

**Delta Nutrients Forms and Ratios Public Workshop: "Role of Nutrients in Shifts in
Phytoplankton Abundance and Species Composition in the Sacramento-San Joaquin Delta"**

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Report prepared by Workshop Panel Members

Dr. Amelia K. Ward, Professor Emeritus
Department of Biological Sciences
University of Alabama
Tuscaloosa, AL 35487

Dr. Hans W. Paerl, Kenan Professor
Institute of Marine Sciences
University of North Carolina at Chapel Hill
Morehead City, NC 28557

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I. INTRODUCTION: Overview and background

The Sacramento-San Joaquin Delta (hereafter, The Delta) is a complex, dynamic ecosystem that is one of the most human-manipulated systems worldwide. It serves as a water source for millions of people as well as critical agricultural and fisheries interests, recreation, and habitat for endangered species among other purposes (Healey et al. 2016a). However, the system also faces unprecedented, multiple, interrelated stressors that have developed over the past several decades that threaten both its ecological and economic value (Luoma et al. 2015). A recent 2016 review concluded that many changes to the Delta brought about by these stressors are irreversible, and that the system as a whole must be managed for “desirable futures” (Healey et al. 2016b). A further confounding factor is that the future includes challenges wrought by climate change that will likely result in more extreme events (e.g., storms, heat waves and droughts) and produce yet another layer of unpredictability in management planning for the Delta (Cloern et al. 2011, Dettinger et al. 2016). Overall, management of the Delta has been described as a “wicked problem” (*sensu* Rittel and Webber 1973), i.e., one that defies a single correct characterization or solution and requires a management strategy that minimizes adverse outcomes and maximizes beneficial ones (Healey et al. 2008, Luoma et al. 2015).

Changes in the Delta’s physical-chemical environment over the last couple of decades, including increased water clarity, have resulted in renewed interest by management entities and others in roles of nutrients in this system (e.g., Dahm et al. 2016). Previously, low light conditions and high concentrations of nutrients, especially inorganic nitrogen, suggested to some that nutrients had little role in regulating primary production in the Delta (e.g., Jassby et al. 2002). However, recently there has been intense focus on two inorganic nitrogen forms, ammonium and nitrate, and their influences on phytoplankton growth and composition and, consequently, as potential seminal drivers of phytoplankton production and food web dynamics in the Delta. Development of the Ammonium Paradox and its counter-arguments has resulted. A summary of the main hypotheses of this conceptual model and supportive and differing experimental results have been succinctly summarized in Senn and Novick (2014) and Dahm et al. (2016).

Several topics related to the recently developed Ammonium Paradox have been discussed in the scientific literature for some time. Some key conclusions endure from the earlier studies: there is an energetic benefit and preference of ammonium as a nitrogen source for algal growth compared to nitrate; many algal taxa can use either ammonium or nitrate to support high growth, although some grow best when supplied with ammonium (especially some cyanobacteria), others with nitrate; and a few require exclusively either ammonium or nitrate (Morris and Syrett 1965, Moss 1973, Morris 1974, Ward and Wetzel 1980, among others). There was also clear recognition in these early studies of interacting factors (e.g., changes in pH of growth medium, light regime, water residence time) that could confound interpretation of results and identification of driving mechanisms from different laboratory studies (e.g., Morris 1974).

Therefore, perhaps it is not surprising, given the physiological intricacies of algal nitrogen metabolism and its sensitivity to external conditions coupled with the extraordinary biological, physical, and chemical complexity of the Delta, that contemporary studies addressing the reliability of the Ammonium Paradox to explain phytoplankton response in the Delta have revealed conflicting results. Two key questions at this juncture are:

- (1) Will continuation of experiments to test the Ammonium Paradox in the absence of a robust understanding of the overall nitrogen/nutrient dynamics and accompanying environmental drivers yield reliable and useful predictions of phytoplankton response to expected changing conditions in the Delta and effective management practices?
- (2) What is the research path forward with regard to nutrients and phytoplankton in the Delta that will result in the best science-based, management practices?

II. CHARGE TO PANEL

The panel members for this workshop were charged to address questions related to nutrient and phytoplankton conditions in the Delta (see full text of questions in Appendix 1). The first three (#s 1-3) focus on design of experiments that could be used to resolve conflicting results from different studies that relate to the Ammonium Paradox. Two others deal with (#4) identification of monitoring/modeling strategies in the Delta that will yield the most effective information on nutrients and phytoplankton response, and (#5) identification of plausible outcomes to management practices relevant to phytoplankton dynamics.

Explanation of panel approach to questions 1-3:

A plethora of scientific articles, some of which support the Ammonium Paradox and others that question it, have led to animated discussions, but perhaps also a premature over-emphasis on only one part of a larger complex of drivers in the Delta that result in observed nutrient and phytoplankton patterns. A narrow focus on two different forms of nitrogen will not yield scientific findings that will result in effective, future management practices. A broader understanding of critical Delta features that drive nutrient distribution, concentrations, forms and biological transformations is now needed to interpret results of previous experiments and forge a management path. Therefore, it is the consensus of the panel that broadening investigations within the Delta in prioritized areas will now lead to a more thorough and accurate understanding of nutrient-phytoplankton relationships, rather than continued, more narrow experiments. Ultimately, whether the Ammonium Paradox is applicable broadly, in 'windows of opportunity' when conditions align over shorter spatial/temporal scales, or not at all in the Delta will likely emerge from these broadened studies.

It is not the intent of the advisory panel to reiterate in this report the detailed cases made for and against the Ammonium Paradox that have appeared in other publications. However, we do share our thoughts on some areas of research that we believe have been under-investigated or not rigorously considered in interpretation of past results and that form part of the rationale for the recommendations that we make here and in the next report sections.

In brief, four primary areas of concern from previous studies include:

- Need for ecosystem-scale integration of the roles and effects of physical processes such as irradiance, temperature and water movement on phytoplankton N uptake, growth and production dynamics.

- Lack of consideration of dynamic within-system nutrient (i.e., N) cycling when considering effects of specific N sources on downstream phytoplankton and associated microbial community structure and function.
- Lack of attention to within-system uptake/transformation processes by bacteria/archaea, especially with regard to nitrification. For example, N uptake rates attributed solely to phytoplankton may also be the result of uptake/transformation by bacteria/archaea, skewing calculations and correlations involving phytoplankton growth and uptake.
- Insufficient documentation of phytoplankton composition in field studies, i.e., species identification, given the recognized variability among species in use of specific N forms. There has not been enough consideration of differences among species within broader taxa groups, e.g., diatoms, in interpretation of N use by phytoplankton.

Past publications have not been devoid of information and commentary on the above areas, but there does appear to be a lack of critical assessment in some cases of how results could have been affected by these factors and, hence, conclusions skewed with regard to support (or not) of the Ammonium Paradox.

The following comments/examples provide further elaboration of our major points above:

Physical influences on phytoplankton nutrient use and growth: First, it is important to not misidentify inorganic N source as a driver of greater or lesser phytoplankton growth when interactions with physical factors such as light availability, temperature, turbulence, and water residence time (flushing rates) are likely the primary drivers. Consider a hypothetical example where phytoplankton may have low growth because of light limitations during mixing events when they may also be assimilating primarily ammonium, since ammonium assimilation is favored over oxidized forms of N under low light. Under subsequent, more transparent conditions in the water column and after ammonium concentrations have decreased, phytoplankton growth increases at the same time nitrate is being utilized. A conclusion of “ammonium inhibition” of nitrate uptake and also lower growth with ammonium as a N source appears to be unwarranted under these conditions if growth is actually lessened by lower light at a time when phytoplankton are also using ammonium. In this scenario, ammonium use by phytoplankton coincided with physical processes (mixing/light) that were the primary drivers of low growth, not necessarily the inorganic N form. These scenarios appear to be supported by conditions in estuaries in China (Xu et al. 2008, 2010) and the Neuse River Estuary, NC, USA (Paerl and Piehler 2008). Within the Delta, the role of turbulence in suspension, settling, and re-suspension of phytoplankton from benthic regions, especially in shallow areas, has not garnered the attention it deserves, e.g., in interpretation of the magnitude of impact of benthic clam grazing and other drivers that influence phytoplankton biomass, production and composition. Delta studies by Lucas et al. (2016) and Kraus et al. (2017) also reinforce the need to consider physical factors that influence phytoplankton, especially when they co-vary with inorganic N concentrations.

Role of within-system nutrient (specifically N) cycling: Nitrogen is a highly mobile nutrient element with many dissolved, particulate and gaseous forms. Numerous studies have shown that riverine, estuarine and coastal waters experience rapid cycling rates between these forms, as well as sediment-water column and water column-atmospheric exchange (c.f., Capone et al. 2008, Paerl and Piehler 2008).

Because of rapid within-system cycling, leading to transformations of soluble, gaseous and particulate forms, it is very difficult, if not impossible, to link upstream discharge of specific forms of N to downstream impacts on phytoplankton and other microbiota community structure. For example, ammonium discharged by the Sacramento Regional County Sanitation District wastewater treatment plant (Regional San WWTP; >50 km upstream from the North San Francisco Bay) can be cycled numerous times (via uptake, nitrification, denitrification, decomposition, ammonification, etc.) before its ultimate N form arrives in receiving estuarine and coastal waters. There is general agreement among researchers that excessive N loading to the Delta and downstream San Francisco Bay plays a role in eutrophication and harmful algal and cyanobacterial bloom dynamics. However, it is highly speculative and naïve to assume that a single form of N (namely ammonium) is ultimately responsible for the undesirable effects of N-driven eutrophication. This is why the National Research Council Report on Sustainable Water and Environmental Management in the California Bay –Delta (NRC 2012) recommended considering TOTAL N input rather than specific N form (e.g., ammonium) reductions from upstream point and non-point sources to help control downstream eutrophication and harmful algal bloom formation.

Roles of bacteria and archaea in N cycling processes: The effects of bacteria and archaea on N uptake and transformation and resulting changes in nutrient concentrations need closer scrutiny in Delta research. In particular, nitrification, a process that can both decrease ammonium and increase nitrate concentrations requires more attention in interpretation of research results. Care must be taken to consider all biological “players” that can affect concentrations of N sources. For example, observations of decreases in ammonium coincident with non-declines in nitrate may not mean that phytoplankton are only using ammonium, but that production of nitrate via nitrification causes no observable change in nitrate concentrations. Also, a steep decline in ammonium concentrations may, in part, be caused by nitrification. Therefore, phytoplankton nitrate uptake could be masked to some extent and decreases in ammonium concentration enhanced by nitrification that results in less obvious decreases in nitrate because of nitrate production and more rapid disappearance of ammonium because of its transformation to nitrate. Although some past Delta research has mentioned nitrification as possibly occurring during nutrient and/or phytoplankton studies (Glibert et al. 2014, Wilkerson et al. 2015), inclusion of nitrification measurements has been infrequent (e.g., Parker et al. 2012, Novick et al. 2015), and in-depth interpretation of the possible effects of this process in explaining research results, specifically with the Ammonium Paradox, has been lacking (e.g., Dugdale et al. 2015, Glibert et al. 2016). Recent studies in the Delta have documented the presence of ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing archaea (AOA) in benthic regions (Damasheck et al. 2015). Both of these groups of organisms drive nitrification, but can differ in some aspects, including affinity for ammonium, an important attribute that could determine where they occur, i.e., in eutrophic vs oligotrophic environments, and whether they compete effectively with phytoplankton for ammonium (Smith et al. 2014). An overall research plan that includes a full array of microbes that drive N transformations in a broadened geographical scope will provide a more complete biogeochemical perspective of Delta N processes.

Phytoplankton species identification: Since it is well-established that growth response to inorganic N form and concentration can vary among species within broad taxonomic groups and even strains of the same species (e.g., Collos and Harrison 2014, Berg et al. 2017), more focus is needed on species identification in field and experimental Delta studies in order to understand the effects of algal composition at the species level when interpreting responses to specific nutrient inputs. Algal species identification is very labor intensive. However, less time-consuming measurements, e.g., of total

chlorophyll *a* or diagnostic photopigments specific to a particular algal group, although useful in many phytoplankton investigations, are not necessarily adequate for studies that seek to unravel complex questions related to specific phytoplankton groups (e.g., diatoms, chlorophytes, dinoflagellates, cyanobacteria) and species nutrient responses, especially with regard to the Ammonium Paradox. A broad-brushed description of phytoplankton communities as ‘diatom-dominated’ or ‘chlorophyte-dominated’ based on pigment analyses appears insufficient to generalize conclusively about phytoplankton response to inorganic N sources based on algal group. A lack of attention to taxonomic detail may be contributing to the inconsistencies in results and interpretation of previous studies addressing the Ammonium Paradox. It is also useful to remember that native phytoplankton communities of mixed species may exhibit different nutrient uptake, growth and productivity attributes as a group than uni-algal laboratory cultures sampled from the same native community and grown under similar conditions. Interspecific competition among phytoplankton taxa and competition with bacteria for nutrients is well-documented (e.g., Tilman 1978) and can be among the drivers determining which algal taxa dominate at any given time.

Despite identification of the above confounding factors with regard to resolving issues with the Ammonium Paradox, the panel does not recommend further studies specifically designed to “prove or disprove” this concept at this time. Rather, we suggest more fruitful research in the future should include thoughtfully designed field studies in broadened, ecosystem-scale, prioritized theme areas described in the next section as a better way to more thoroughly illuminate phytoplankton-nutrient interactions in the complex Delta landscape and, ultimately, make progress on Delta nutrient management strategies.

During the panel discussion in Sacramento (November, 2016), we decided we would not address ecological stoichiometry issues in great detail because it was a secondary topic dependent on Ammonium Paradox tenets. Since we are recommending a much-broadened research approach that does not include additional experiments directed at resolving the Ammonium Paradox, the topic of ecological stoichiometry became moot. We also note that others have published serious concerns about data sets and methods used to substantiate ecological stoichiometry as a predictor of biological community (foodweb) structure in the Delta (e.g., Cloern et al. 2012, 2014), and these concerns provide additional reasons to not pursue this particular approach in Delta research and management at this time. The below text provides further clarification of our conclusions on this topic:

The “ecological stoichiometry” hypotheses, as proposed by Glibert et al (2011) and Glibert (2010), argue that high ammonium concentrations or elevated N:P have played a primary role in the decline of pelagic fish species in the Delta-Suisun by causing shifts in the phytoplankton community toward assemblages that inadequately support higher trophic levels. Glibert et al. (2011) state: “...management strategies to date have not reversed fish declines because they have not addressed the ultimate cause of the change at the base of the food web and the complex role of nutrient form and quantity. The present study supports the premise that reduction of the NH_4^+ effluent into the Bay Delta is essential to restoring historic pelagic fish populations and that until such reductions occur, other measures, including regulation of water pumping or manipulations of salinity, as has been the current strategy, will likely show little beneficial effect.”

The basis for applying “ecological stoichiometry” to the Delta is a statistical analysis of a 30-year (1975-2005) data set of phytoplankton cell counts (monthly observations) by the California Department of Water Resources Environmental Monitoring Program for the Delta-Suisun system. However, a recent re-analysis of that same dataset identified major data-quality issues that result in large uncertainties in

estimated phytoplankton abundance (Senn 2016). For large portions of the data, the counting methodology led to extremely low numbers of enumerated cells per sample, e.g., one Suisun Bay station at which community composition for >15% of the dates was based on only a single cell being counted, and the overall mean for the entire record was 6 cells counted per sample.

Given the questions about whether, in fact, a selective decline in diatom biomass occurred following the mid-1990s when ammonium discharge from Regional San wastewater treatment plant increased, a thorough reanalysis of available data with consideration of data quality is warranted. As an example, a recent review of phytoplankton community structure and biomass for the Sacramento River end member (USGS stations 3-657) and subsequently extended to Suisun Bay (Stations 6-657), based on cell counts and biovolumes, and then verified by HPLC-based phytoplankton group analysis, showed that diatom biomass, as a percent of total phytoplankton biomass, actually increased between the critical 1992-1999 and 2000 and 2005 periods (San Francisco Bay Nutrient Technical Workgroup and Steering Committee 2015, R. Kudela, Pers. Comm.) (Figure 1).

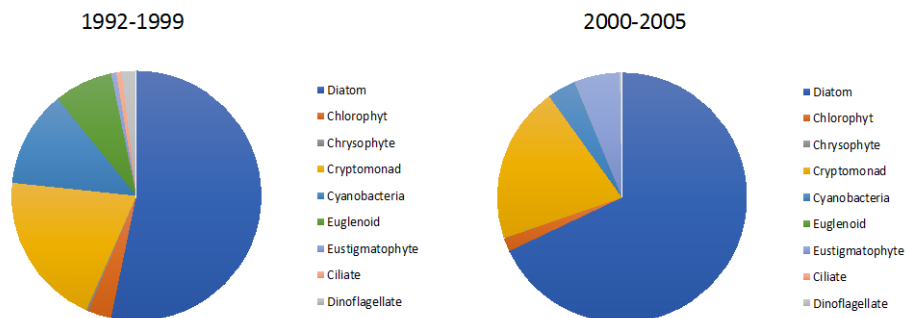


Figure 1: Cell biovolume-based determination of phytoplankton community structure and relative contributions to total biomass among major phytoplankton groups for sites noted in the text and for the time periods of 1992-1999 vs. 2000-2005. Data are from the USGS time-series with data analysis provided by the San Francisco Bay Nutrient Technical Working Group Steering Committee (2015) and R. Kudela (Pers. Comm.).

We submit that analytical limitations as well as re-examination of phytoplankton biomass data by the SF Bay Nutrient Technical Working Group Steering Committee precludes a conclusion that a phytoplankton community “shift” away from diatoms has occurred. Accordingly, the cascade of ecosystem changes

proposed by Glibert (2010) and Glibert et al. (2011) that depends on changes at the primary producer level is neither statistically nor technically sound.

Lastly, arguments based on ‘ecological stoichiometry’ (Glibert 2010, Glibert et al. 2011) are not directly transferrable to shallow-water ecosystems, such as the Delta-Suisun Bay regions, because sediment-water column nutrient exchanges dominate N and P cycling. One cannot reliably infer ratios of elements and forms with consistency, as the ecosystem is not biogeochemically static in time and space, limiting the usefulness of this approach.

III. Future Research on Phytoplankton – Nutrient Interactions in the Delta

Upon review of pertinent materials related to current understanding of phytoplankton responses to nutrients in the Delta, and especially with regard to the Ammonium Paradox, the advisory panel has reached the conclusion that a broadened research approach is required to make progress in this area. Below we provide a narrative that identifies a broadened conceptual framework and also integrates several research theme areas we believe are necessary to advance phytoplankton/nutrient investigations and knowledge.

(a) The Delta as a nutrient enriched ecosystem:

It is important to place Delta research in the broadened conceptual framework of tropho-dynamics. Macro- (nitrogen, phosphorus, silicon) and micro- (trace metals such as iron) nutrients are essential for supporting and sustaining primary and secondary production in aquatic ecosystems, including the Delta and down-gradient San Francisco Bay. However, excessive nutrient inputs that exceed the assimilative capacity of resident microbes and higher plants can lead to altered community structure and proliferation of species that may have undesirable effects on biogeochemical cycling, food web dynamics, habitat conditions, environmental and human health. There are numerous examples of the negative effects of nutrient over-enrichment, or “too much of a good thing” in estuaries worldwide (D’Elia 1987, Smetacek et al. 1991, Nixon 1995, Paerl 1997, 2008; Boesch et al. 2001, Cloern 2001, Elmgren and Larsson 2001, Conley et al. 2009, Paerl et al. 2014) and in the Delta (Dugdale et al. 2007, Lehman et al. 2008, Meyer et al. 2009). These include: 1) Accelerated primary production (eutrophication); 2) Selective stimulation of harmful (i.e., toxic) algal bloom (HAB) species, including cyanobacteria in the upper Delta; 3) Shifts in phytoplankton community structure to more opportunistic “weed” species; that may 4) induce changes in food web structure and trophic transfer; and 5) enhance the potential for bottom water hypoxia and anoxia due to increased sedimentation of autochthonous-organic matter.

Excessive nutrient inputs to the Delta also highlight the need for improved quantitative understanding of transformation processes and fate of nutrients as they move through the Delta and ultimately to San Francisco Bay. Novick et al. (2015) concluded that the Delta was an “important biogeochemical reactor for N” and emphasized the importance of N assimilation, nitrification, denitrification and burial processes for determining N distribution and fate. They also noted large uncertainties in these areas and the need for more process measurements linked to physical processes and better modeling efforts, all of which are consistent with a broadened biogeochemical research perspective recommended in this report. Efforts must also be made to incorporate impacts on biota of seasonal variations in water flow that determine nutrient transit through the Delta (timing of flux), i.e., rapid transit during winter high flow versus nutrient retention during summer low flow when biota are most active. Accurate estimates of nutrient input and output (mass balance approach) for the Delta are critical for understanding

influences of Delta processes on nutrient forms and concentrations both within the Delta and in down-gradient environments.

(b) Role of water flow in understanding Delta phytoplankton dynamics:

The Delta ecosystem is composed of aquatic environments with different water residence times (or flushing rates) that vary seasonally and annually. This hydrological complexity is compounded further by strong flow, salinity and other gradients as water moves into the down-gradient San Francisco Bay. In turbid, highly tidally mixed, well-flushed, nutrient enriched estuaries like San Francisco Bay and the Delta, light availability, water residence time and grazing (or filter feeding) may be the primary factors limiting phytoplankton production (Cloern et al. 1983, Alpine and Cloern 1992, Cloern and Duford 2005, and Jassby 2008). Here, both N and P are often plentiful (i.e., exceeding the half saturation constants for growth) and, hence, N:P supply ratios or different chemical forms are unlikely to have a significant effect on shaping phytoplankton community structure and function. However, there are poorly-flushed regions of the upper Delta, where there is a shift from tidal dominance to (river) flow dominance. In these regions, water residence time may be long enough (especially during low flow periods) for nutrients to be thoroughly assimilated. Under these conditions, nutrient limitation may potentially occur (Lehman et al. 2013, Parker et al. unpublished), and nutrient enrichment could impact the structure and function of primary and secondary producers. This potential scenario requires further investigation, especially under protracted drought periods, when residence time is relatively long, nutrient limitation will most likely occur and, hence, nutrient enrichment impacts would be most significant. In this regard, water delivery rates and water residence can vary on short (diel) and longer term (seasonally, inter-annually) time scales, leading to the possibility for nutrient limitation, especially if low flow, drought conditions prevail in the future.

In upstream regions of the Delta, where tidal influence is minimal, and water withdrawals and diversions have taken place, flow and residence time have been significantly altered. Recent studies in the Delta and elsewhere have shown that such hydrologic alterations can have profound effects on phytoplankton community structure (Lucas 2009; Lucas et al. 2009, 2016). In addition, geomorphology (and changes therein) of the Delta can affect water movement, residence time and biological responses, including primary production, phytoplankton biomass and composition. Human-made alterations of flows and residence times play an integral role in mediating these changes. For example, Monsen et al. (2007) provide an example of how the placement of a barrier in the south Delta radically changed flushing times and water quality.

In either up-gradient or down-gradient environments, when flow is reduced and water residence time increases, phytoplankton will have longer periods of time to assimilate nutrients and increase biomass (as blooms) before being transported out of the system. This scenario benefits phytoplankton overall and, more specifically, those species that have generally slow growth rates, since under the influence of reduced flushing (longer residence time), these species will more effectively compete with faster-growing species for nutrients and other resources. Most cyanobacteria, including harmful bloom forming types, exhibit relatively slow growth rates (Paerl and Huisman 2009). Hence, in a more conducive, longer residence time system, conditions will become more favorable for their dominance, especially if nutrient supplies are adequate to sustain blooms (Paerl 2008, Paerl and Huisman 2009). In recent years, the non-N₂ fixing, potentially toxic, bloom-forming cyanobacteria, *Microcystis* spp., has increased in dominance in slow-moving fresh to oligohaline waters of the upper Delta (Lehman et al. 2008, 2013). This genus appears to have benefitted from the combined effect of increased residence

time, possibly warmer water conditions (which would enhance growth rates), more intense stratification, and excessive nutrient loading. Furthermore, buoyant, colony-forming cyanobacterial genera like *Microcystis* escape both benthic and planktonic grazing, thereby minimizing top-down controls on blooms.

(c) Irradiance as an interacting factor in determining phytoplankton nutrient response:

Solar radiation is clearly a powerful influence on phytoplankton growth and nutrient uptake, including N assimilation. The key energy source available for phytoplankton primary production and N assimilatory processes is photosynthetically-active radiation (PAR: 400-700nm). Energy costs depend on irradiance; at high irradiance levels, cells are not energy-limited, but at reduced irradiance, the cell's overall energy budget can be affected (Turpin 1991). This impact may be manifested as changes in the photosynthetic quotient, chlorophyll *a* per cell production, nutrient assimilation and resultant growth rates (Thompson et al. 1989).

Phytoplankton have the capacity to adapt to the light environment in which they reside in species-specific ways. In consistently low light environments, e.g., some taxa respond with higher chlorophyll *a* concentrations per cell and others with saturation of photosynthesis rates at lower light intensities than would occur if they were growing at high light intensities (e.g., Jørgensen 1969). Photoinhibition responses are well-known among phytoplankton exposed to very high light intensities, e.g., near water surfaces. Therefore, it is critically important to consider the previous light history experienced by phytoplankton when interpreting phytoplankton responses to different N sources, e.g., in terms of instantaneous rates of photosynthesis, N uptake rates, and chlorophyll concentration.

An understanding of effects of light intensity on assimilation of inorganic N sources such as ammonium and nitrate by phytoplankton is especially important. It is well known that it is energetically more favorable for phytoplankton to grow on ammonium compared with nitrate because reductant does not need to be expended to reduce nitrate to ammonium before N can be assimilated, allowing cells to save approximately 20% or more on energy costs, and for the ammonium uptake system to be less limited by light than the nitrate uptake system in phytoplankton (Syrett 1981, Thompson et al. 1989, Levasseur et al. 1993, Cabrita et al. 1999, Clark and Flynn 2002). In addition to the energetic expenditure, reduction of nitrate to ammonium requires processing of N through an extra enzyme pathway, which at high growth rates can lead to an enzymatic "bottleneck". The "bottleneck" may result in lower N and protein contents, leading cells grown on nitrate to appear more N stressed (Wood and Flynn 1995, Page et al. 1999) and exhibit lower growth rates (Paasche 1971, Thompson et al. 1989, Turpin 1991, Clark and Flynn 2002).

If both the "energetic" and "bottleneck" effects impact growth rates, they can do so in opposite ways. For example, if the energetic effect dominates, then we would expect that the difference in phytoplankton growth rates on nitrate versus ammonium may increase with decreasing irradiance because the extra energy cost for reducing nitrate to ammonium (for assimilating N into cellular constituents) is more pronounced at lower irradiance. Conversely, if the bottleneck effect is more dominant, we would expect that the difference in phytoplankton growth on nitrate versus ammonium will be largest at high growth rates, commonly achieved at medium irradiances, and smallest at low growth rates, commonly achieved at low or photoinhibiting irradiances. Therefore, the bottleneck effect may operate in a manner opposite of what would be expected from the energetic effect. Although both these effects may impact phytoplankton physiology simultaneously (i.e., photosynthetic

quotient or chlorophyll *a* per cell), results from several carefully conducted culture studies appear to demonstrate that the bottleneck effect has a greater impact on growth rates compared with the energetic effect (Paasche 1971, Thompson et al. 1989, Turpin 1991, Wood and Flynn 1995).

In turbid estuarine systems, including the San Francisco Bay Estuary and Delta, the possibility exists for these two effects to operate interactively (simultaneously), varying in time and space relative to N supply, irradiance and the degree of N limitation. Paerl and Piehler (2008) demonstrated this effect, with regard to impacts of equimolar supplies of ammonium and nitrate provided in *in situ* bioassays conducted with water samples collected along the axis of the turbid Neuse River Estuary, North Carolina (Figure 2) (adapted from Paerl and Piehler 2008).

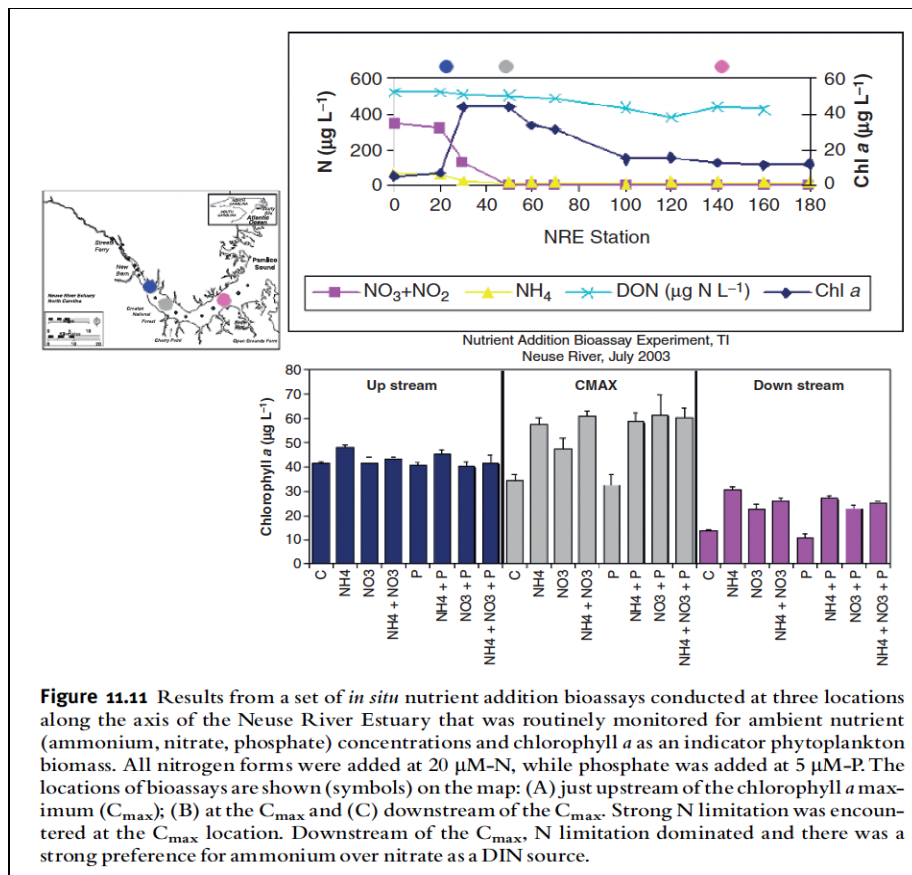


Figure 2. *In situ* nutrient bioassays in the Neuse River Estuary showing response to N and P additions with conclusions of strong N limitation and preference for ammonium.

The influence of photoinhibition on nitrification is also important in interpreting the impact of light on overall nitrogen dynamics. As with phytoplankton N uptake, nitrification can affect concentrations of nitrate and ammonium and, in some cases, phytoplankton may compete with ammonia-oxidizing microbes for ammonium, especially in ultra-oligotrophic environments (e.g., Smith et al. 2014). Ammonia-oxidizing bacteria (AOB) have been known for many years, but the recent discovery of ammonia-oxidizing archaea (AOA) that differ from AOB in several important attributes, including response to light, has stimulated studies investigating niche separation of these organismal groups and, ultimately, their roles in determining overall distribution and activity of nitrification (Merbt et al. 2012, Damashek et al. 2015). In general, AOB and AOA appear ubiquitous in many aquatic environments,

including oceans, estuaries, and inland waters (Merbt et al. 2012 and references therein). However, Horrigan and Springer (1990) concluded that photoinhibition of ammonium oxidation was less important in estuaries than in oceanic environments. More recent studies investigating responses of AOB and AOA to various environmental features appear to support this earlier conclusion in that AOB growth is less photosensitive than AOA growth (Merbt et al. 2012), and AOB tend to dominate in some estuarine environments, especially those impacted by agricultural inputs (Wankel et al. 2011, Damashek et al. 2015). Future studies on N processes in the Delta and downgradient estuarine environments would benefit from investigations of nitrification and other N transformation processes in both benthic and pelagic regions, effects of light on these processes, and a determination of the magnitude of benthic-overlying water couplings, which could affect phytoplankton-nutrient interactions.

(d) Roles of N, P and grazers in determining phytoplankton growth and composition:

In estuarine ecosystems, both N and P have been shown to play interactive roles in controlling primary production (Fisher et al. 1992, Paerl 2009, Paerl et al. 2014). Both the *amounts* and *ratios* of N and P inputs and resultant concentrations can determine the structure and function of primary producers. The median DIN concentration in the Delta is $\sim 28 \mu\text{M}$ and median phosphate is $\sim 2 \mu\text{M}$. In the context of the roles that ratios of N and P may be playing there, it should be noted that these concentrations are both 10 times higher than half saturation constants (Cloern and Dufford 2005). Given the very high concentrations of both N and P in the Bay Delta, it is difficult to envision how ratios of two non-limiting nutrients play a role in shaping communities. The *chemical forms* of these nutrients can play additional roles in modulating community responses. Lastly, there are synergistic and antagonistic interactions among limiting nutrients, for example N and P co-enrichment often leads to greater degrees of biostimulation than N or P alone (i.e., they may be co-limiting) (Elser et al. 2007, Paerl et al. 2016a).

With respect to the influence of *chemical forms* of nutrients as possible stressors on the Delta system, it has been proposed (the Ammonium Paradox) that the reduced form of N, ammonium, may play a selective role by inhibiting the growth of diatoms in mesohaline to full salinity regions of the Delta and San Francisco Bay regions (Dugdale et al. 2007). This scenario would depend on N being limiting in this region, vs. light and flushing/transport and grazing as limiting factors, all of which should be considered contemporaneously. If common and widespread, this type of inhibition could have food web, nutrient and carbon cycling ramifications, since diatoms are considered a desirable food source for most zooplankton, planktivorous fish and shellfish species; although it should be pointed out that dinoflagellates and cryptophytes, which are plentiful in these regions, are also a good food source. The ammonium inhibition argument is based on open ocean observations of a strong preference for nitrate as the N source in diatom populations and laboratory observations that show high levels of ammonium can inhibit the uptake of nitrate in diatoms (Dortch 1990). These observations have led Dugdale and colleagues to propose that ammonium discharge from upstream wastewater treatment plants (in particular the Regional San WWTP) is high enough to lead to inhibition of nitrate uptake in downstream, diatom-dominated waters (e.g., Suisun Bay). Furthermore, it has been pointed out that there has been a general decline in diatom biomass since the mid-1990s, and that the amount of ammonium discharged by the Regional San WWTP (and possibly other WWTPs) has shown a parallel increase. However, recent work by Berg et al. (2017) has shown that resident diatom species recently isolated from the Bay Delta do not show ammonium “inhibition” of either nitrate uptake or growth when incubated at light and temperature levels reflecting natural conditions. Furthermore, Esparza et al. (2014) showed that elevated ammonium levels (far higher than the $4 \mu\text{M}$ $\text{NH}_4\text{-N}$ that Dugdale et al. suggested was “inhibitory” to diatom nitrate uptake and growth) discharged to Suisun Bay actually stimulated diatom growth and bloom formation.

Although the idea of ammonium inhibition of diatom growth remains controversial, the preference for ammonium (Flores and Herrero 2005, Paerl and Piehler 2008) and increased growth with that N form by cyanobacteria (Blomqvist et al. 1994) are well documented. As noted above, increased blooms of *Microcystis* in some areas of the Delta have caused concern in recent years (Lehman et al. 2008, 2013). *Microcystis* is indicative of nutrient-enriched conditions worldwide (Reynolds 1987, Paerl 2008, Paerl et al. 2016b). In particular, this genus tends to dominate in waters that are receiving excess N, since it is a non-N₂ fixer and, hence, reliant on externally-supplied forms of N (Paerl et al. 2016b). Therefore, it appears that the combined effect of increased residence time and excessive N loading (possibly combined with a warming trend) is conducive to *Microcystis* bloom formation (Paerl and Huisman 2008, 2009). In order to sustain *Microcystis* blooms, both N and P supplies must be adequate. Therefore, while N appears to be the main nutrient stressor (i.e., at times supplied in excess), P supplies must also be available. Excessive N loading may also become a problem in South San Francisco Bay, which is a relatively poorly-flushed part of the greater SFO Bay and is prone to problematic (including potentially toxic genera) algal (dinoflagellate and other flagellates) blooms. We note that the high N and P levels in San Francisco Bay, combined with the concern about potential water-quality degradation, have motivated creation of the San Francisco Bay Nutrient Management Science Strategy (<http://sfbaynutrients.sfei.org>).

Overall, there is evidence that when physical conditions permit (i.e., increased residence time, elevated temperatures and enhanced vertical stratification), nutrients can play an increasingly important role in the control of phytoplankton production, bloom formation and persistence in parts of the Delta system. Nitrogen appears to be the nutrient most instrumental in enhancing biomass and bloom formation, although a potential secondary role of P should not be ignored. Therefore, there is agreement that N input reductions from both point (wastewater inputs) and non-point sources (agricultural and urban runoff) will help improve water quality conditions in the Delta and possibly parts of San Francisco Bay (e.g., South SF Bay). There is less certainty as to whether reducing one form of biologically-available N is preferred over another (i.e., nitrate vs. ammonium, vs. dissolved organic N). Because different forms of N are biologically available and readily cycled between the water column and sediments, the prudent approach is to control TOTAL N inputs from both point and non-point sources, which will ensure that undesirable algal bloom formation in regions prone to such events is minimized (NRC 2012). There is less certainty as to the role P inputs play in the control of algal production and bloom formation. If P plays a role as a limiting nutrient, it is likely to be during freshwater blooms, but this has not been established. The degree to which N reductions should be practiced is at present uncertain and requires a combined research (i.e., bioassays, N transport, fate and cycling studies) and modeling approach that takes both physical and chemical forcing features, as well as the interactive effects of grazing and light limitation, into consideration.

Also, while it is generally recognized that the Regional San WWTP is a highly significant point source N contributor to the Bay's N budget, there is no reason to believe that the ammonium fraction of the N in the effluent is any more detrimental to the Bay's phytoplankton community composition (i.e., the decline in diatoms) than other biologically utilizable N fractions in the effluent (e.g., oxidized DIN and DON) or unknown contaminants. One aspect that has largely been ignored is the potential for contaminant concentrations to covary with ammonium. In Southern California, a recent study demonstrated that enhanced nutrient discharge from wastewater treatment suppressed algae because of the co-occurrence of disinfection byproducts that heavily impacted phytoplankton, but not heterotrophic bacteria (Kudela et al. 2017). These compounds are known to exist in the Sacramento and San Joaquin Rivers (Chow et al. 2007) and are only one example of unsampled contaminants that could

co-occur with ammonium in discharge. The discharge point of this plant is also well upstream (>50km) from the Bay proper (e.g., Suisun Bay) where diatom and other phytoplankton taxa preferred by grazers have declined. This distance allows for both inorganic and organic N species released by the plant to be cycled and change forms many times before they enter the Bay proper (Figure 3). Therefore, imposing specific reductions on ammonium to minimize the “Ammonium Paradox” effect many km downstream seems unwarranted and, from a biogeochemical perspective, unjustifiable. If N over-enrichment is of concern, it seems more logical and justifiable to target and reduce TOTAL N discharge from this and potentially other wastewater treatment plants and agricultural inputs impacting N loading to the Bay (NRC 2012).

Overall, reductions of ammonium from the Regional San WWTP represent a positive application of technology to affect N loadings, with possible ramifications for the receiving waters, but a cascade of ecosystem responses appears unlikely as ammonium is not the sole driver of phytoplankton throughout this strongly light-limited ecosystem. Future studies that are planned to compare pre- and post-ammonium reduction from the Regional San WWTP and other WWTPs would greatly benefit from an approach that incorporates a full set of potential physical, chemical and biological drivers and controls of phytoplankton biomass and composition as discussed in other parts of this report.

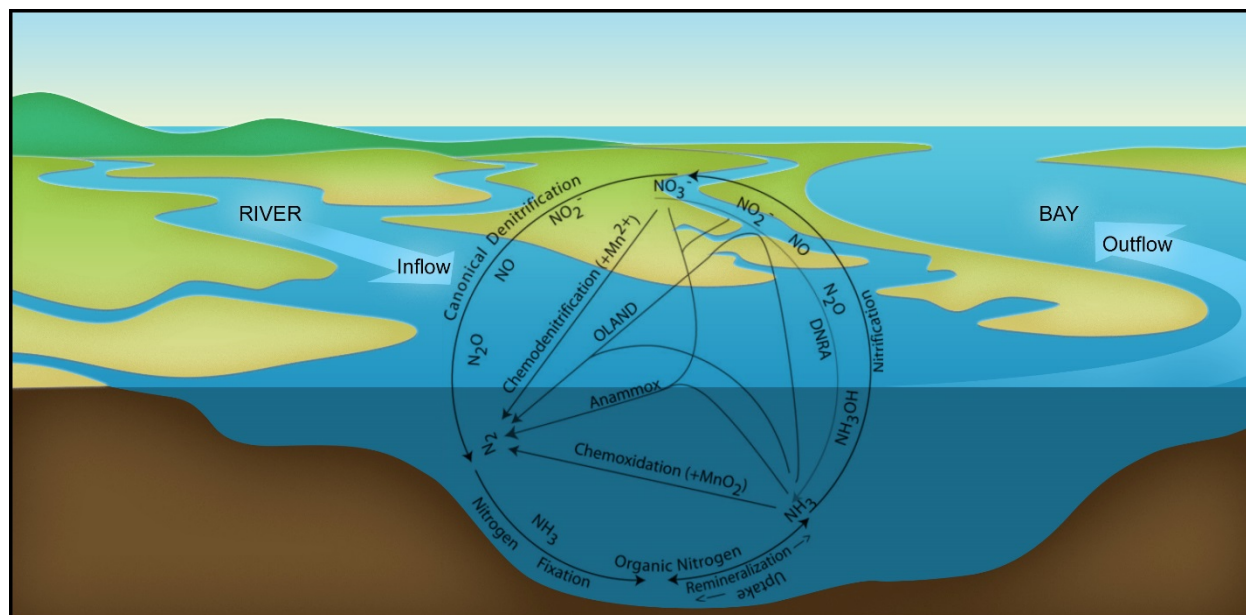


Figure 3. Conceptual diagram showing the multiple microbial, sediment-water column and dissolved-gaseous transformations that impact the chemical forms and fates of N in the riverine-estuarine continuum (N cycle from Brandes et al. 2007).

The effects of grazers on phytoplankton and food webs in general have focused primarily on the introduced clam, *Corbicula fluminea*, and the later invasion of the Asian clam, *Potamocorbula amurensis*. Brown et al. (2016) described the invasion of *P. amurensis* as causing an ‘abrupt change’ in the estuarine food web beginning in 1987, including a 5-fold decrease in phytoplankton biomass in Suisun Bay and the western Delta (Alpine and Cloern 1992), and a decrease in algal cell size accompanied by an almost total decline in diatom production. These conclusions are supported by Jassby (2008), Jassby et al. (2002), Thompson et al. (2008), Cloern (1984, 2010) and others, who have

pointed out that the decline in diatom biomass in Suisun Bay and other locations took place immediately after the proliferation of *P. amurensis*, an abundant grazer capable of quantitatively removing vast amounts of phytoplankton biomass. In this regard, Figure 4, adapted from Cloern et al. (2014), shows that (1) chlorophyll-*a* declined abruptly after the clam introduction; and (2) chlorophyll-*a* had no trend (up or down) during the period 1987-2011 when ammonium load and N:P increased significantly. The estuary did not behave in a manner consistent with the Ammonium Paradox explanation of a chlorophyll *a* decline and diatom loss.

It appears that several environmental factors co-vary with the decrease in diatom biomass starting in the mid-1990s. Also, we note that in addition to decreases in diatom biomass, other phytoplankton taxa decreased in biomass at this time, at similar locations, indicating that the phytoplankton decline was not solely due to diatoms. This latter observation would tend to support the argument that “top down” grazing controls exerted by invasive benthic bivalve grazers can control phytoplankton biomass (Lucas et al. 2016).

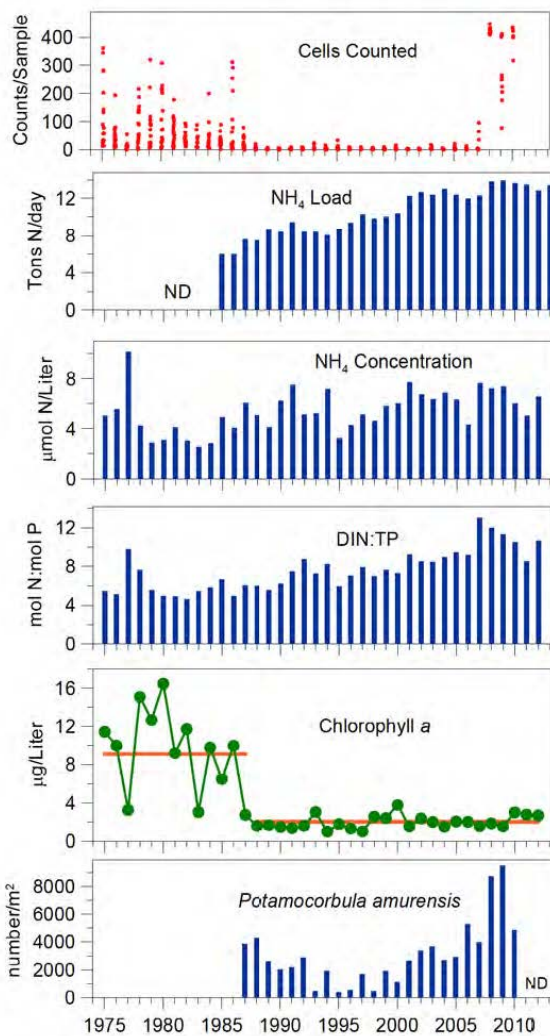


Figure 4. (Figure and caption copied from Cloern et al. 2014) Top panel: number of cells or colonies counted in phytoplankton samples collected at IEP-EMP station D7. Bottom panels show mean annual: NH₄ loading from SRWTP; NH₄ concentration and N:P ratio in Suisun Bay (means of measurements at stations D7 and D8); chlorophyll-*a* concentration in Suisun Bay (means of measurements at stations D7 and D8); and *Potamocorbula amurensis* abundance (station D7-C). The orange lines in the chlorophyll-*a* panel demarcate a 1987 change point in mean chlorophyll-*a* concentration, synchronous with the establishment of *Potamocorbula* in Suisun Bay. There was no significant trend of chlorophyll-*a* concentration before or after 1987, nor was there a decadal trend in chlorophyll-*a* mirroring the increases in NH₄ concentration and N:P ratio. ND means not determined.

(e) Roles of macrophyte beds in nutrient generation, transformation and export:

Wetland ecosystems are well-known as sites that support highly productive and diverse biota as well as zones of nutrient transformations and gas flux primarily associated with aquatic plants and microbial communities attached to plant surfaces and sediments (e.g., Stanley et al. 2003, Wetzel 2006, Mitsch et al. 2009, Stanley and Ward 2010). They are particularly well-known for their impacts on nitrogen transformation via the processes of nitrification, denitrification, and nitrogen fixation because of their roles in retention of some nutrients (e.g., nitrate) and export of others (e.g., dissolved organic matter and ammonium). However, wetlands as sinks or sources of nutrients can vary depending on a variety of factors, including aquatic plant composition, density, seasonal changes, and hydrological patterns, among others (Stanley and Ward 1997, reviewed by Mitsch and Gosselink 2007). Wetlands that form interfaces between upgradient riverine environments and estuaries can be especially important modulators of nutrient inputs into near coastal areas (Pennock et al. 1999, Ward et al. 2016.).

Wetland areas in the Delta once included marshes composed of emergent aquatic macrophytes that formed expansive tules dominated by *Scirpus* and *Schoenoplectus* spp. (Kimmerer et al. 2008, Meyer et al. 2009). It is likely that these native marshes played significant roles associated with wetlands as noted above. However, very little of these wetland areas remains, and aquatic plants in the Delta landscape are now composed of very different types of macrophyte communities, which include invasive species of Brazilian waterweed (*Egeria densa*) and water hyacinth (*Eichhornia crassipes*) (Dahm et al. 2016). Both of these species grow in free-floating form (*E. densa* can also grow submersed, attached to sediments) that typically results in dense, surface mats of aquatic vegetation that impede boat travel and also cause extensive, sub-surface changes. The thick surface mats create a low-light environment in the underlying water column that can cause pH and low-oxygen conditions inhospitable for growth of phytoplankton and other photosynthetic organisms (Wetzel 2001). Conversely, in some locations, rapidly developing phytoplankton blooms could impede light penetration sufficiently to reduce growth of submersed aquatic vegetation (e.g., Hauxwell et al. 2003). Very little is understood about the current roles of Delta macrophyte communities that might affect phytoplankton composition and growth in other areas of the Delta, including nutrient retention, regeneration, transformation, and ultimately quality and quantity of nutrient transport into areas beyond the macrophyte beds.

Recent reviews of macrophyte status in the Delta note that areal coverage across the Delta is still low: 3% for *E. crassipes* and 11% for *E. densa* (Dahm et al. 2016), but possibly expanding with two-fold increases of submersed and five-fold increases in floating aquatic vegetation reported from 2008 to 2014 (Macrophyte Science Work Group 2015). Expansions of floating macrophyte invasives would be expected to continue and even enhanced with increased water residence time and warmer temperatures (Wilson et al. 2005), conditions anticipated under current climate change predictions for the Delta (Cayan et al. 2009, Cloern et al. 2011). The invasion of additional non-native, macrophyte species into the Delta from nearby environs also seems likely. Although nutrient requirements for invasive species are clearly met in the Delta environment, little is known about specific nutrient thresholds that support high levels of production, i.e., whether a strategy of decreased TN might also be required to impede macrophyte growth. Lack of knowledge in this area hinders efforts to predict how changes in nutrient input to the Delta affect invasive macrophyte growth, areal expansion, and also potential effects on phytoplankton.

The advisory panel agrees with conclusions from the review publications cited above, including: (1) sporadic surveys conducted to date in the Delta of macrophyte coverage and composition are

inadequate for robust analysis of macrophyte change over time, (2) lack of investigations of nutrient dynamics within plant beds (e.g., production, water column- sediment exchange, plant and sediment nutrient sequestration) impedes understanding of the role of these beds in Delta nutrient cycling, and (3) development of a biogeochemical model that addresses nutrient fate and transport and that includes macrophyte beds is needed.

(f) Modeling as a tool for integrated understanding of phytoplankton-nutrient dynamics:

There is a critical need to link hydrodynamic models to biogeochemical models in order to advance Delta research for a more broad-scale understanding of nutrient-phytoplankton interactions. Addressing this need is very challenging, not only because the Delta is large and complex, but also because there is currently no organizational framework nor adequate funding to meet modeling needs. A strategic plan, focused commitment to modeling goals, and inter-agency leadership and cooperation are required to move successful modeling efforts forward.

Some Delta researchers agree that good 1-, 2-, and 3-dimensional hydrodynamic models do exist for the Delta, but most are not open source or public domain. Unfortunately, biogeochemical models that could be linked to them are under-developed and will require more information across the heterogeneous Delta landscape on process rates (e.g., denitrification, nitrification, DIN uptake) for model validation and calibration. These conclusions are consistent with panel recommendations that large-scale, prioritized field studies addressing nutrient-phytoplankton dynamics are the necessary next steps that will lead to successful Delta management strategies. A coordinated plan that links expanded field measurements to relevant models is needed.

A recent Modeling Science Workgroup White Paper (Trowbridge et al. 2016) provided a modeling framework for Delta nutrient management, including a thoughtful overview of the current status of models in Delta research. The authors emphasized that the complexity of the Delta required model use to allow evaluation of how multiple, interacting factors affect ecosystem response to nutrients, including the relative importance of a variety of physical and biological features on phytoplankton composition and production. The current narrow focus of individual research projects does not produce the broad-scale hydrodynamic and water quality tools needed by the community to address the Delta landscape as a whole. Below are key points from that paper that the panel views as most relevant to this report:

- Existing hydrodynamic and water quality models used in the Delta are inadequate because they do not include a broad enough suite of processes nor do they have all of the desired model characteristics such as accessibility, credibility, scalability, and a large enough user community.
- A successful modeling effort will include not just model development relevant to Delta management needs, but also a team that includes data managers and technologists who prepare data for models and work with an interdisciplinary team of scientists to ensure consistency with conceptual models.
- An effective governance process that is not overly complicated to guide modeling efforts, coordinate agency interactions, and evaluate funding is needed to produce a set of hydrodynamic and water quality tools available to state and federal agencies, universities, stakeholders, and consultants.

- A phased implementation approach is recommended, e.g., starting with an addition of nutrient modules to existing hydrodynamic models and then building complexity in the model(s) from this first step.
- Use multiple models that are appropriately groomed to answer relevant questions; some answers may require sophisticated 3-D models, whereas others will be less complicated.

Summary and Knowledge Gaps:

Current Delta research requires an approach that includes focus on a broad array of drivers that influence nutrient forms and concentration as well as phytoplankton growth, production, and composition. The Delta is a complex environment where many factors drive events on different time and space scales. It is highly unlikely that one factor, e.g., ammonium concentration, is the main driver over all of these spatial scales or is even the primary driver in any given situation. A preference for ammonium among some phytoplankton based on energy costs, especially with cyanobacteria (e.g., *Microcystis*), is well documented. However, the observation of *preference* for ammonium does not necessarily extrapolate successfully to a generalized conclusion of ammonium *inhibition* of nitrate uptake among diatoms as a group in field conditions. Inadequate attention to interacting physical factors such as light and water flow (including water retention time) as well as under-investigation of an array of bacterial and archaeal N processes (e.g., nitrification, among others) is likely confounding conclusions from past Delta research.

Grazing effects on phytoplankton have primarily focused on introduced/invasive clams. However, other grazers such as micro- and meso-zooplankton, have contributed one-third to one-half of total grazing on phytoplankton, with all three classes of grazers consistently suppressing phytoplankton biomass accumulation (Kimmerer and Thompson 2014). The controls on and factors influencing zooplankton grazer effects compared with clam grazing on phytoplankton need further clarification. Also, there has been virtually no evaluation of protist grazers, such as ciliates and flagellates, on phytoplankton.

The influences of the complex and diverse landscape of the Delta on nutrient flux also require closer scrutiny. For example, recent efforts to restore floodplain and tidal wetlands as well as expansion of submersed and floating aquatic vegetation (Brown et al. 2016) emphasize the increasing need to understand how material flux into and out of these habitats affects nutrient form and concentration in other parts of the Delta and the down-gradient estuary.

Finally, there is an urgent need for models that address the heterogeneous Delta landscape as a whole. Models that link existing hydrological models with new biogeochemical ones are especially critical. These goals are daunting for a number of reasons, including the need for additional field data across habitats for improved biogeochemical models, an interdisciplinary team of data managers, technologists, and scientists, coordination of teams across multiple agencies and academic institutions, and funding sources.

IV. Outcomes of Future Management Strategies in the Delta

The advisory panel strongly recommends a management strategy of the Delta that is based on broadened research objectives, including a focus on multiple nitrogen forms (not just nitrate and ammonium and including DON), other nutrients (e.g., phosphorus), and their biological transformations.

The general increase of nutrients in the Delta associated with changing land use and increases in agriculture, among other causes, along with other features of eutrophication have resulted in prolific growth of phytoplankton that thrive under nutrient-rich conditions as well as expansion of invasive macrophytes. Nutrient inputs to the Delta are projected to increase as the human population and its activities continue to grow in California. *

Current efforts to limit ammonium inputs from wastewater treatment plants will likely succeed in reducing biomass of specific phytoplankton that prefer that nitrogen form, including some cyanobacterial taxa, e.g., *Microcystis*. However, cyanobacteria, other phytoplankton taxa and macrophytes may flourish on diverse inorganic and organic forms of nitrogen (and other nutrients) that are produced down-gradient from the original ammonium source (Figure 3). If management strategies include efforts to curtail eutrophication in the Delta, including decreases in overall nutrient input, then alleviation of negative consequences from excessive nutrients, described in a previous section, will also likely occur.

Although consequences of eutrophication in estuaries and inland waters (as well as its reversal) are well documented (see citations in previous sections), specific predictions of phytoplankton attributes under any Delta management strategy are confounded by unknowns related to future climate change. Among the many factors that may intersect with future management efforts, climate change looms among the most prominent (Dettinger et al. 2016). Therefore, the advisory panel has focused primarily on this feature with regard to future outcomes of management strategies and its likely consequences to nutrient, phytoplankton interactions in the Delta.

Climate Change

Overview: Climate change is a major driver of historical and future water quality and tropho-dynamic changes in the San Francisco Bay-Delta system (hereafter Bay Delta), which has been transformed from a tidal, freshwater marsh of the early nineteenth century to one that is leveed and converted to subsided islands, with a complex network of channels (Lund et al. 2010). Western regions of the United States have already experienced changes in hydrology since the mid-twentieth century, and such changes have been shown to be consistent with the increases in greenhouse gasses (Bonfils et al. 2008). Projected changes in primary drivers of climate change, including rising temperatures, changing precipitation amounts and patterns, and sea level rise, will result in significant impacts to the Bay Delta proper (Cloern et al. 2011), its tributary watersheds, and the water resources it supplies to Central and Southern California (Chung et al. 2009).

There is extensive information on impacts of climate change in the Bay Delta region (Climate Action Team 2010, Cayan et al. 2008, 2009; Field et al. 1999). This includes a systems approach for understanding the natural variability in the region's climate (Redmond and Koch 1991, Greshunov et al. 2000), detection and attribution of historical changes in climate (Bonfils et al. 2008), and quantification of potential changes in primary stressors of climate through analyses of the General Circulation Model (GCM) predictions (Cayan et al. 2009), statistical downscaling (Maurer and Hidalgo 2008, Hidalgo et al. 2008), impacts of projected sea level rise (Knowles 2008), and the sensitivity of the water resources system to climate change and sea level rise (USBR 2008). However, relatively few studies have been conducted to quantify the impacts of warming, consequent changes in hydrology, and sea level rise on the ecology of the Bay Delta region. Efforts have been underway to link climate, hydrology, and ecology in the Bay-Delta-River-Watershed system for predictive purposes (CASCaDE 2010).

A conceptual diagram depicting how climate (changes) will impact hydrologic and habitat conditions relevant to primary producer (phytoplankton and benthic macro- and microphytes) in the Bay Delta system is shown in Figure 5 (from NRC Report 2012). Global warming due to anthropogenic greenhouse gasses (Intergovernmental Panel on Climate Change-IPCC 2007, 2012) is the primary driver for changes in climate and sea level rise. The other primary driver, natural variability, manifests itself in the form of multi-decadal changes in precipitation and temperature patterns (Pagano and Garen 2005), intra-decadal variations associated with El Niño/Southern Oscillation (ENSO) (Redmond and Koch 1991), and the North Pacific Oscillation (Pierce 2005). Typically, temperature variability in this region is somewhat buffered compared to interior, continental areas because of proximity to the Pacific Ocean, whereas changes in precipitation are naturally more extreme (Dettinger et al. 2016). Nevertheless, Pagano and Garen (2005) demonstrated that California regional water quality and habitat are experiencing an unprecedented sequence of wet years along with multi-year extreme droughts that exceed natural variability. Ocean-Atmospheric patterns will also elevate sea levels along the west coast during El Niño years (Cayan et al. 2008).

IPCC (2007, 2012) suggests, based on models, that there is no discernible change in the future ENSO amplitude and frequency. However, the multi-decadal changes in climate and particularly the occurrence of major droughts (such as those that occurred during the 1930s and 1990s in the Bay Delta region) should be investigated further as such variations could have irreversible impacts to the Delta ecosystem under the present condition. The Delta is at a “tipping point” (Lund et al. 2010), and natural variations which are of extreme nature could pose significant threats to the sustainability of the Bay Delta system.

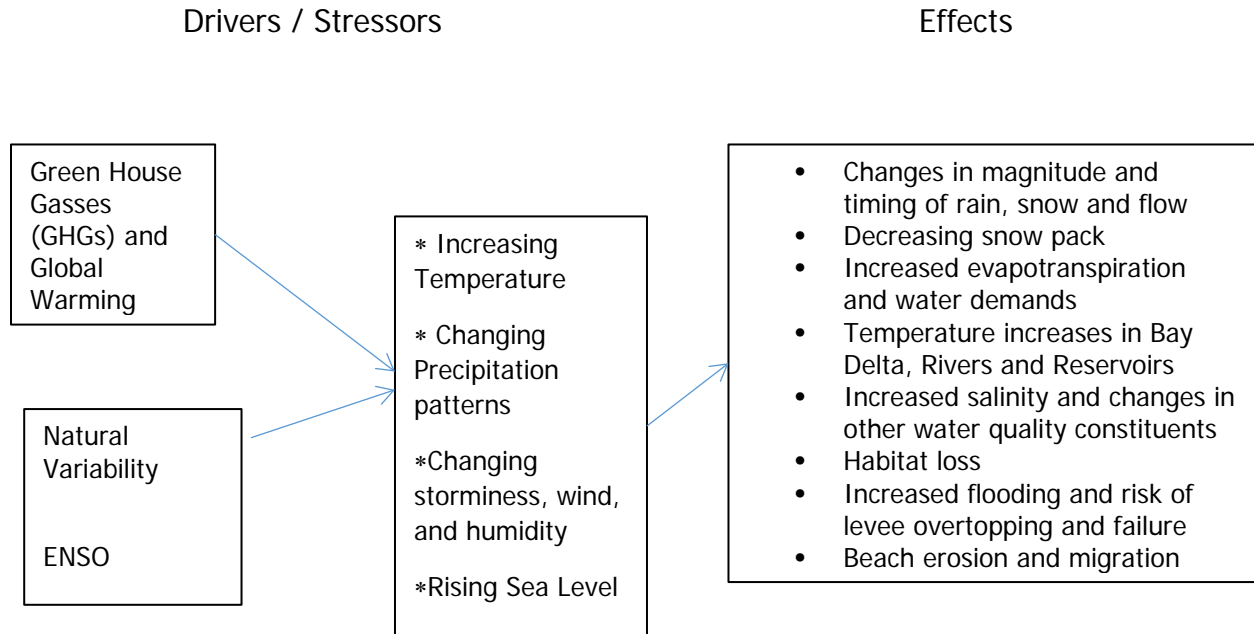


Figure 5. Conceptual framework for assessing climate change impacts on water quality and habitat conditions in the Bay Delta region (adapted from NRC Report 2012).

Overall, the mid-century warming is in the range of 1°C to 3°C, which will increase to 2°C to 5°C by the end of the 20th century (Cayan et al. 2009). The models also showed that there is greater warming in the summer than in winter and that the interior will be warmer than the coast. This asymmetry in temporal

and spatial warming will have a significant impact on precipitation patterns (snow versus rain) and the snowmelt in the tributary watersheds of the Bay Delta system. Compared to the historical period, spring temperatures are projected to be much warmer, particularly during the second half of the century, and cause a significant reduction in April 1st snowpack, a key indicator of water supply for the following summer and fall. The duration of the extreme warm temperatures extend from two months (July-August) to four months (June to September) (Climate Action Team 2010). Heat waves are also projected to increase in frequency and magnitude.

Precipitation in the Bay Delta region of California has a strong Mediterranean climate pattern with much of the annual precipitation occurring during the cooler part of the year, i.e., November to March (Climate Action Team 2010) and, under future climate scenarios, this pattern is not expected to change. Models suggest that future climate will continue to exhibit significant inter-annual and decadal variability, as in the historical observations, but there appears to be a tendency for drying (less precipitation) particularly during the mid to late 20th century (Cayan et al. 2009). The reduction in precipitation could be as much as 10 percent, although not all models demonstrated such a change, particularly during the early part of the 21st century. There is significant uncertainty in the precipitation projections of downscaled global climate models. Regardless of such uncertainties in precipitation projections, increases in temperature, consistently projected by all models, and the subsequent effect on snowmelt may result in a significant change in the timing of flows in the tributary rivers of the Bay Delta region.

Sea Level Rise (SLR) is another climate change driver which will have a significant impact on Bay Delta hydrodynamics and salinity conditions (Mount 2007, Lund et al. 2010). Higher ocean levels, particularly in the presence of tides, and the storm surges which may be exacerbated by ENSO conditions, will increase water depths and push salty water further inland, affecting vertical mixing. The effect of sea level rise depends on the future projections of its magnitude. Historical rate of sea level rise at the Golden Gate has been estimated to be about 2 mm/yr (equivalent to about 0.2 meters over the 20th century). IPCC (2007, 2012) has predicted that, by 2100, global SLR will be in the range of 0.18 to 0.59 meters, although many researchers have noted that such estimates do not include future sea level increases due to potential rapid loss of ice from places such as Greenland and Antarctica (e.g., see Rahmstorf 2007, and Vermeer and Rahmstorf 2009). Based on an empirical relationship between SLR and the global temperature developed by Rahmstorf (2007), a higher range of SLR, 0.7 to 1 meter by the mid-century and 0.5 to 1.4 meters by the end of the century, has been proposed by the Independent Science Board of CALFED (Mount, 2007). Using the same methodology, Chung et al. (2009) have proposed probability distributions of SLR for 2030 through 2090. USACE (2009) has also provided guidance for incorporating SLR into planning, engineering and design of USACE projects, and such guidance is in the form of three sets of curves through the 21st century, representing historical rate of rise, intermediate and high rates of rise. The progression of SLR through time in this guidance was based on a polynomial curve suggested by the NRC (2012) and a 21st century SLR of 0.4 to 1.5 meters. The above range of estimates is representative of what is used elsewhere in the USA and should be useful for investigating SLR impacts in the Bay Delta region until better estimates become available.

Climate change effects on nutrient inputs, phytoplankton ecology and water quality: As shown in Figure 4, climate change will have a variety of impacts on both natural and human systems in the Bay Delta region. In terms of hydrologic changes, one of the key results of warming will be to alter the precipitation patterns and the water runoff characteristics. Under warmer conditions, precipitation

during the winter will occur more as rain instead of snow and, as a consequence, the April 1st snowpack has been and will continue to be declining (Chung et al. 2009, Mote et al. 2005), most likely even in rainy years as we are experiencing in winter 2017. Clearly, current and projected changes in rainfall and temperature regimes will alter hydrologic and nutrient loading patterns. This means that both timing and quantities of nutrient loads associated with discharge will change. One potential scenario is earlier and potentially larger non-point source loads of nutrients associated with agricultural activities, urban storm water and other diffuse sources entering the Bay Delta. Projected more extensive droughts from spring into summertime will translate into reduced flushing and longer water residence times, as well as more extensive salt intrusion in the Delta region, all of which could have significant impact on phytoplankton and macrophyte community structure and function. In particular, significant late winter-spring runoff events followed by protracted summer-fall drought conditions tend to support the “perfect storm” scenario for stimulating and supporting summer nuisance cyanobacterial (i.e., *Microcystis*) bloom events in the relatively slow moving, long residence time flooded island and tract regions of the upper Delta (Lehman et al. 2008, Lucas et al. 2009, Paerl et al. 2016b).

Spring nutrient pulses from the largely freshwater (as opposed to snowpack, which would retard nutrient runoff until later in the year) discharge pulses in late winter/early spring will deliver nutrients to entrained (“appendix”) regions in the lower Bay where they may serve as nutrient sources for subsequent summer-fall blooms. South San Francisco Bay, which is the poorest-flushed region of the Bay will be particularly susceptible to this scenario. Nutrients discharged from local wastewater treatment plants, in combination with more stagnant conditions due to protracted summer droughts, will no doubt play an additional role in enhancing the bloom potential in this region. Lastly, “trapped” nutrients from early snowmelt and elevated spring runoff entering the Bay from the Sacramento and San Joaquin watersheds should also be considered in potentially supporting such blooms.

Predicted increases in summer temperature are also likely to play a role in determining phytoplankton growth rates and dominance by specific taxa. In particular, certain cyanobacterial bloom taxa (e.g., *Microcystis*, *Cylindrospermopsis*, and less so *Anabaena* and *Aphanizomenon*), thrive at relatively high temperatures ranging up to 35-40°C (Paerl and Huisman 2008, 2009; Paerl et al. 2011), giving them a distinct growth advantage over taxa such as diatoms and dinoflagellates that prefer cooler conditions. In addition, warming of surface waters will enhance vertical density stratification, which will benefit those phytoplankton taxa able to control their position in the water column by buoyancy regulation (e.g., bloom-forming cyanobacterial species) and flagellar swimming (all flagellated taxa). Accordingly, the combination of protracted summer droughts and warmer temperatures is a potent formula for enhanced cyanobacterial bloom potential in the upper Delta track and flooded island regions, while dinoflagellates and other flagellated taxa will benefit in more saline, downstream regions.

Elevated temperatures will also affect an array of metabolic activities. For example, they will enhance rates of respiration and microbial mineralization, which will lead to enhanced cycling of organic matter and release of inorganic nutrients, potentially making them more available for supporting primary production and phytoplankton bloom formation.

Sea level rise will alter salinity regimes, affect vertical stratification and tidal flux in the Bay Delta. Changes in any of these characteristics will affect phytoplankton community composition and biomass; some in more predictable ways (e.g., increased vertical stratification will favor more motile taxa), while others in less predictable ways (effects of horizontal transport on residence times and taxa having differential growth rates).

Increased upstream, saltwater intrusion will interact with changes in downstream, freshwater flow and water withdrawal from the Delta in a complex way. The recent historical records already show changes in timing of flows from the headwaters of the Sierra Nevada region (Vicuna and Dracup 2007, Dettinger et al. 2004, Stewart et al. 2005, Kapnick and Hall 2009). Previous studies have shown that the timing of change is very clear, likely attributable to temperature changes, but there is no clear indication that the streamflow volumes have changed significantly. However, the work to date show that future temperature increases will continue to cause changes in streamflow timing particularly during the second half of the 21st century, and such projected changes have been shown to exceed those from natural variability (Maurer et al. 2007). Chung et al. (2009) have shown that on average, 50% of the annual inflows to Lake Oroville shifts from mid-March to mid-February (about 36 days), and that the annual runoff fraction during the snowmelt period of July through April will decrease from about 35% to about 15% in the case of a 4°C warming scenario.

Very few studies are available to translate the air temperature increases under warming scenarios to corresponding changes in water temperature. A statistical regression model, developed under the CASCaDE (2010) project has demonstrated some promise for predicting water temperatures in the Delta. However, hydrodynamic models which simulate the impacts of air temperature changes, mixing, and flow distributions are needed to provide more accurate estimates of temperature and water quality changes in the future.

V. RECOMMENDATIONS

The Delta is a large and complex landscape that requires an integrated and holistic approach to problem-solving and management. Over the past decade, a number of reports, white papers and journal articles, including some with explicit recommendations, have emerged that addressed various facets of Delta research. The advisory panel acknowledges these previous efforts and offers the following recommendations that build on past publications/recommendations and are constructed from a synthetic overview of topics related to current and future phytoplankton-nutrient interactions.

- (1) Future Delta research should address phytoplankton-nutrient dynamics from a conceptual framework that incorporates system-wide eutrophication phenomena and consequences, including 'recovery' from eutrophication if nutrient inputs decrease. Excessive nutrients trigger a constellation of physical, chemical, and biological responses that form the contextual backdrop of nutrient effects on phytoplankton community productivity, growth, and composition.
- (2) There is a need for careful focus in future Delta research on physical factors, such as hydrology and irradiance, as interactive drivers of observed phytoplankton response to nutrients. Water flow determines direction and magnitude of nutrient (and salinity) flux as well as water residence time, both of which directly impact nutrient form and concentration and subsequent phytoplankton response. Water movement can also affect water clarity, especially in shallow regions, where resuspension of sediments increases turbidity and, hence, availability of light needed for phytoplankton nutrient uptake and growth. Instantaneous measurements of nutrient and carbon uptake can be strongly influenced by the previous light environment of phytoplankton, a topic that needs thoughtful consideration in design and interpretation of future field and laboratory research.

- (3) A broadened spatial approach to nutrient monitoring (e.g., to include nitrogen, phosphorus, silicon, iron, trace metals, and dissolved organic matter, including DOC and DON) concomitant with measurements of phytoplankton and other microbial processes related to nutrient sources, their uptake and transformation is an especially critical need. Delta research would benefit from a strategy that encompasses total nitrogen, i.e., both inorganic and organic forms, as well as phosphorus, as key nutrients determining phytoplankton growth and composition. Among N transforming processes, nitrification has been highlighted in previous sections of this report, but other microbial N processes should not be ignored. A thoughtful research design that incorporates different chemical forms of nutrients, conditions under which one or more may be limiting to phytoplankton, effects of microbial nutrient transformations, and potentially growth-controlling and community-structuring physical factors (e.g., light, temperature, water residence times) and biological controls (e.g., grazing) that intersect with phytoplankton response to nutrients is key to a holistic, biogeochemical perspective of the Delta.
- (4) Research on effects of grazers on phytoplankton biomass, productivity, and composition needs to continue. The impact of clam grazers on phytoplankton has been well-documented, but far less is known about zooplankton and protist grazers, e.g., where, when and under what conditions they have most significant impact on phytoplankton growth and composition. It is clear that grazing is an important top-down control on phytoplankton, and more in-depth studies that include the full array of grazers are needed along with how grazing interacts with nutrients (as described above) to determine phytoplankton growth and composition.
- (5) The diversity of Delta habitats needs to be more fully integrated into research plans that seek better understanding of fate of nutrients and their effects on phytoplankton. The relatively recent expansion of invasive macrophytes as well as on-going restoration of wetlands and floodplains suggest a growing role for these types of environments in nutrient retention, transformation, and export in the Delta. Also, macrophyte beds and wetlands in general represent regions where there can be close connectivity among sediments, the anoxic processes and end products they generate, and the overlying water. Therefore, it will become increasingly important to understand how these habitats contribute to nutrient forms and concentrations that influence phytoplankton growth and composition in pelagic regions.
- (6) An integrated understanding of nutrient dynamics and phytoplankton response across multiple spatial scales and diverse landscapes and in the face of emerging climate change demands a much expanded modeling effort. Currently, there is a lack of adequate biogeochemical models that can link with existing hydrological ones. Biogeochemical models can only be improved with an expanded field effort that provides much needed microbial process measurements. More efforts are also required to establish collaborations across agencies, organization of personnel with appropriate modeling and data management expertise, and additional funding to meet modeling goals.

After completion of this report, the authors were asked to suggest studies that exemplify the type of broadened perspective that we are recommending in future Delta research. We cannot provide an exhaustive list, but suggest that Delta scientists begin this process by examining information available for NSF Long Term Ecological Research sites, such as the Plum Island Ecosystems LTER (<https://lternet.edu/sites/pie>) and the Florida Coastal Everglades LTER (<https://lternet.edu/sites/fce>).

These sites do not exactly reproduce the ecological and management challenges of the Delta, but do provide overviews of scientific strategies that might be helpful to Delta researchers as they develop future interdisciplinary, collaborative research.

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APPENDIX 1

The white paper authors received a Charge¹ to guide outcomes of the Nutrients and Phytoplankton workshop (Nov 29-30, 2016) and white paper. Detailed Questions from the Charge document are as follows:

- (1) Can differences in experimental conditions (for example, light levels, temperature, duration of experiment, pH, salinity, grazing, initial experimental conditions, phytoplankton species and genetics, and others) explain different results from different researchers for the ammonia paradox and ecological stoichiometry hypotheses?
- (2) What bench-scale/mesocosm/field experiments would test the ammonia paradox and ecological stoichiometry hypothesis in the Delta and in Suisun Bay? In controlled tests, what are the appropriate and ecologically relevant nutrient concentrations and ratios to use as experimental variables?
- (3) What factors should be considered in the experimental designs:
 - a. What are the appropriate and ecologically relevant temporal scales (hours, days, weeks) at which to evaluate the ammonia paradox and ecological stoichiometry hypotheses in the Delta?
 - b. What is the duration and frequency of occurrence of the time frame where the ammonia paradox is believed to be important?
 - c. What are the appropriate and ecologically relevant nutrient concentrations and ratios to use as experimental variables?
 - d. What modeling or other work should precede the experiments to identify the nutrient concentrations and ratios that will result in situ from management actions underway?
- (4) What nutrient monitoring, special studies, and modeling are recommended to track changes in nutrient levels and phytoplankton responses in the Delta? Note that presenters will be asked to make predictions in their oral presentations based on their understanding of the mechanisms affecting phytoplankton abundance and species composition about how the Delta and Suisun Bay will respond to the expected nutrient state change and to describe experiments to test the predictions. The panel will review and comment on the appropriateness of both the predictions and experimental design.
- (5) What is the range of potential outcomes, regarding biological impacts, of future management in the Delta? In other words, what can reasonably be expected, in terms of phytoplankton abundance, biomass, species, composition, and what are the justifications for those predictions?
- * (6) How does the Delta Estuary fit into the global spectrum of river-dominated estuary systems across multiple parameters? Based on its particular characteristics (e.g., habitat types, morphology, flow/tidal flux/retention time, light/turbidity, seasonal nutrient loads and forms and food web components), what can we anticipate about the Bay-Delta's responses, in comparison with responses to changes in nutrient loads observed in other estuaries?

¹ Charge document is available:

http://www.waterboards.ca.gov/centralvalley/water_issues/delta_water_quality/delta_nutrient_research_plan/science_work_groups/2016_112930_deltanut_wkshp_charge.pdf

- * During a teleconference in January, 2017, Janis Cooke and remaining panel members at that time (A. Ward, H. Paerl, A. Quigg) agreed that a detailed answer to the second part of question #6 was largely beyond the scope of this report. Examples and citations from other estuary systems are included within the report text. Predicting the responses to planned nutrient changes in the Delta is complicated by the difficulty of predicting responses to climate change impacts. Anticipated climate change impacts and potential effects on nutrients and phytoplankton are discussed (pg. 19-22).

Addendum to Delta Nutrient Forms and Ratios Workshop Report

This addendum was prepared by Central Valley Regional Water Quality Control Board staff and the Delta Nutrient Research Plan Stakeholder and Technical Advisory Group (STAG). At its 12 June 2017 meeting, the STAG proposed adding information and references regarding changes resulting from population growth.

Subject: Additional Information Regarding Future Nutrient Loads Entering the Delta

The paper states that “nutrient inputs to the Delta are projected to increase as human population grows in California” (pg. 19). This statement acknowledges that, in general, nutrient inputs to the environment increase with growth of the human population and associated changes in land uses. Absent deliberate actions to manage nutrients, the increasing trend would be expected to continue. To estimate the actual impacts on Delta waterways of predicted human population growth, however, effects of anticipated nutrient management efforts should be considered.

Modeling through 2030 predicts that loads of total nitrogen and total phosphorous to surface waters in the Sacramento and San Joaquin River watersheds would decrease under a scenario that includes population growth and planned nutrient management (Systech, 2011; West Yost Associates, 2011). The estimates were prepared for the Drinking Water Work Group during development of the Central Valley Water Board’s Drinking Water Policy. Modeling of future loads was performed assuming changes in land use and population based on State and city general plan estimates of population growth through 2030 and associated increased in point source discharge volumes and conversion of agricultural land to accommodate population growth (but no other agricultural land use changes). Assumptions of nutrient management under a planned future scenario were: wastewater treatment facility improvements required under current NPDES permits, but not yet implemented; new urban development occurring under implementation of stringent (2010) NPDES regulations for storm water controls; and 2% reduction in loadings of nitrogen, phosphorous, and organic carbon through general management practice implementation by irrigated agriculture.

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