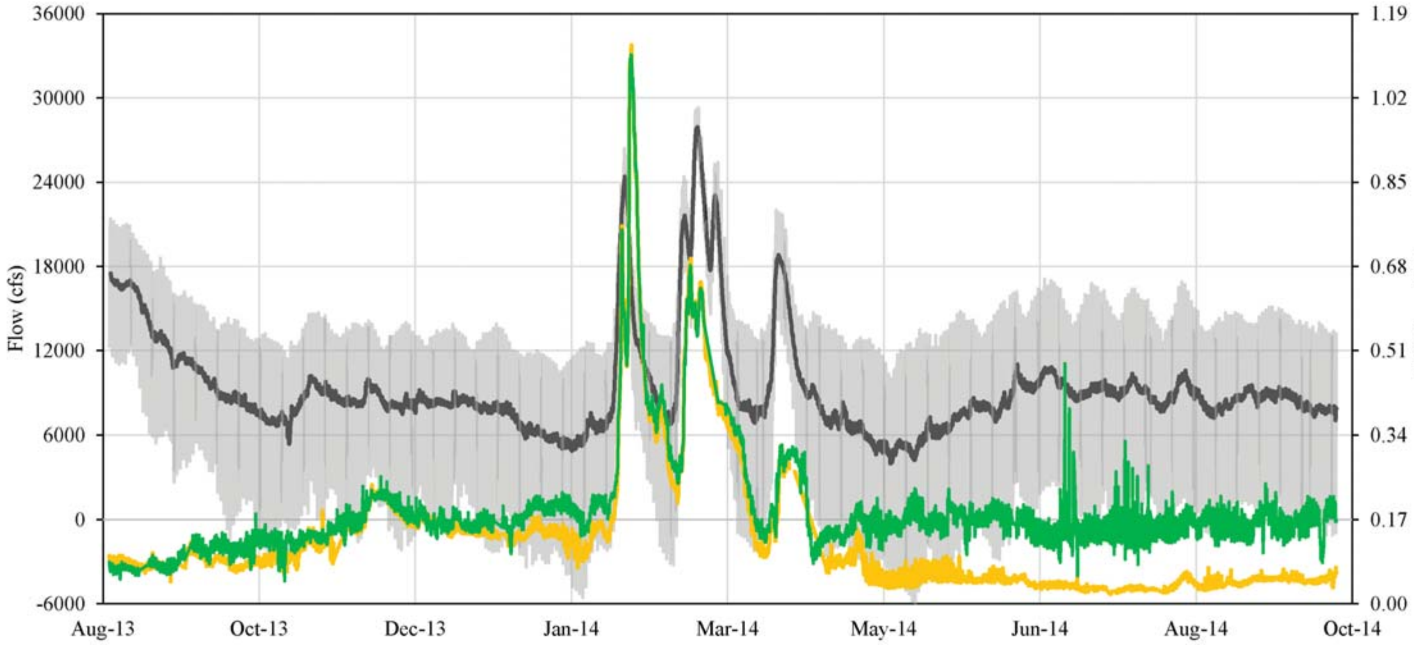

Figure 10 Instantaneous (grey) and tidally averaged (black) flow of the Sacramento River at Freeport (FPT) plotted with nitrate concentrations measured at the continuous monitoring stations located at FPT (yellow) and Walnut Grove (WGA, green) from August 2013 to October 2014. Figure from O'Donnell 2014.

Spatial Applications of High Frequency Sensors

Recent studies have also demonstrated how high-frequency sensors may be used to improve our understanding of environmental processes by mapping spatial variability in rivers, lakes and estuaries, often in conjunction with fixed-station measurements (Downing et al., forthcoming; Gilbert et al. 2013; Hensley et al. 2014; Wild–Allen and Rayner 2014; Crawford et al. 2015). These examples include the Columbia River Estuary, where fixed station and mapping data allowed researchers to identify nutrient sources and transformations across a salinity gradient, and thus identify key transition zones (Gilbert et al. 2013). In Florida, longitudinal profiling of several rivers permitted nutrient removal “hot spots” to be located (Hensley et al. 2014). In the north Delta, Downing et al. (forthcoming) mapped the spatial variation in water isotopes, from which they calculated water residence time (Figure 12), an important ecological parameter related to many biogeochemical processes—and one previously not possible to quantify from field measurements. Using concurrent measurements of concentrations, they calculated rates of ecosystem uptake of nitrate, comparing how rates varied in areas with different amounts of wetlands. To assess the outcomes of the ongoing upgrades of the SRWTP and other management actions, quantitative estimates of nitrate uptake and transformation by various environmental compartments in the Delta are needed to model nutrient cycling.

Continuous Nutrient Measurements in the Delta

Continuous sensor measurements have begun in the Delta only recently. There are no published compilations or assessments of the data, although the data are available on the web in real time (*http://waterdata.usgs.gov/nwis*) and in daily reports via subscription. At present, eight continuous nutrient monitoring stations currently operate in the Delta (Table 1), with nitrate the only nutrient parameter reported from every site, and phosphate and ammonium reported intermittently on an event basis (Figure 11). The objectives for establishing these stations include determining drivers for available nutrients and quantifying nutrient dynamics as related to phytoplankton uptake. The stations

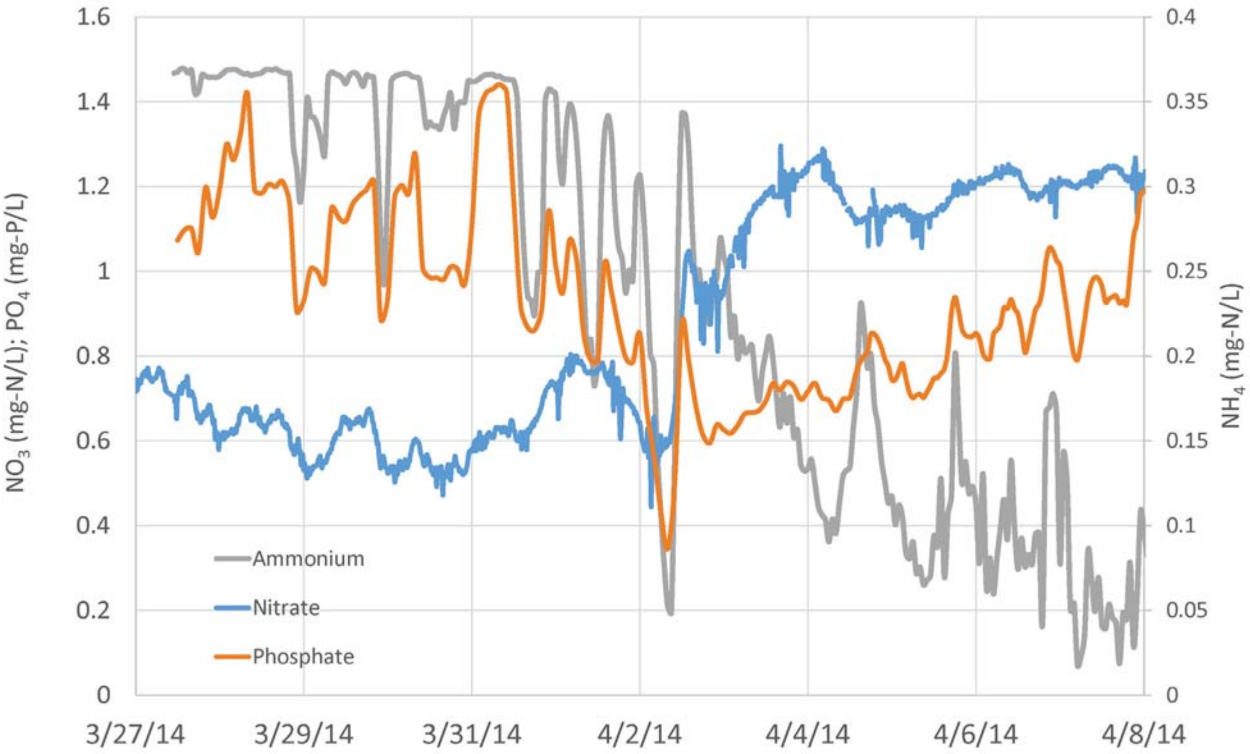

Figure 11 Time series of nitrate, phosphate and ammonium from March 27 to April 8, 2014 in the Sacramento River at Walnut Grove, CA

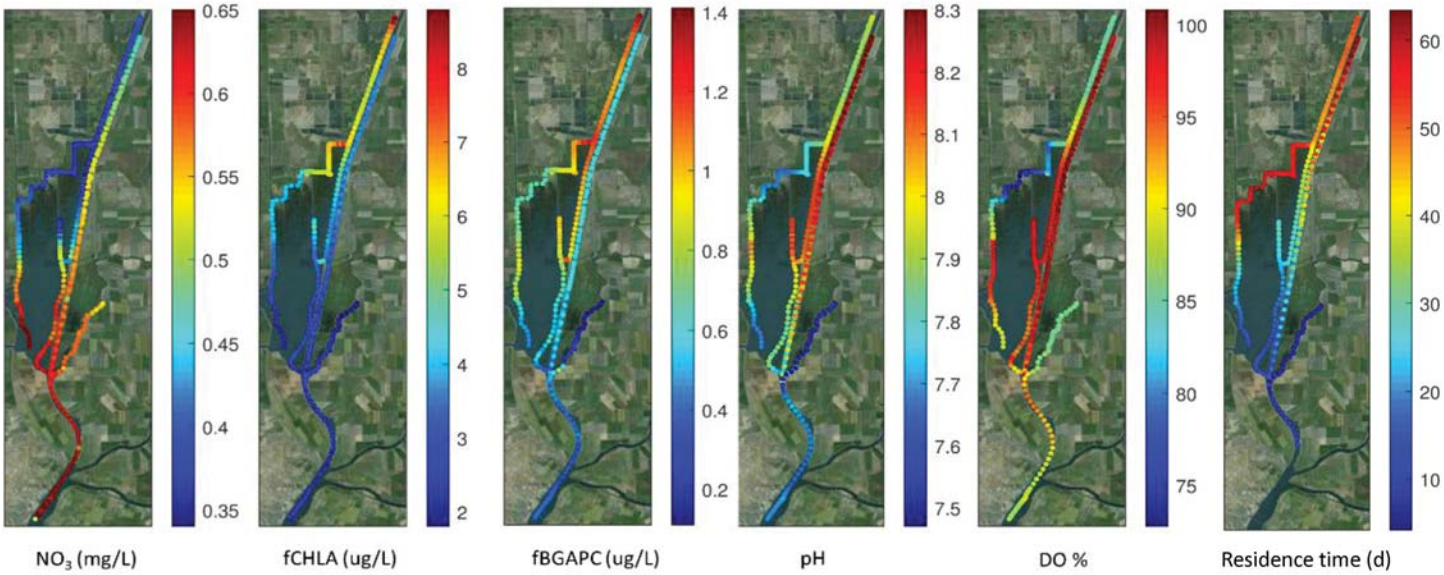

Figure 12 Concurrent high speed mapping of nitrate [NO_3^-], Chlorophyll fluorescence [fCHLA], Phycocyanin fluorescence [fBGAPC], pH, Dissolved oxygen [DO%] and water residence time (days) show how environmental gradients are related to residence time. Data were collected on October 1, 2014, over a period of approximately four hours starting at the flood to ebb transition.

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also directly support efforts to elucidate effects of wastewater effluent from the SRWTP on downstream nutrient concentrations and food web dynamics. Additional continuous nutrient measuring stations are planned.

Sensor Networks

Several recent papers have explored the advantages of building networks of nutrient monitoring stations to improve understanding of how ecosystems function at the landscape scale (Johnson et al. 2007; Crawford et al. 2015; Pellerin et al. 2016). Data from sensor networks can be used to quantify constituent sources, calculate transport times, and calculate transformation rates, which together can generate new insights and quantitative estimates of ecosystem processes. Rigorous evaluation of these data can inform current monitoring programs by quantifying the uncertainty and bias obtained from lower-frequency measurements, and can help design future sampling programs that take into account cost and accuracy (Hirsch 2014; Jiang et al. 2014).

However, as use of *in-situ* sensors becomes more common, to ensure data comparability and quality, there must be a concerted effort among users to develop, improve, document and adhere to community protocols for operation, maintenance and calibration. Further, users need to develop tools to effectively carry out quality assurance/quality control on the large volumes of data such networks generate, and to improve the visualization and analysis tools necessary to make these data useful to managers, policy-makers, and other scientists in a timely manner, preferably in near real time (Johnson et al. 2007; Pellerin et al. 2016).

A long-term commitment to high-frequency monitoring in the Delta will improve the ability to quantify how ecosystem processes are affected by events such as storms (Saraceno et al. 2009) and drought (Outram et al. 2014). This will help to more rapidly identify abrupt state changes and to recognize long-term change against a background of continuous variability, as well as the data necessary to resolve processes at short time-scales (Pellerin et al. 2009). These data can also be used to calibrate, validate, and improve models that water managers and policy-makers rely on to make decisions and to identify periods where water quality parameters either exceed or are below critical thresholds (Carey et al. 2014). Further, these data can help reduce uncertainties in models, and thereby improve assessments related to water management actions and/or climate variability (Pellerin et al. 2016). As an integrated understanding of ecosystem processes results from such data and synthesis, the development, implementation, and evaluation of water-management strategies and policies will be advanced (Cassidy and Jordan 2011; Outram et al. 2014; Pellerin et al. 2014).

RESEARCH NEEDS AND DIRECTIONS FOR DELTA NUTRIENTS

There are many research needs and directions for studying nutrients within the Delta, and recent reports, workshops, and symposia have put forth many useful recommendations. We focus on four

Table 1 Current USGS nutrient monitoring stations in the Delta

Site name	Site abbreviation	NWIS station number	Date established	Latitude	Longitude
Decker Island	DEC	11455478	1/24/2013	38.093333	121.736111
Cache Slough	CCH	11455450	2/1/2013	38.212778	121.669167
Liberty Island	LIB	11455315	7/15/2013	38.242222	121.686111
Walnut Grove	WGA	11447890	8/21/2013	38.257778	121.517222
Sacramento River at Freeport	FPT	11447650	8/30/2013	38.456111	121.500278
Liberty Cut	LCT	11455146	1/31/2014	38.328850	121.667531
Deep Water Ship Channel	DWS	11455335	4/11/2014	38.256111	121.666667
Toe Drain North of Stair Steps	TOE	11455139	8/19/2014	38.365180	121.637730
San Joaquin River at Vernalis	SJV	11303500	1/21/2015	37.676111	121.265278

research areas that we believe will prove fruitful: (1) coupling continuous sensor data for nutrients with similar sensors for dissolved oxygen and temperature to estimate daily rates of primary production and ecosystem respiration along with nutrient stoichiometry; (2) linking existing hydrodynamic models of the Delta with appropriate water-quality processes that involve dissolved nutrients; (3) measuring key rates of nutrient uptake and transformation in habitat types off main channels including sloughs, backwaters, tidal marshes, macrophyte beds, and aquatic sediments; and (4) exploring the use of stable isotopes to trace the movement and fate of effluent-derived nutrients within the Delta.

The Delta has an extensive network of monitoring stations that measure flow (Burau et al. 2016), conductivity, temperature, turbidity, chlorophyll, pH, and dissolved oxygen (*http://waterdata.usgs.gov/nwis*). Daily dissolved oxygen patterns—when coupled with data on temperature, barometric pressure, and light regime—can be used to estimate gross primary production and ecosystem respiration in aquatic ecosystems as pioneered by Odum (1956) and now widely used in various aquatic ecosystems (Grace et al. 2015). Metabolism estimates can also be coupled to continuous nutrient sensor data to examine both elemental stoichiometry and the coupling of primary production and ecosystem respiration to the uptake of nutrients such as ammonium, nitrate, and phosphate (Cohen et al. 2013). Few places anywhere have the combined measurements of flows, fixed stations for basic water quality, and the network of high-frequency nutrient stations (Table 1) that are found in the Delta. This presents an excellent opportunity to estimate daily rates of primary production and ecosystem respiration that are linked to nutrient uptake and stoichiometry.

Hydrodynamic modeling of the Delta is well developed and mature with several existing models applied to portions of—or the totality of—the Delta (Trowbridge et al. 2016). The linking of these hydrodynamic models to water-quality models that focus on the transport and fate of nutrients is a logical next step. Trowbridge et al. (2016) offered recommendations to make this connection between hydraulics and nutrient biogeochemistry a reality for the Delta. Key recommendations included good data management, phased implementation of the coupled models, selecting the right model—or models—for the task, rigorous quality assurance, and regular workshops between modelers and biogeochemists. If resources can be found to develop these tools, an excellent opportunity exists to make progress at this interface between modeling and nutrient biogeochemistry.

Much of what we know about nutrients in the Delta has been gathered from samples collected where larger boats can travel. Locations that are less commonly sampled include sloughs, backwaters, tidal marshes, macrophyte beds, and aquatic sediments. Key processes that take up nutrients (e.g., uptake by attached bacteria, fungi, algae, and aquatic macrophytes) and transform nutrients (e.g., nitrification and denitrification) are concentrated in these rather than open-water habitats. Novick et al. (2015) have made an initial estimate of ~30% internal losses for N within the Delta, and the roles for various habitat types in the uptake by biota or loss to the atmosphere through denitrification remain an important unknown. Current planning and some initial implementation of large-scale restoration within the Delta through EcoRestore (*http://resources.ca.gov/ecorestore/*) heighten the need for rate measurements on key processes that cycle nutrients in these parts of the Delta.

A large-scale natural experiment is in the offing for the Delta because the Sacramento Regional County Sanitation District has broken ground on the EchoWater Project (*http://www.regionalsan.com/echowater-project*) that will upgrade the SRWTP, which serves about 1.4 million people. This upgrade will reduce ammonium inputs in the north Delta from the plant by 95% or more, and substantively reduce overall inorganic nutrient inputs by 2021. Effluent N has a distinctive isotopic signal that allows effluent nitrogen to be traced within the Delta. Effluent water is generally enriched in the heavier isotope of nitrogen (^{15}N) compared to the lighter isotope (^{14}N), and, therefore, a natural tracer is available to study the transport, uptake, transformation, and role in food webs of effluent nitrogen (Costanzo et al. 2005; Miller et al. 2010). This large-scale experiment, if adequately documented, could yield far-reaching insight into the dynamics of nutrient cycling within the Delta.

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CONCLUSIONS

An ever-changing Delta has encouraged a re-evaluation of the roles for nutrients within it. At the turn of the millennium, nutrient levels were high, nutrient limitation was rare, and regulation of primary production resulted from factors other than nutrients (Jassby et al. 2002). As Delta waters became clearer (Schoellhamer et al. 2016), and *Microcystis* blooms became commonplace and invasive aquatic macrophytes became more pervasive, questions arose about the effects of concentrations, chemical form, and elemental stoichiometry of N and P on the structure and productivity of the open-water algal community. There has been a resurgence in interest in nutrients and their roles within the Delta. Good, long-term data on nutrients allow the status and trends of Delta nutrients to be assessed, and an emerging network of high-frequency nutrient sensors allows high resolution studies on the availability, transport, and fate of dissolved nutrients in Delta waterways. We highlight four emerging opportunities of interest relating to nutrients within aquatic ecosystems of the Delta. The first is how a major, nearly completed upgrade to the SRWTP will affect the primary producers and food webs of the Delta. The second is the opportunity to couple high temporal and spatial resolution estimates of primary production and ecosystem respiration to nutrient uptake and the elemental stoichiometry of C, N, and P. The third is addressing how tidal marsh restoration and floodplain re-connection within the Delta will affect nutrient biogeochemistry. The fourth is linking hydrodynamic models of the Delta to a growing understanding of biogeochemical processes within the tidally dominated Delta. Nutrients are most definitely of growing interest within the Delta, and future changes to the Delta allow some fundamental hypotheses about nutrient biogeochemistry of this rapidly changing landscape to be tested.

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NOTES

Larry Walker Associates. 2015. N and P data graphs for Delta stations. Developed by Larry Walker Associates for use by the Delta NNE science work groups. Available from: 707 Fourth Street, Suite 200, Davis, CA 95616 or email: *infolwa@lwa.com*.