PRIMARY PRODUCTION IN THE SACRAMENTO-SAN JOAQUIN DELTA

A SCIENCE STRATEGY TO QUANTIFY CHANGE AND IDENTIFY FUTURE POTENTIAL

USGS
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DELTA SCIENCE PROGRAM
DELTA STEWARDSHIP COUNCIL

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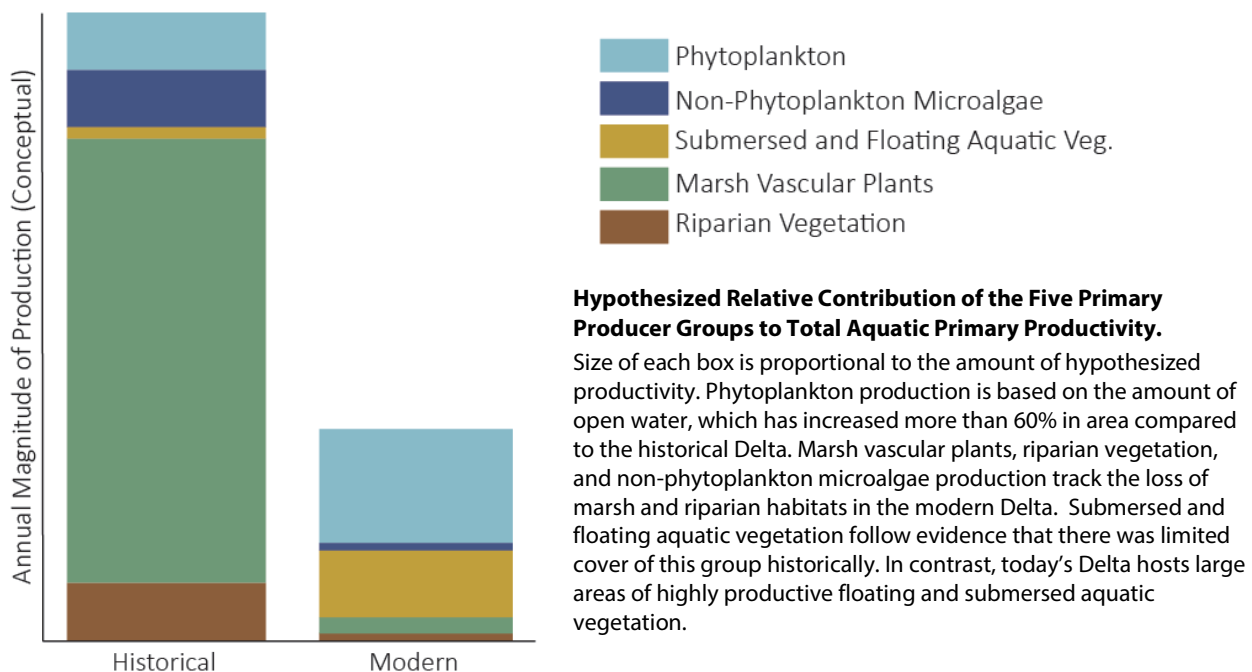Erica Spotswood[1]

Table of Contents

EXECUTIVE SUMMARY

Today's Sacramento-San Joaquin Delta is an unusually low-productivity estuary. The constraints on primary production and the relative importance of different production sources to the food web are major ecological uncertainties in the Delta system. Understanding how the extensive historical changes in the Delta landscape have altered primary production has the potential to inform restoration planning and management across the region.

The Delta Landscapes Project (SFEI-ASC 2014) has recently produced information that allows us, for the first time, to answer questions about historical primary production and carrying capacity from quantified changes in the areal extent and spatial configuration of habitat types in the Delta since the mid-19th century. Our focus is on estimating primary production because the *potential* capacity of ecosystems to support fish, bird and other wildlife populations is set by primary production – the supply of food required to produce animal biomass. Landscape change in the Delta suggests the following two hypotheses:

Hypothesis 1: Landscape change has significantly reduced Delta primary production supporting fish, birds and other wildlife.

The landscape change analysis in *A Delta Transformed* (SFEI-ASC 2014) quantifies the profound transformation of land cover in the Delta, showing that the formerly extensive marshes, floodplains, and woody riparian areas have largely been lost. We hypothesize that the magnitude of primary production available to wildlife has been greatly reduced by this habitat loss, and therefore the capacity of the Delta to support large populations of native wildlife has been reduced proportionally.

Hypothesized Relative Contribution of the Five Primary Producer Groups to Total Aquatic Primary Productivity.

Size of each box is proportional to the amount of hypothesized productivity. Phytoplankton production is based on the amount of open water, which has increased more than 60% in area compared to the historical Delta. Marsh vascular plants, riparian vegetation, and non-phytoplankton microalgae production track the loss of marsh and riparian habitats in the modern Delta. Submersed and floating aquatic vegetation follow evidence that there was limited cover of this group historically. In contrast, today's Delta hosts large areas of highly productive floating and submersed aquatic vegetation.

Hypothesis 2: The Delta has been transformed from an ecosystem largely dependent upon marsh-based production to one dependent upon production by aquatic plants and algae.

While the number of primary producer groups is probably roughly the same, the proportion of their contribution to total primary production has likely shifted. This is important for two reasons. First, the quality and availability of organic matter (OM) to consumers varies across the primary producer groups (e.g., plants vs. algae). Second, if the portfolio of primary production has become less diverse, then resilience of food webs has been reduced by restricting the types of food available to consumers. Thus, shifts in primary producer communities are expected to drive shifts in the relative abundance of consumers that depend on food derived from specific primary producers.

A Science Strategy

This report provides a Science Strategy for testing the above hypotheses by developing an "order-of-magnitude" estimate of primary production and potential carrying capacity for the Sacramento-San Joaquin Delta, both historically (c. 1850) and today.

A Three-Phase Science Strategy for Estimating Delta Primary Production
Phase 1 (this report): Design a strategy and research plan for calculating order-of-magnitude estimates of primary production in the historical and modern Delta. This strategy and a research plan for Phase 2 were developed during a three-day Workshop held in 2015, and are laid out in this document.
Phase 2: Carry out calculations and modeling as outlined in Phase 1. This effort will rely on existing data and will not involve new data collection. Results of this analysis will be published in a peer-reviewed journal and communicated to the local regulatory and scientific community.
Phase 3: Build a multi-year monitoring and modeling program that will address uncertainties and data gaps identified in Phases 1 and 2.

Outputs from this study will inform Delta management in two ways. First, it will measure losses in the Delta's capacity to produce food for its native biota. Resource managers need to know the relative importance of individual stressors on the ecosystem, and this information will provide a quantitative basis for understanding the consequences of landscape change as one component of a multi-stressor problem. Second, results from this study will provide restoration practitioners with a new approach for establishing targets and performance measures based on the ecosystem functions that will be amplified by different restoration actions. Knowledge of which functions have been most lost can be useful for deciding which functions to prioritize for restoration.

Within this report we describe:
- A conceptual model that serves as a roadmap for this project to help us understand the mechanisms of Delta primary production historically and today.
- An approach that will be used in Phase 2 to quantify primary production in the historical and contemporary Delta for each of the following primary producer groups: (1) phytoplankton (suspended microalgae); (2) non-phytoplankton microalgae (growing in/on sediments or on surfaces); (3) vascular plants growing in tidal marshes (e.g. tules); (4) aquatic vascular plants that are rooted or float on the water surface, and associated macroalgae; and (5) riparian plants growing on the edge of waterways which contribute fallen wood and litterfall as a food source for aquatic consumers.
- An approach for estimating the potential energy available (i.e. the bioavailability) to consumers in a common currency for Phase 2 of this project.
- A simple model that would describe exchanges between marsh and channel habitats as a part of Phase 2, as a first attempt to integrate physical transports into our production estimates
- Additional considerations around drivers of changes, physical transports, and consequences for consumers.

CHAPTER 1: INTRODUCTION

Habitat restoration in the Sacramento-San Joaquin Delta is expected to help support the recovery of native biota by re-establishing some of the ecosystem functions lost as a result of landscape change. In this report, we outline a Science Strategy to discover how human transformation of the Delta landscape altered one vital ecosystem function — primary production. California's Sacramento-San Joaquin Delta is a highly altered ecosystem bearing little resemblance to the habitat mosaic, hydrological system, and biological communities that existed in the early 19th century (Whipple et al. 2012). Change in the Delta has taken many forms, including massive-scale landscape transformations, water consumption and diversion, contaminant inputs, and introductions of non-native species. The Delta once supported a rich array of native plant and animal species that contributed to California's exceptional biological diversity (Mooney and Zavaleta 2016), and losses of native plants, mammals, resident and migratory birds, endemic fish and their invertebrate prey are the result of pressure from multiple stressors. Population declines of Delta-dependent species and the emergence of non-native plants and animals were primary motivations for California's 2009 Delta Reform Act (CA Water Code §85054) which established a state goal of "protecting, restoring, and enhancing the Delta ecosystem", as a goal co-equal to water supply reliability.

This goal of ecosystem restoration in the Delta is enormously challenging because of the magnitude and diversity of human stressors that have reduced the carrying capacity of the Delta to support its once abundant communities of native plants, birds, fish and wildlife. Success at meeting California's goal will require actions to reverse or mitigate effects of all such impacts. Making the actions effective requires scientific understanding of the mechanisms through which each stressor caused population losses of native biota. One key element of California's Delta-recovery plan is EcoRestore, which plans to restore 17,500+ acres of floodplain habitat, 3,500 acres of managed wetlands, and 9,000 acres of tidal and sub-tidal habitat within the next 5 years (http://resources.ca.gov/ecorestore/).

Our focus in this report is primary production because the *potential* capacity of ecosystems to support fish, bird and other wildlife populations is set by primary production – the supply of food required to produce animal biomass. Today's Sacramento-San Joaquin Delta is a low-productivity ecosystem. Most primary production is contributed by phytoplankton (Jassby & Cloern 2000) whose photosynthesis supplies about 70 grams of new carbon biomass per square meter per year (Jassby et al. 2002). This ranks Delta phytoplankton production in the lowest 15% of the world's estuaries (Cloern et al. 2014), and low primary production is one constraint on meeting California's goal of restoring and enhancing the Delta ecosystem.

But is low primary production an inherent attribute of the Delta, or is it largely a consequence of landscape change? What was the historical primary production and the associated potential carrying

capacity of the Delta, and how has it changed? Could restoration actions increase carrying capacity, and by how much?

Until recently, ecosystem restoration strategies for the Delta have largely relied on fairly vague "guiding images" (Palmer et al. 2005) that have been derived from mostly qualitative knowledge of the historical Delta. Due to the recent advances in quantifying many aspects of the historical Delta landscape, it is now possible to add a new, quantitative dimension to these guiding images. Specifically, the Delta Landscapes Project (SFEI-ASC 2014) has recently produced information that allows us, for the first time, to answer questions about historical primary production and carrying capacity from quantified changes in the areal extent and spatial configuration of habitat types in the Delta since the mid-19th century. For example, tule-dominated wetlands sustain exceptionally high rates of primary production (Atwater et al. 1976), and their areal coverage has decreased 98% from 193,000 to 4,000 hectares. On the other hand, open water aquatic habitat area has increased 62% from 16,000 to 27,000 hectares (SFEI-ASC 2014).

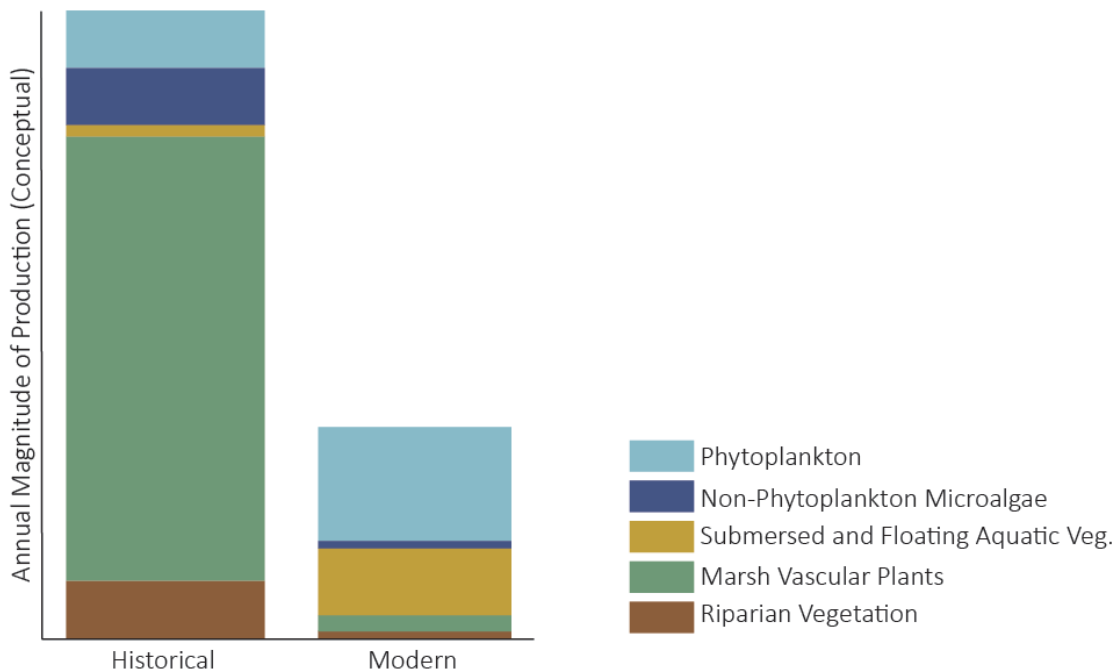These changes over time suggest two hypotheses (Figure 1):

Figure 1. Hypothesized Relative Contribution of the Five Primary Producer Groups to Total Aquatic Primary Productivity. Size of each box is proportional to the amount of hypothesized productivity. Phytoplankton production tracks the amount of open water, which has increased more than 60% in area compared to the historical Delta. Marsh vascular plant, riparian vegetation, and non-phytoplankton microalgae production track the loss of marsh and riparian habitats in the modern Delta. Submerged and floating aquatic vegetation tracks with evidence that there was limited cover of this group historically. In contrast, today's Delta hosts large areas of highly productive floating and submerged aquatic vegetation.

Hypothesis 1: Landscape change has significantly reduced Delta primary production supporting fish, birds and other wildlife.

The landscape change analysis in *A Delta Transformed* (SFEI-ASC 2014) quantifies the profound transformation of land cover in the Delta, showing that the formerly extensive marshes, floodplains, and woody riparian areas have largely been lost. We hypothesize that the magnitude of primary production available to wildlife[1] has been greatly reduced by this habitat loss, and therefore the capacity of the Delta to support large populations of native wildlife has been reduced proportionally.

Hypothesis 2: The Delta has been transformed from an ecosystem largely dependent upon marsh-based production to one dependent upon production by aquatic plants and algae.

While the number of primary producer groups is probably roughly the same, the proportion of their contribution to total primary production has likely shifted. This is important for two reasons. First, the quality and availability of organic matter to consumers varies across the primary producer groups (e.g., plants vs. algae). Second, if the portfolio of primary production has become less diverse, than resilience of food webs has been reduced by restricting the types of food available to consumers. Thus, shifts in primary producer communities are expected to drive shifts in the relative abundance of consumers that depend on food derived from specific primary producers.

In this report, we describe a Science Strategy to test these hypotheses by: (1) estimating annual primary production of five plant and algae groups based on the areal extent of different habitat types in the historical and contemporary Delta, (2) estimating availability of this primary production as a food resource to first-order consumers, and (3) creating a simple two-box model describing transports between marsh and channel habitats.

Results from these studies are expected to reveal how, and by how much, landscape change has affected the energetic carrying capacity of the Delta. This will allow Delta ecosystem restoration efforts, including EcoRestore, to develop much more detailed and explicit restoration visions and goals, measurable and quantitative targets, and more accurate and reliable assessments of likely outcomes.

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1. We do not consider agriculture in our approach for estimating primary production because, at an "order-of-magnitude" scale, most of the agricultural production in the Delta goes towards supporting people rather than wildlife. However, we recognize that agriculture does provide key food resources to some wildlife species in the Delta, particularly waterbirds, which merits further consideration in later stages of this effort (Phase 3).

Summary of Landscape Change in the Delta

The extent, configuration, and diversity of flooded habitats in the Delta have been wholly transformed, affecting the size and location of high productivity habitats such as tidal marshes and shallow-water areas. These areas feature high residency time of water and biota, which are important factors for maintaining food webs that support a diverse array of consumers. Landscape changes that have affected these factors include loss of marsh plain complex, changes in channel type and connectivity, transformation of riparian areas, and the introduction of invasive species. All of these changes have implications not only for the amount of primary production, but also for the relative proportion of primary producers in the Delta today. These landscape changes are summarized briefly here; see *A Delta Transformed* (SFEI-ASC 2014) for more details.

The most striking conversion has been of marsh emergent wetland habitats to terrestrial land uses: 98% of marshes have been converted to agricultural and urban uses (Figure 2). Historical marshes (c. 1850) were composed of a complex matrix of habitat types, including emergent marshes, shrub-scrub wetlands, and ponded areas, formed as floodwaters met the tides. Modern land management has fundamentally altered this landscape by disconnecting floodwaters from wetlands, widening and deepening channels, and diking and draining wetlands. The suite of historical marsh habitats has been largely converted to agricultural land cover, supported by a system of levees and channels that have very different characteristics than the historical land cover. While agricultural landscapes provide wildlife support today, they are not equivalent to the processes and species supported by marsh habitats. These new land cover types support very different forms of primary production than they did historically, converting aquatic primary production in these areas to terrestrial production for human uses.

A major feature of wetland transformation has been the loss of connection between land and water, both daily and seasonally. Despite marsh fragmentation, which increases the edge-to-area ratio, the marsh-edge zone, where exchanges of organic matter occurs, has decreased by more than 72% overall. Along with the dramatic decrease in marsh area, this has meant that opportunities for exchange of water and materials has been dramatically reduced. Coupled with this change has been a reduction in the duration of flooding. This loss of extent and type of flooding reduces the area of potential aquatic primary production in time and space, reducing what is available to consumers in the aquatic food web by restricting when and where they are able to access food.

Changes in Flooding Patterns. In the historical period, the largest area of inundation occurred during the spring months when both the Sacramento and San Joaquin rivers were in flood stage; while the driest part of the year was in the fall when flood stages had diminished and rivers were again confined to low-flow channels. In the contemporary Delta, the largest area of inundation occurs during the winter months when the Yolo Basin floods; while the driest conditions occur in the fall, when the wetted area does not exceed that caused by tidal forcing. Duration, frequency, and depth of flooding has been dramatically reduced in the modern Delta. Based on estimates in the Delta Historical Ecology Investigation and Delta Transformed reports, and on Dayflow model analyses (SFEP 2015), we estimate

that average historical high flooding conditions in marshes and floodplains lasted about 6 months, averaged about three feet in depth, and occurred 40-50% of the years. Comparatively, because of water management, modern flooding events last just a few weeks, are probably shallower than they were historically, and occur in only 20% of years.

Inter-Annual Variability in flooding patterns. During dry years, water was confined mainly to channels and marshes within reach of tidal inundation cycles. Transport of detritus from higher elevation habitats to waterways would be reduced under dry conditions. Even in dry years though, the historical connection of habitats would still have moved detritus and organisms from the upper watersheds into and throughout the Delta more than in modern times (Figure 3; see Appendix A).

During wet years, tidal flooding patterns were augmented by riverine flood events, which activated the movement of sediments, plants, and animals. Higher elevation habitat types such as willow thickets, willow riparian scrub or shrub, and seasonal wetlands became inundated during extreme events, expanding the area, magnitude and diversity of primary production in both tidal and non-tidal/seasonally wetted habitat types. Exchanges among habitat types in the historical Delta would have been much higher than those we see today because habitat connectivity was greater historically.

Channel type and connectivity: Loss of small, dead-end channels. The channel network in today's Delta is much more highly connected, with larger channel sizes than the Delta of the past (see Appendix D). This transformation has included the diking and filling of a formerly extensive network of small, dendritic dead-end sloughs interspersed among the marsh plain; the creation of new, straight conveyance channels which cut off natural meanders; the widening of the lower reaches of some channels combined with the accidental flooding of leveed islands, creating areas of wider and deeper open water; and the filling of smaller floodplain channels along with creation of levees. All of these changes have resulted in a reduction of the diversity of physical habitats available to primary producers, and a much lower residence time of water within the channel network, with implications for algal and planktonic growth within these habitats.

Transformation of riparian processes within large fluvial channels. Riparian land cover in the Delta has been reduced by 60%, and what remains is more fragmented and narrow. The narrow bands now present have a relative lack of structural diversity and lack the microtopography, vegetative structure, and moisture gradients that once characterized riparian zones in the Delta. Many of the hydrologic and geomorphic processes that make riparian areas self-sustaining have been interrupted in today's Delta. The present configuration largely disconnects land from water during flood stages because of the confinement of channels inside levees, reducing the process of cutoff channel formation and attendant formation of slow-moving water habitats. The loss of habitat complexity has meant the attendant loss of shading and structure that supported temperature control and reduction of allochthonous inputs both to the river channels, and also from rivers to downstream areas.

Exotic Species Invasion. Landscape transformation has created opportunities for introduced species to thrive in settings that were formerly absent in the Delta. Invasive species themselves can also transform

habitats, creating a feedback loop whereby they contribute to their own continued growth and spread, and also likely facilitate additional species invasions. Today's Delta hosts 62.5% greater area of open water, with tiny areas of marsh embedded in it, and much of this area is populated with non-native species of clams, floating and aquatic vegetation, and fishes (see Appendix B for more details). This suite of invasive plants and animals takes advantage of the relative abundance of the deeper, open water provided by larger channels and flooded islands. Primary production in these areas is high, and the physical structure provided by the floating and aquatic vegetation hosts epiphytic algae as well as primary consumers within its roots and leaves. The effect of these new species is another major uncertainty in the Delta food web puzzle.

a) Historical

b) Modern

Marsh

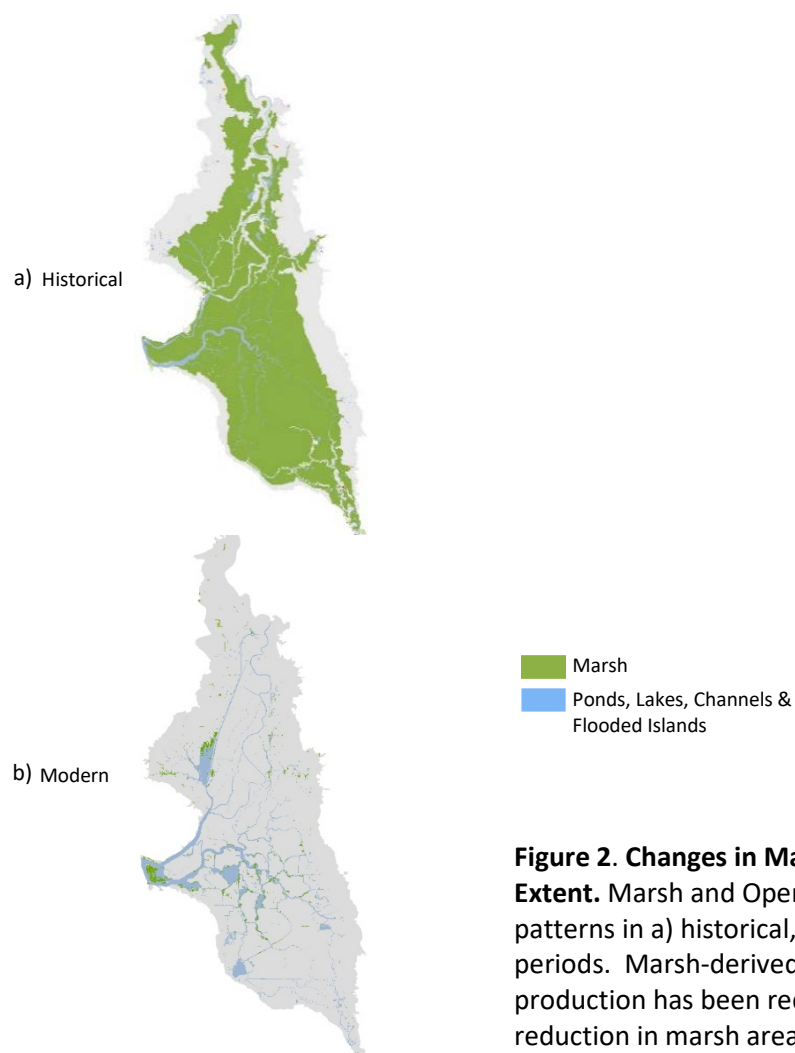Ponds, Lakes, Channels & Flooded Islands

Figure 2. **Changes in Marsh Habitat Extent.** Marsh and Open Water Habitat patterns in a) historical, and b) modern periods. Marsh-derived primary production has been reduced due to reduction in marsh area (Modified from SFEI-ASC 2014).
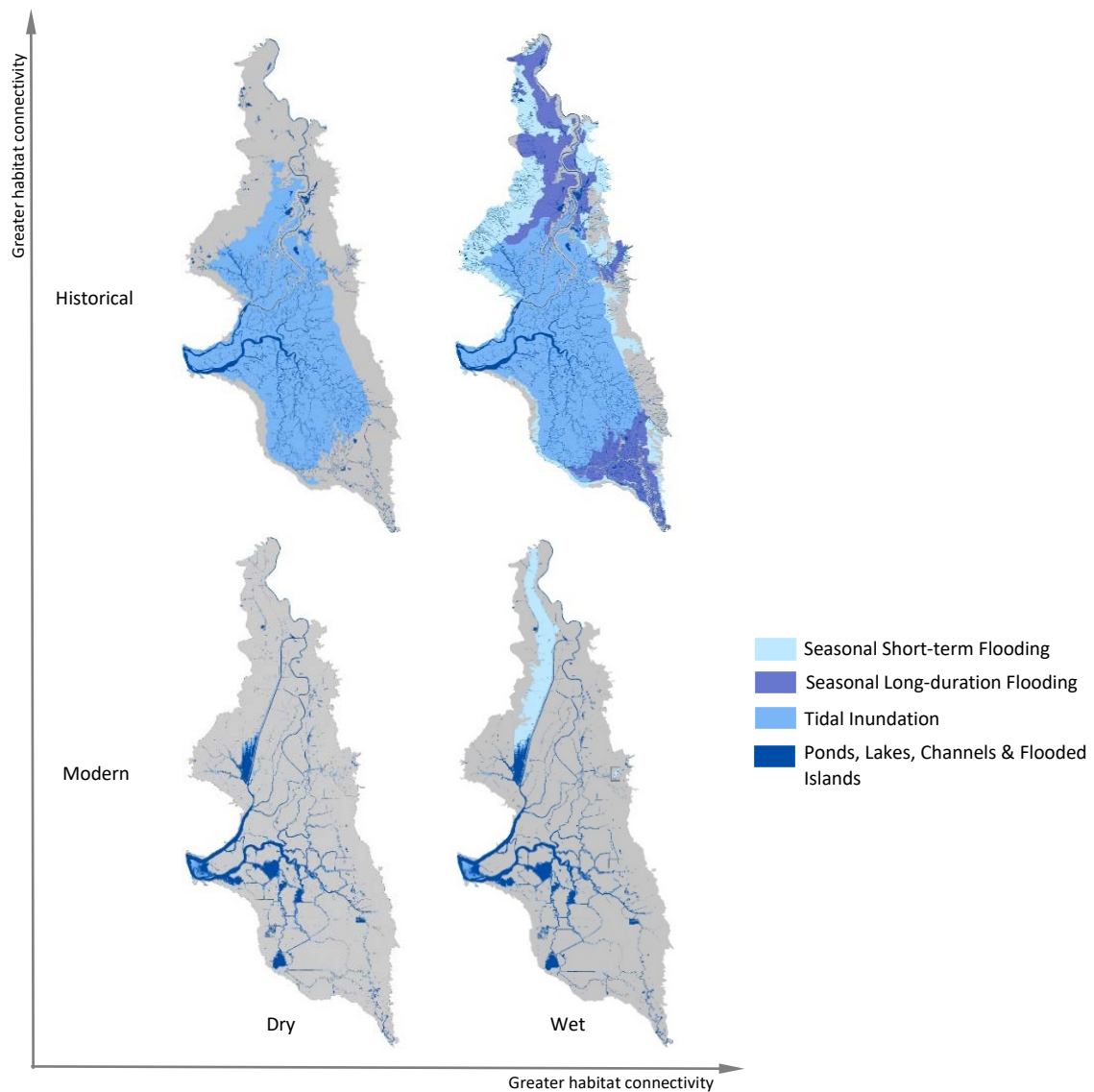
Figure 3. **Changes in Flooding Patterns in the Historical and Modern Delta.**
Inter-annual variability in flooding within the historical and modern Delta during
wet and dry years. Flooding increases connectivity between wetland and open
water habitats (Modified from SFEI-ASC 2014).

CHAPTER 2: A SCIENCE STRATEGY WITH THREE PHASES

This report provides a Science Strategy for developing an "order-of-magnitude" estimate of primary production and potential carrying capacity for the Sacramento-San Joaquin Delta, both historically (c. 1850) and today. This chapter lays out the three-phased approach for this Science Strategy and provides a summary of the project's conceptual model. Chapter 3 describes our approach for generating estimates of primary production for each of the five different primary producer groups identified in this report. Chapters 4 and 5 describe the fate of primary production in terms of biotic transfers through the food web and physical transports through the Delta. Chapter 6 summarizes the near-term next steps for this project.[2]

Science Strategy

An initial key step in the development of the Science Strategy was a three-day Workshop held in October 2015. During the Workshop, an interdisciplinary team of local and national experts discussed a number of issues related to changes in primary production in the Delta and how to quantify them. From this, a Science Strategy with components grouped into three successive phases emerged.

The first component of this Science Strategy is the identification of questions, hypotheses, and study approaches during a research planning phase - Phase 1. The Workshop initiated Phase 1 and this report is the primary Phase 1 product. Workshop participants were asked to develop approaches for estimating primary production, its bioavailability, and transport. An initial conceptual model was developed (see Appendix A), and many caveats and issues were raised at the Workshop, which we capture in Appendix B. This information was then used to further develop the overall science strategy (Phases 2 and 3), including the following research components:

1. Developing a conceptual model of: (a) environmental factors that regulate primary production by marsh, riparian, floating and submersed vascular plants, attached/benthic macroalgae, microalgae and phytoplankton; (b) the role of water transport in regulating primary production and movement of producer biomass across the Delta landscape; and (c) nutritional value and routing paths of producer biomass into food webs supporting fish, bird and other wildlife populations.

2. Identifying data requirements and methods for estimating annual primary production by each producer group, and considering how data gaps could be filled.

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2. Current information from the scientific literature is referenced throughout this report to explain and contextualize our Science Strategy, however this report is not intended to serve as comprehensive literature review of primary production in the Delta.

3. Developing a set of steps to estimate annual production in the historical and contemporary Delta, using habitat areas from the Delta Landscapes Project and comparing annual production in wet vs. dry years.
4. Developing a process for converting annual primary production by each producer group into a common currency as a metric of nutritional value and accessibility to consumers.
5. Designing a two-box model as a first step to learn how tidal and riverine transport influences system primary production and its availability to aquatic consumers. Developing experimental designs that, in conjunction with modeling, would be sufficient for estimating historical and contemporary water and material exchanges between habitats like marsh plains, dendritic channels, distributary channels, and bays.

The intent of Phase 2 is to implement these research components and produce the first quantitative estimates of annual primary production by five producer groups in the historical and contemporary Delta, considering variability between wet and dry years and the variable quality of food produced by the different primary producer groups. Products of Phase 2 will be a scientific article co-authored by workshop participants, and communications of results to interested stakeholders. Phase 2 establishes the foundation for more robust analyses based on new modeling and data collection in Phase 3.

The intent of Phase 3 is to refine the results from Phase 2 and reduce uncertainties arising from key data gaps, assumptions about historical environmental conditions, and the "static" approach used in Phase 1 that does not represent effects of tidal- and seasonal-scale water movements that connect(ed) habitats of the contemporary and historical Delta. The more dynamic approach employed in Phase 3 will revolve around a large scale study that integrates new field measurements with numerical models to refine and deepen our understanding of how Delta primary producers and their support of biological productivity have changed, and to provide more reliable and realistic quantitative estimates.

A Three-Phase Science Strategy for Estimating Delta Primary Production
Phase 1 (this report): Develop a strategy and research plan for calculating order-of-magnitude estimates of primary production in the historical and modern Delta. This strategy and a research plan for Phase 2 were developed during a three-day Workshop held in 2015, and are laid out in this document.
Phase 2: Carry out calculations and modeling as outlined in Phase 1. This effort will rely on existing data and will not involve new data collection. Results of this analysis will be published in a peer-reviewed journal and communicated to the local regulatory and scientific community.
Phase 3: Build a multi-year monitoring and modeling program that will address uncertainties and data gaps identified in Phases 1 and 2.

Conceptual Model

The following conceptual model is a roadmap to help us understand the mechanisms of Delta primary production historically and today. Our objectives were to build a conceptual model that would characterize how energy created from net primary production transfers to consumers, and to understand how this energy is transported among different habitat types in the Delta, historically and today.

We started by characterizing the components and processes of the historical Delta food web:

- Dominant primary producers in five producer groups: phytoplankton, non-phytoplankton microalgae, emergent marsh vegetation, submersed and floating aquatic vegetation, and riparian vegetation
- Primary production rates, and abiotic and biotic factors regulating those rates
- Spatial and temporal distribution of total organic matter production
- Direct and indirect consumption by primary consumers
- Transport of production to, through, and out of the Delta.

Delta food webs are considered at two scales over space and time in the conceptual model: (1) the Delta as a system embedded in a wider landscape, and (2) exchanges among Delta habitat types. The model is presented here in only two figures (Figures 4-5); see Appendix A for a more detailed description of the conceptual model.
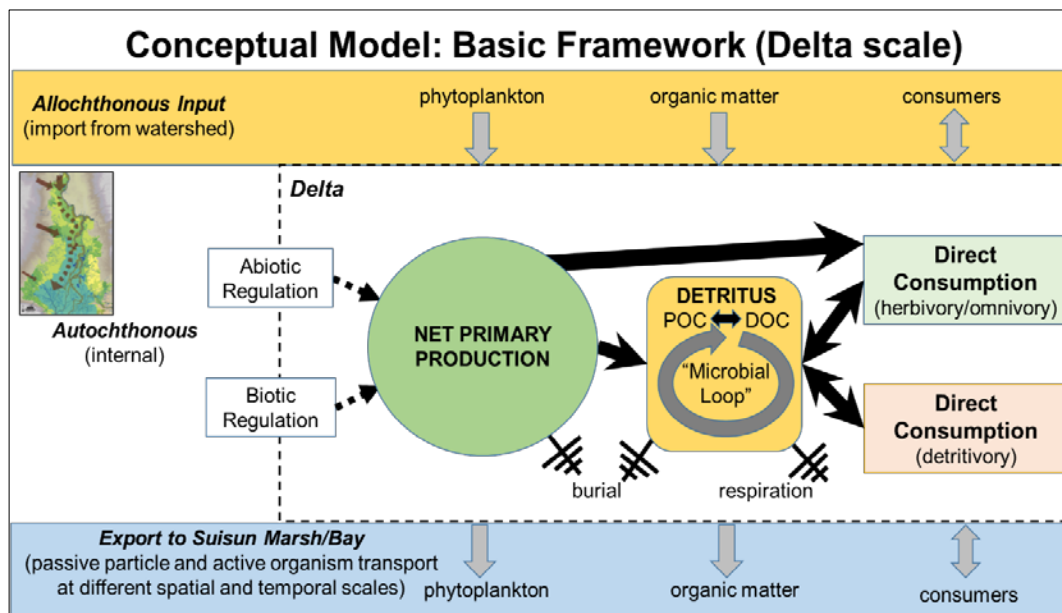

Figure 4. Basic conceptual model framework of primary production at Delta scale.

Allochthonous Inputs. In a system-scale view, living and dead (detrital) organic matter and consumer organisms are imported into the Delta from the surrounding watersheds, and contribute to the total production coming into the system. The primary inputs from the watersheds come in the form of dissolved organic matter, phytoplankton, zooplankton and insects, and detritus. Fishes and many other animals also move into and through the system either passively with flows or actively through migrations.

Internal Production Processes. **(a) Regulating Factors.** Factors regulating net primary production are both abiotic (e.g. light, turbidity, temperature, nutrients, spatial area and volume available to primary producers) and biotic (e.g. biochemical processes, consumption patterns). (**b) Routing of Energy.** Some of the energy primary producers create is consumed in respiration, and all primary producer assemblages, including phytoplankton, lose some proportion of their standing stock to sinking and burial of senescent organic matter in sediments. The remainder is potentially available to consumers, and the simplest pathway for energy to travel in is direct consumption. However, much is routed to the food web through a "microbial loop", in which dead organic matter is utilized by bacteria and fungi that are in turn consumed by flagellates and ciliates.

Exports from the System. Though exports could be derived from our proposed estimate of production within the Delta, it is not within the scope of our assessment to estimate Delta exports of production.
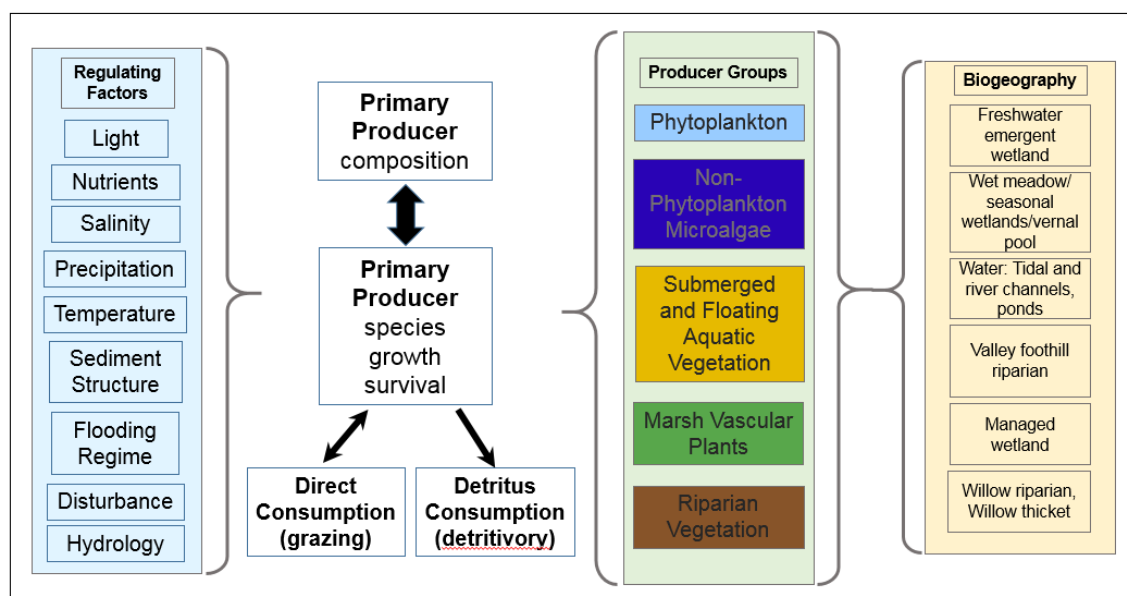

Figure 5. Components and factors regulating the composition, growth, survival and trophic output of different primary producer assemblages occurring in different habitat types.

Factors Affecting the Primary Producer Assemblage. Abiotic factors such as light availability and temperature will affect primary production; these are listed in "Regulating Factors". We expect that abiotic and biotic regulating factors will differ across habitat types, and as a consequence, the producer assemblage will vary in proportion depending on the factors present within each habitat type. For this conceptual model, we adopted the habitat types in the Delta Transformed report (SFEI-ASC 2014), in the "Biogeography" column. Within each of these habitat types, different proportions of primary producers, i.e., "Producer Groups", would be present.

CHAPTER 3: PRIMARY PRODUCER GROUPS

Our conceptual model begins with the identification of five primary producer groups that contribute to Delta-wide primary production: (1) phytoplankton (suspended microalgae); (2) non-phytoplankton microalgae (growing in/on sediments or on surfaces); (3) vascular plants growing in tidal marshes (e.g. tules); (4) aquatic vascular plants that are rooted or float on the water surface, and associated macroalgae; and (5) riparian plants growing on the edge of waterways which contribute fallen wood and litterfall as a food source for aquatic consumers. While many of these groups contain a diverse array of producers within them, the groupings reflect similar habitat associations and fields of study which lend themselves to a common approach for estimating production at a coarse scale.

In this chapter we describe the approach that will be used to quantify primary production in the historical and contemporary Delta for each group in Phase 2. We provide a short description of the relevant habitat types, environmental controls on primary production, how those controls vary in space and over time, the data required as model inputs, and data gaps as a source of uncertainty in model calculations. In these descriptions we try to be transparent about the assumptions and limitations of the proposed Phase 2 calculations so that our estimates can be easily revised as new data becomes available, and as our thinking evolves, in Phase 3.

In Phase 2 we will make four estimates of primary production for each producer group: historical and modern Delta, wet year and dry year. Wet and dry year conditions were discussed in the workshop based on available data from the Delta Landscapes Project. Our approach will be to use estimated extents of flooding to contribute to primary production estimates. Areas for 'wet year' and 'dry year' conditions will be calculated by taking the yearly minimum and maximum extents for wet and dry conditions in historic and modern maps from the Delta Transformed project. We will also characterize the change in frequency of "wet year" conditions, which will allow us to understand the consequences of flooding frequency for primary production over time.

Photo Credit: Sarah Pearce

Phytoplankton

Phytoplankton are microscopic primary producers suspended in water and transported with currents. They are present in all aquatic habitat types – rivers, estuaries, lakes, sloughs, ponds, and inundated flood plains. Phytoplankton photosynthesis is an important, and often the dominant, source of organic matter to fuel metabolism in estuaries. With the exception of cyanobacteria, the common groups (diatoms, dinoflagellates, smaller flagellates) are rich in protein, lipids including essential

Photo credit: James E. Cloern

fatty acids, and are a high-quality food resource for consumers. As a result, fisheries production in estuarine-coastal ecosystems is strongly correlated with annual phytoplankton primary production. Preliminary calculations from a nutrient-phytoplankton-zooplankton model (Cloern 2007), recent data about areal extent of open water habitat, and assumptions of past nutrient loading and turbidity indicate that phytoplankton photosynthesis fixed about 4,000 tons of carbon in the historical Delta annually compared to 23,000 tons produced annually in today's Delta (Jassby et al. 2002).

Controls on phytoplankton in the Delta include:

- Areal extent of open water aquatic habitat, which determines potential primary production
- Sunlight energy as daily incident photosynthetically active solar radiation (PAR)
- Water depth, which is one factor that determines solar radiation available to phytoplankton (Cloern 2007) and, as a result, phytoplankton growth rate (Lopez et al. 2006)
- Turbidity from particle scattering and light absorption by dissolved organic matter, which is the second factor that determines light availability to phytoplankton (Cloern 1987)
- Water temperature that regulates rates of photosynthesis and respiration (Cloern 2007)
- Nutrient (N and P) supplies and concentrations (Jassby et al. 2002)
- Water residence time as determined by tidal and river flows (Jassby 2008)
- Losses to grazers including microzooplankton (e.g. ciliates), mesozooplankton (e.g. copepods), bivalves and other filter feeders (Kimmerer and Thompson 2014)
- Water diversions from today's Delta that export phytoplankton biomass equivalent to 25% of within-Delta primary production (Jassby et al. 2002).

Spatial and temporal variability of the controls

The spatial extent of aquatic habitat (and therefore its contribution to Delta primary production) varies over three important time scales: (1) the 2.4-fold increase in perennial open water habitat since the 1800s (SFEI-ASC 2014), (2) the seasonal expansion of aquatic habitat as flood plains are inundated, and (3) the tidal oscillations that expand/contract the areal extent of aquatic habitat, especially on spring tides. Water depth also changes over these three time scales. For example, mean water depth is higher in the contemporary Delta because of river channelization and loss of tidal sloughs. Nutrient supplies and concentrations are likely much higher in the contemporary Delta compared to the historical Delta. Turbidity has also probably changed, but the direction of change since the 1800s is unknown. Spatial gradients of turbidity between the modern North Delta (high sediments and turbidity) and modern South Delta (low turbidity) impose spatial gradients on phytoplankton photosynthesis.

Approach for estimating production

A standard approach for measuring phytoplankton primary production is to incubate water samples at different depths after additions of C-14 labeled CO_2, and then measuring the assimilation of labeled CO_2 into phytoplankton cells. This method has been applied across the Delta by USGS to develop an empirical model that estimates daily primary productivity from chlorophyll-a, PAR, water depth, and turbidity. The model was applied to a monthly time series of these four quantities measured by the IEP-EMP, yielding estimates of annual phytoplankton primary production at 21 sites across the Delta for the period 1975-1986 (Jassby et al. 2002). Therefore, we have good estimates of phytoplankton primary production in the contemporary Delta (mean~70 g C m^{-2} yr^{-1}), and its annual variability (factor of 5). Since those studies, (Lehman et al. 2007) measured primary production in the Yolo Bypass, so we also have good estimates of the substantial phytoplankton production in that large flood plain when it is inundated.

A grand challenge remains to develop plausible estimates of phytoplankton primary production in the historical Delta. We can compare two different approaches to obtain one measure of uncertainty of historic primary production: (1) use existing empirical models that relate estuarine primary production to key habitat attributes such as water depth, tidal amplitude, turbidity, residence time, and nutrient loading; (2) use the nutrient-phytoplankton-zooplankton model calibrated for the contemporary Delta (Cloern 2007). Implementation of both approaches will require a number of assumptions, some bolder than others. Reasonable first-order assumptions can be made that seasonal patterns of water temperature and solar radiation, and phytoplankton growth- and grazing-rate parameters have not changed significantly since the 1800s. We can test that assumption with model sensitivity analyses. The largest uncertainties will come from unknown nutrient loading and turbidity in the historic Delta, and these knowledge gaps will also yield highly uncertain estimates of historic primary production by submersed vascular plants. We can explore and compare several approaches for estimating historic nutrient loading (e.g., hindcasting trends of N and P concentrations in the Sacramento and San Joaquin rivers, applying empirical relationships between population and nutrient runoff from land) and turbidity (e.g., explore measurements from Delta analogs, apply empirical relationships between turbidity and

depth in different regions of the Delta). Another large uncertainty is in accounting for phytoplankton biomass that is produced as water is transported by tides across marsh surfaces, thus expanding phytoplankton habitat on tidal scales. One possible solution is to develop a simple model for computing this component of production as it varies with tidal cycles of marsh inundation and the diel cycle of solar radiation. See "Exploratory Modeling of Exchanges Across Habitats" in Chapter 5.

Aerial extent of aquatic habitats by depth category, for both wet and dry years, can be calculated from data layers developed for the Delta Transformed Report (SFEI-ASC 2014) and Historical DEM (SFEI-ASC, UC Davis, and RMA, in progress) projects.

Models to Apply in Phase 2

Empirical models of phytoplankton primary production take forms like:

$$P_\mathrm{g} = \psi BI_0 z_\mathrm{p} = 4.61\psi\frac{BI_0}{k}$$

where P_g is daily gross primary productivity (g C m^{-2} d^{-1}), Ψ represents ecosystem-specific photosynthetic efficiency, B is phytoplankton biomass as chlorophyll-*a* concentration, I_o is daily PAR, and k is the light attenuation coefficient (Jassby et al. 2002).

Mechanistic models are usually sets of coupled differential equations, such as these, to compute daily values of nitrogen concentration (N), phytoplankton biomass (P) and zooplankton biomass (Z):

$$\frac{d\mathrm{N}_1}{dt} = \mathrm{NS}_1 + \mathrm{NR}_1 - \mathrm{NU}_1 - C \times (\mathrm{N}_1 - \mathrm{N}_2),$$

$$\frac{d\mathrm{P}_1}{dt} = \mathrm{PG}_1 \times \mathrm{P}_1 - \mathrm{PM} \times \mathrm{P}_1 - \mathrm{GR}_1 - C \times (\mathrm{P}_1 - \mathrm{P}_2),$$

$$\frac{d\mathrm{Z}_1}{dt} = \mathrm{ZG}_1 \times \mathrm{Z}_1 - \mathrm{ZM}_1 - C \times (\mathrm{Z}_1 - \mathrm{Z}_2),$$

Required inputs are initial conditions for N, P and Z plus daily values of PAR, water temperature, turbidity, and water exchange rates between habitats of different depth.

Non-phytoplankton Microalgae

Non-phytoplankton microalgae are a diverse group composed of microscopic unicellular and filamentous algal species (primarily diatoms, cyanobacteria, and chlorophytes) that inhabit a range of aquatic habitats in the Delta. This group of primary producers is a major source of fixed carbon for many aquatic food webs. Microalgae that grow attached to the surfaces of aquatic plants and macroalgae are termed periphyton. Benthic microalgae (also known as
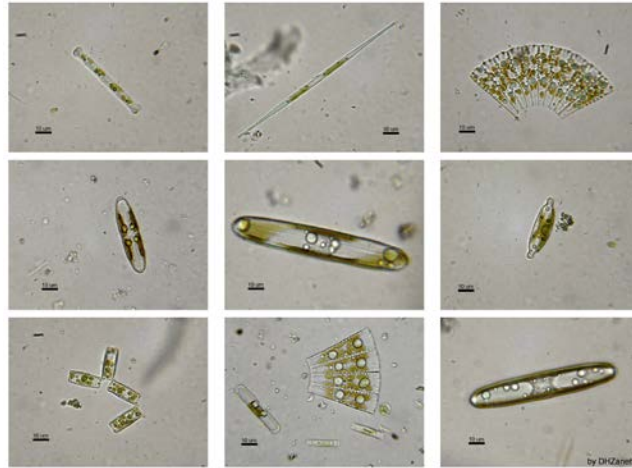

Photo Credit: Damián H. Zanette

microphytobenthos or epipelic microalgae) are found in the upper few millimeters of sediments and may be either motile (epipelic) or attached to individual sand grains (epipsammic). In general, non-phytoplankton microalgae can be found wherever there is sunlight and sufficient moisture to prevent desiccation. This includes subaerially exposed sediments that retain their moisture, plant stems immersed in water, and permanently submerged habitats. In the Delta, the non-phytoplankton microalgae can be categorized into three major groups for estimating the magnitude of primary production: benthic microalgae, epiphytes on emergent wetland vegetation, and epiphytes on submersed/floating aquatic vegetation. The primary change in primary production by this group from the historical to the modern Delta is a reduction in total aquatic area available for habitation.

Controls on non-phytoplankton micro-algae:

The main controls and habitat features important for determining the biomass and primary productivity of the non-phytoplankton primary producer group are:

- Water Level – sufficient water moisture is needed to prevent cell desiccation
- Water Movement – turbulence due to high wave activity or strong currents can dislodge attached epiphytes or resuspend benthic microalgae
- Substrata Types – fixed (stems) vs. mobile (sediments) will determine biomass and community composition
- Temperature – photosynthetic rates will vary with temperature
- Light (quality & quantity) – *in situ* irradiance and available wavelengths determine photosynthetic rates
- Habitat Available (number of stems/plants) – constitutes surface area available for epiphytes
- Nutrient Concentrations – nutrients (primarily N & P) are necessary for growth
- Heterotrophy (grazers) – grazers may remove epiphytes and benthic microalgae

Spatial and temporal variability of the controls on production

The spatial and temporal variability in water levels and the subsequent areal coverage of wet habitat types is a major feature that exhibits an overriding control on non-phytoplankton primary production. Seasonal growth and senescence of emergent aquatic vegetation determines both the areal extent of epiphyte growth (number and condition of stems) and the amount of light available (plant canopy density) for microalgal photosynthesis. Temporal variations in water turbidity determines the ambient irradiance for benthic microalgal and epiphyte productivity.

Approach for estimating production

The approach for a first-order estimate of primary production for the three primary producer groups (benthic microalgae, epiphytes on emergent vegetation, and epiphytes on submersed/floating aquatic vegetation) will rely on a range of areal primary productivity values (g C m^{-2} yr^{-1}) for similar habitat types obtained from published rates in the scientific literature. These rates will be multiplied by the areal estimates for the different habitat types (freshwater emergent wetland, floating/submersed aquatic vegetation, and open water) for the historical and modern conditions.

The data needs for making the primary productivity estimates as described above are mainly accurate measures of the respective habitat areas covered by water during wet and dry conditions for the historical and modern conditions. Areal coverages of submersed / floating aquatic vegetation (SAV/FAV) are also needed for the historical and modern conditions. One major unknown for performing these calculations is an accurate estimate of the areal/spatial distribution and biomass of microalgae in the Delta including the vertical distribution of periphyton biomass on plant stems. There are also no data quantifying seasonal changes in primary productivity and the effects of water turbidity on microalgal photosynthesis. Similarly, there are no data about grazing rates on microalgae, which may be a major determinant of net ecosystem primary production.

A major assumption implicit using the approach above is that the distribution of non-phytoplankton microalgae biomass is homogeneous within each of the habitat types. Biomass distributions are clearly not homogeneous, but it is assumed that averaging over large habitat areas will incorporate this variability. A primary caveat of this approach is the assumption that the literature values for non-phytoplankton microalgae primary productivity reflect values in the Delta region.

Areal rates for primary productivity (g C m^{-2} yr^{-1}) will be multiplied by the estimated areas of the three habitat types (freshwater emergent wetland, floating/submersed aquatic vegetation, and open water) under wet and dry conditions for both historical and present scenarios.

The first-order approximation of non-phytoplankton primary production described above will not employ numerical models. For subsequent Phases (3) of this project, the benthic microalgal production model of Pinckney and Zingmark (1993), which uses a habitat-specific approach, will be modified for *in situ* environmental conditions characteristic of the Delta Region. Epiphyte production on emergent aquatic vegetation will use the model developed by Jackson et al. (2006). Benthic microalgal productivity and biomass measures for Suisun Bay as reported in Cohen et al. (2014) and Guarini et al. (2002) will be used to initialize the models.

Marsh Vascular Plants

Vascular plant communities in tidal freshwater wetlands typically contain a range of grasses, sedges, shrubs, and trees. In the Delta, the relict wetlands are dominated by emergent macrophytes and scrub-shrub communities. The dominant emergent macrophytes include bulrushes (*Schoenoplectus californicus, S. acutus, S. americanus,* and hybrids), cattails (*Typha angustifolia, T. latifolia, T. domingensis,* and hybrids), and common reed (*Phragmites australis*) (Atwater and Hedel 1976; Reed 2002). The scrub-shrub communities mainly contain willow (e.g.,

Photo Credit: Judith Z. Drexler

Salix laseolepis), buttonbush (*Cephalanthus occidentalis*), and dogwood (*Cornus sericea*) (Drexler et al. 2009). In total, the Delta contains ~80 plant species and ~5.4 at the subplot scale (7 m^2) (Atwater and Hedel 1976; Vasey et al. 2012).

The main differences in the vascular plant communities of the historic (intact and undrained) vs. current Delta are (1) the loss of large wetland expanses, which likely contained *several* plant communities across elevational gradients and hydrogeomorphic zones, and (2) the addition of several highly invasive plants to the current Delta such as Himalayan blackberry (*Rubus armeniacus*), perennial pepperweed (*Lepidium latifolium*), and giant cane (*Arundo donax*). Such changes have led to losses in wetland biodiversity, ecosystem function, and habitat quality (Blank and Young 2002; Reynolds and Boyer 2012; SFEI-ASC 2014).

Primary productivity of Delta wetlands has thus far only been measured in marshes (both restored and historic) dominated by emergent macrophytes. The range of aboveground peak live biomass in the Delta spans from ~920 – 2500 g m^{-2} yr^{-1} (Miller and Fujii 2010, 2011; Schile et al. 2014). Belowground peak live biomass ranges from ~900-1800 g m^{-2} yr^{-1} (Miller and Fujii 2010, 2011). The studies by Miller and Fujii were conducted in restored freshwater marshes that were impounded and may differ in productivity from naturally tidal wetlands.

Controls on vascular plant productivity in the Delta include:

- Climate: growing season length, day length/insolation, air temperature, river discharge
- Marsh elevation, water depth
- Water temperature
- Nutrient status (N, P, and K)
- Elevation of the marsh platform
- Hydroperiod
- Salinity range

- Disturbance including floods, drought, insect infestation, and invasive species
- Contaminants including heavy metals, herbicides, pesticides, and fertilizers.

There are few if any reports on how these controls affect plant productivity in the Delta. Due to its mild climate and very long freeze-free period (approximately 296 days based on statistics for nearby Sacramento (Western Regional Climate Center 2014), the Delta has high annual wetland plant productivity. Currently, the major limitation on wetland productivity in the Delta is available land for marsh migration and/or future wetland restoration. The main factors of concern regarding future wetland productivity are sea-level rise, potential impacts from drought, and the continuing spread of invasive species (Reynolds and Boyer 2012; SFEI-ASC 2014; Swanson et al. 2015).

Approach for Estimating Production in the Delta

Although a range of approaches exist for estimating vascular plant productivity, from field-based to remote sensing (e.g., Hawbaker et al. 2009; Miller and Fujii 2010; Byrd et al. 2014), a simple way to obtain an acceptable estimate of productivity is to employ the well-known relationship between vascular plant productivity and marsh plain elevation first applied to smooth cordgrass (*Spartina alterniflora*) by Morris et al. (2002) (Figure 6). In this approach, a parabolic relationship is established from aboveground productivity of local vegetation or aboveground organic matter accumulation rates if no vegetation data are available (Kirwan and Guntenspergen 2012; Swanson et al. 2015).
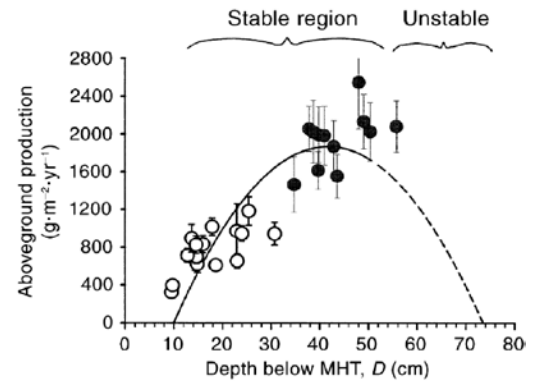

Figure 6. Relationship between vascular plant productivity and marsh plain elevation.

The parabolic equation describing Mo, the annual mass of organic matter accumulated per unit area [$M L^{-2} T^{-1}$], at a given elevation, z, is:

$$Mo(z) = (a + b)(z - MHHW)(z - MLLW)$$

where a and b are constants with units of [$M L^{-4} T^{-1}$] for aboveground and belowground production, respectively, fit to the measured organic matter accumulation rates in the surface layer (0 to 2 cm) of each peat core at the elevation of the marsh surface where the core was collected (Swanson et al. 2015). If actual aboveground productivity values are available, then these can be used in the place of organic matter accumulation rates.

Data requirements

In order to best apply this simple modeling approach using marsh elevations, aboveground plant productivity data are needed. In the Delta, few published above or belowground productivity data are available for naturally tidal wetlands (i.e., un-impounded marshes). However, such data may soon be

published. Therefore, vascular plant productivity could be estimated using either plant productivity data or organic matter accumulation rates as shown above. Clearly, it would be best to use both approaches and see how different the estimates are. Additional data requirements include cover estimates (areas) of current tidal wetland communities in the Delta.

Unknowns

The main unknown for the purpose of estimating wetland plant productivity in the current Delta is the lack of any productivity data for Delta scrub-shrub wetlands. However, there are estimates for willow productivity in the western United States that could possibly be used to estimate the scrub-shrub wetland productivity in the Delta for Phase 2 (e.g., Balian and Naiman 2005; Peinetti et al. 2009). Refining this estimate could be a task for Phase 3, and would require a comparison of riparian willow stands from elsewhere in the West to those of the Delta to see if their basic characteristics (i.e., height, diameter, tree density, and age class) are similar enough to justify their use in estimating Delta scrub-shrub productivity.

Assumptions and caveats

Due to limited data availability, we would need to either (1) estimate the primary productivity of vascular plants in the Delta as being entirely composed of emergent plant communities or (2) use literature values for scrub-shrub communities from elsewhere to approximate the productivity of such communities in the Delta together with known productivity for emergent marsh. Either approach would provide an acceptable first order estimate for comparing the dramatic change in primary productivity between the current and historic Delta.

High priority data and knowledge gaps

The following studies would serve to greatly improve estimates for vascular plant productivity in the Delta:

- Above and below-ground biomass studies in emergent and scrub-shrub wetland communities in the Delta
- Linkage of above studies with remote sensing approaches

The resulting productivity data could be used with newly published carbon gaseous flux data (Hatala et al. 2012; Knox et al. 2015) to run marsh sustainability models such as the Marsh Equilibrium Model (which can now incorporate gaseous fluxes of carbon) in order to determine the future fate of tidal wetlands in the Delta.

Submersed and Floating Aquatic Vegetation

The submersed and floating aquatic vegetation in the Delta includes at least 19 species of vascular plants (reviewed by Boyer and Sutula 2015). There are roughly equal numbers of native and non-native species present. The most common native species include the rooted, canopy-forming sago pondweed (*Stuckenia pectinate*; shown at right), the submersed coontail (*Ceratophyllum demersum)*, and the floating pennywort (*Hydrocotyle umbellata*). Common non-native species include the submersed Brazillian waterweed (*Egeria densa*) and the floating water hyacinth (*Eichhornia crassipes*) and water primrose (*Ludwigia* spp., a mix of *L. hexapetala*, *L. peploides*, and perhaps *L. grandiflora*). In addition, we include

Photo Credit: Katharyn E. Boyer

macroalgae in this overall group of producers, which may be attached to the vascular aquatic macrophytes or to hard substrate, or may be detached as floating mats. In general, aquatic macrophytes are valued for their provision of habitat and food to invertebrates, fish, and birds, although the morphology, stoichiometry, life history, and abundance of each species determine the form and magnitude of its contribution (e.g., Jepson 1905; Meerhoff et al. 2003; Toft et al. 2003; Brown and Michniuk 2007; Schultz and Dibble 2012). Invasion by non-native species is a major change in this producer group between historic and modern periods, and increased prevalence of deeper water likely supports greater production now than in the marsh-dominated system of the past.

Controls on submersed and floating macrophytes in the Delta

(See Anderson 2008 for conceptual model and Boyer and Sutula 2015 for detailed review):

- Solar radiation, which supports photosynthesis of all producers (and can be especially limiting to submersed species such as *Egeria*; Marín et al. 2009)

- Suspended particles (high turbidity), which affect light penetration to submersed species (but which can be removed from suspension by these species, thus enhancing production; Hestir et al. 2015); less important to canopy forming rooted species upon reaching the water surface in spring (e.g., *Stuckenia*) and floating species

- Water depth, which limits distribution of most rooted macrophytes to < 5m (e.g., *Egeria*, Durand 2014); not important for floating species, except in shoreline establishment

- Water residence time: when high, encourages establishment and accumulation of floating and submersed macrophytes locally, but water movement is needed for dispersal

- Water temperature: warmer supports several invaders (up to a point, e.g., 30°C for *Egeria*, Borgnis and Boyer 2015), but freezing reduces abundances (e.g., of water hyacinth, Spencer and Ksander 2005)

- Salinity: freshwater supports many species including several invaders. Salinity intrusion into the Delta favors native *Stuckenia* over introduced *Egeria* (Borgnis and Boyer 2015)

- Nutrient (N and P) supplies and concentrations, although the relative importance of nutrients versus other factors is poorly understood, and several invasive macrophytes have increased greatly in abundance in recent years despite relatively steady nutrient concentrations (Boyer and Sutula 2015)

- Competition among species: e.g., floating species such as water hyacinth shade submersed species such as *Egeria* (Khanna et al. 2012), and green filamentous macroalgae can form heavy mats on *Egeria* and *Stuckenia* (Boyer, pers. obs.), potentially decreasing light or nutrient availability to the vascular plants.

Spatial and temporal variability of the controls

Submersed and floating aquatic vegetation covered roughly 4,400 hectares of the Delta in 2014 (Khanna and Ustin, unpublished data). This included 2880 hectares of submersed vegetation, dominated by *Egeria*, and 1,550 hectares of floating vegetation, composed of roughly half water hyacinth and half *Ludwigia* spp. (and very little native pennywort, which was previously more common). The spatial extent of particular species is determined in part by regional gradients in a number of factors, including salinity (higher in west than east) and turbidity (higher north than south), and local differences in water depth and residence time. Fluctuations in water depth due to tides probably have minimal effects, other than to decrease light penetration to submersed species on the higher tides. Large temporal fluctuations in the areal extent and biomass of this producer group over the past decade are poorly understood.

Remote sensing data indicate submersed vegetation cover ranged from 1,730 to 3,220 ha over the period of 2004-2014, while floating vegetation cover ranged from 310 to 1,550 ha (Khanna and Ustin, unpublished data). Little of this fluctuation Delta-wide appears to relate to control programs that apply herbicides, although there is evidence of local control (Santos et al. 2009; Khanna et al. 2012). Higher salinities in the West and Central Delta in a recent series of drought years may be contributing to expansion of *Stuckenia* in this region (Borgnis and Boyer 2015; Boyer et al. 2015) and increased water clarity (Schoellhamer 2011) is likely improving conditions for submersed species in general. A five-fold increase in cover of floating invaders between remote sensing surveys in 2008 and 2014 may be explained, in part, by a decreased occurrence of frost over the period. How abiotic controls on submersed and floating macrophytes differ in today's Delta compared to historical conditions is uncertain. Nutrient supply is probably greater today than in the historical Delta (see Appendix B), and there may be a greater extent of open water than historically.

Approach for estimating production

Estimating production in the modern Delta could be approached by first using remote sensing and ground-truthing to determine cover of the species that compose the submersed and floating aquatic vegetation, including vascular species and macroalgae. There have been many advances in the remote sensing approach (e.g., Hestir et al. 2008; Santos et al. 2009, 2012; Khanna et al. 2012); however, ground-

truthing is critical to this endeavor, in part because spectral signatures can be obscured (e.g., by green algae attached to *Egeria*) or confused among species (Santos et al. 2012). Once the acreage that each species covers in the Delta is determined, a net production rate for that species (most likely taken from literature values as tons of C/hectare/year) can be multiplied by the acreage, to establish a first order estimate of production for that species for the whole Delta (and then estimates for all species, or at least the dominant ones, would be summed). One caveat: cover estimates have swung so dramatically over the ten years of remote sensing described above that it is difficult to know how representative of "modern" times any one year can be, and thus a range of estimates could be made to encompass this variation.

Estimating production in the historical Delta could begin by determining the acreage of aquatic habitat < 5 m in depth, using maps that have been developed by the San Francisco Estuary Institute. A list of native species currently present, plus any that were known from historic accounts, could be binned by depth to estimate acreage of each, and literature values of production for each species could be used to quantify primary production as described above. Difficulties with this approach include that the relative abundance of species cannot be known with any certainty for the historical Delta. We could use relative abundances of native species from modern times as a proxy, but exactly how present-day competition from invaders, or differences in nutrient concentrations, turbidity, salinity fluctuations, or other factors may have changed relative abundances of native species will be difficult to surmise (with the exception that macroalgae can probably be assumed to have contributed little production historically if nutrient levels were substantially lower). Another caveat is that some species that are considered native today may actually have been very early introductions following European settlement of the region; e.g., *Ludwigia peploides* (P. Baye, pers. comm.). Despite these uncertainties, it is likely that order-of-magnitude calculations of production can be made.

Models to Apply in Phase 2

Simple models to estimate production of aquatic plants typically use a mass-balance approach such that change in standing crop over time (S) is a function of the rate of biomass production through gross photosynthesis (P) and biomass loss due to respiration (R) and plant washout and decay (L): $S = P - R - L$. Models of aquatic plant production typically estimate gross photosynthesis as the sum of net photosynthesis and dark respiration, measured as the rate of change of dissolved oxygen or inorganic carbon in the surrounding water, or the rate of ^{14}C incorporation by the plants (See review by Carr et al. 1997). There have not likely been such estimates for aquatic plants in the Delta, but these measures could be pursued. However, because most of the plants in the Delta (including the natives) have broad distributions, a first pass at estimating Delta-wide production would take the approach described in the previous section, using literature values of production rates combined with acreages of plant cover.

Riparian Vegetation

Riparian vegetation is found in transitional terrestrial/semi-aquatic zones regularly influenced by flowing water; zones extending from stream edges to upland communities. The ecological importance of riparian vegetation in maintaining the structure, productivity and resilience of the adjacent aquatic community is universally accepted. Riparian productivity and diversity are intimately linked to the structure of the physical habitat – a mosaic created and maintained by inherent nutrient, sediment and biogeochemical processes, by seasonally variable energy

Photo Credit: Sarah Pearce

and flow regimes, and by herbivory and other biotic processes. Riparian vegetation is a source of energy for adjoining aquatic systems via transfer of plant litter and riparian arthropods and, as well, modulates the movement of sediments, nutrients and other chemicals from uplands to adjacent waters. Under natural conditions, large animals (e.g., elk, beaver) significantly influence nutrient and energy flows by altering the hydrologic and geomorphic characteristics of riparian zones and by consuming and redistributing energy and nutrients across system boundaries. Connectivity, via the timing and extent of flows as well as movements and types of animals, is a fundamental requirement for maintaining viable riparian vegetation and the many ecological services it provides.

Main Controls on Production (Habitat Features)

- Topography, including microtopography
- Water (flood/drought) and sediment regimes
- Lateral channel migration
- Fire
- Soil characteristics and nutrient supply
- Herbivory
- Invasive species and contaminants

Spatial and Temporal Variability of the Controls (Past and Present)

Historically, riparian vegetation in the Delta covered large continuous corridors along the major rivers and tributaries. Riparian communities differed broadly between the north and south Delta. Riparian gallery forests in the north Delta were composed of oak and sycamore canopies, and an understory of alder, willow, blackberry and other species. This valley foothill riparian cover occupied around 13,560

ha, and willow scrub occupied about 1,210 ha. Riparian forests in the north Delta were characterized by a tree density of about 124.5 stems/ha (Whipple et al. 2012). In south Delta rivers and distributaries, riparian forests established on levees were more mixed in their composition, about 12% (730 ha) were dense areas of willow thicket, underbrush and briars, and around 80% (2,510 ha) were thickly covered mostly with larger oaks (Whipple et al. 2012).

Generally speaking, modern Delta riparian zones have been transformed by land use changes and are comparatively narrow, discontinuous, and dominated by willow and invasive understory plants. Channel cutoff formation and other fluvial processes are now greatly reduced due to artificial levees and water control management and structures. Despite this, riparian forests continue to provide important habitat for a diverse suite of species. Calculations of total woody riparian area for the historical Delta are 17,244 ha, and for the modern Delta are 6,890 ha (SFEI-ASC 2014). This dramatic loss of total area is likely coupled with changes in riparian processes in the Delta. Total riparian productivity may be smaller in proportion to the habitat loss. Changes in species composition from larger oaks and sycamores to mostly smaller willows and scrub species has also likely shifted the quality of the litterfall and dead wood. Thousands of kilometers of riparian zones existed and still exist upstream of the Delta, and we expect there are major OM contributions from these areas during floods.

Approach for Estimating Production

Techniques for estimating organic matter contributions from riparian zones to the Delta depend on whether the focus is on contemporary or historical values, and on whether the litter is primarily leaf fall or large wood. The detailed process used to calculate riparian production will depend on the specifics of the data available, which will be investigated further at the start of Phase 2. Some important considerations are discussed below.

Litter – Contemporary: For Phase 2, the first step would be a comprehensive literature search (e.g., including graduate theses, USDA technical reports) to reveal quantitative measurements from specific locations in the Delta. If information is not forthcoming, a rough estimate from data and equations developed for other riparian systems can be made. For instance, in a large number of temperate biomes where litterfall has been quantified, annual inputs range from ~300 – 600 g C/m^2/yr. The range depends on the age of the riparian community more than the species composition, with average values attained at 50-100 years of age. Total Delta inputs can then be estimated by extrapolating input rates with data on riparian acreage and stand characteristics (e.g., young vs. old). Riparian inputs transported from areas upstream of the Delta can be estimated from data on suspended and bed loads. This information can be refined in Phase 3 with field studies. The total amount of annual litterfall (leaves, needles, small wood) can be quantified by placing litter traps in locations stratified by community type and age (Naiman et al. 2005).

Litter – Historical: Perhaps the best approach is to use modern equations and rates to approximate litterfall (e.g., O'Keefe and Naiman 2006). Total inputs can be estimated by extrapolating input rates with data on riparian acreage and stand characteristics (e.g., young vs. old) in Phase 2. Riparian inputs

transported from areas upstream of the Delta are problematic but in Phase 3, paleo cores from associated wetlands could be investigated and may provide insights on major events.

Wood – Contemporary: Under the best of circumstances, quantitative measures of wood inputs from riparian forests are problematic as they tend to be patchy and unevenly distributed in time. The best approach for Phase 2 may be to estimate inputs from either known meander rates of stream channels (i.e., the meander capturing wood from the adjacent forest) or from known tree mortality schedules (i.e., life history characteristics). There are several techniques used in forestry to establish mortality schedules. Total inputs should be estimated for decadal periods or longer due to their episodic and patchy nature.

Wood – Historical: The extent and condition of riparian zones are poorly quantified for historic conditions but insights on vegetative characteristics and their spatial distribution can be gleaned from analyses of historical ecology (e.g., Whipple et al. 2012). In addition, early snagging programs (e.g., USACE and others) conducted to improve river navigation often kept semi-quantitative records of snags removed from channels. As well, modern paleo and geologic analyses of channel meandering provides insights into historical rates (e.g., Harvey 1989). Total inputs and standing biomass (decadal scale or longer) could be approximated from accounts in historical journals, the areal extent of riparian coverage, extrapolation of data from other regions, and knowledge of tree life history characteristics.

Total Riparian Production = Riparian Area x production factors (litterfall) + production factors (wood)

Additional Considerations

Understanding Plant Life History Strategies: Root storage and litter release of OM and nutrients (e.g., non-native knotweed vs. native species)

Biochemical Composition: Lignin and nitrogen-related processes; quality based on species chemistry

Decomposition Dynamics: Aerobic and burial processes; fresh and saltwater reactions

Data Needs and Availability

The following table summarizes data availability and identifies needed information to calculate estimates of riparian production.

Data	Needed For?	Available Data(Modern)	Available Data (Historical)
Riparian width	Estimating riparian area	Yes, Estimate from Delta Landscapes GIS Layers	Yes (largely anecdotal), Whipple et al. 2012
Riparian length and bank cover	Estimating riparian area and determining patchiness	Yes, Estimate from Delta Landscapes GIS Layers	Yes (largely anecdotal), Whipple et al. 2012
Plant species	Community composition, general structure, and approximating age	Yes, Warner and Hendrix 1984, Katibah 1984	Yes (largely anecdotal), Whipple et al. 2012
Tree diameters	Approximating age and height	Yes, Estimate from other systems? Field investigations	Limited, Whipple et al. 2012
Plant chemistry	Estimating decomposition rates and bioavailability	Yes, Literature search	Yes, can be determined from contemporary tissues
Nutrient availability	Estimating decomposition rates and bioavailability	Yes, Literature search	Yes, can be determined from contemporary tissues
Litterfall	Estimating annual inputs of leaves, needles, small wood	Yes, Literature search, quantitative estimates and reviews of other systems (e.g., O'Keefe and Naiman 2006)	Can be determined from modelling contemporary forest inputs (possibly from Cosumnes River studies)
Woody inputs	Estimating decadal inputs of large wood, snags	Literature search, dynamic river models, USGS and USACE data bases on channel dynamics. Can estimate from channel meander rates, knowledge of riparian vegetation characteristics (species, demographics, longevity).	Can possibly estimate from channel meander rates, knowledge of riparian vegetation characteristics (species, demographics, longevity)
Fire regimes	Estimating patchiness, mortality	Known? Literature search of other systems (e.g., Pettit and Naiman 2007)	Estimate from paleo cores from adjacent wetlands? New research required
Invasive species	Changes in community composition and litter chemistry	Known? Literature search for Delta	Probably very few
Soil characteristics	Determining potential for riparian species and productivity	Yes GIS data layers, USGS	Yes, if one can infer that modern soil maps reflect historical conditions
Contaminants	Artificial limitation of productivity and changes to litter quality	Yes EPA and USDA databases	Probably very few, and limited quantities

Assumptions and Limitations

- Dry/Wet years are approximately equal for litterfall. However, litterfall/OM exchanges may be greater in wet years with more riparian production entering adjacent habitats.

- Litterfall (leaves, needles and small wood) is normally 300-600 g C/m^2/yr; lowest in early successional riparian communities (< 50 yrs old).

- Decadal inputs of woody material can be "accurately" estimated from channel meander rates and riparian forest characteristics (if generally known).

- Inputs transported from riparian communities upstream of the Delta are not estimated.

- Riparian contributions from buried materials exhumed or eroded by channel meandering are not estimated. This may be substantial at specific locations during floods.

High Priority Data and Knowledge Gaps

- Relative contributions of OM from riparian forests as compared to OM contributions from other Delta sources
- Aquatic habitat and productivity losses from removal of dead wood from channels
- Site specific characteristics of riparian vegetation from multiple Delta locations
- Changes in bioavailability of riparian-derived OM caused by widespread invasive species

CHAPTER 4: USE OF PRIMARY PRODUCTION BY CONSUMERS

In this section, we outline an approach for estimating the energy available to primary consumers from the five producer groups that would be carried out in Phase 2. During the Workshop, participants discussed many facets of food web relationships, including biotic transfers through the food web, and the portfolio of food sources consumers eat in the Delta. See Appendix C in which we consider the pathways through which primary

Photo Credit: Sarah Pearce

production could be routed through the food web, and provide a more detailed discussion of primary consumption, including a discussion of possibilities for future research.

Approach for estimating organic matter contributions: a common currency

Due to differences in food quality, the quantity of organic matter produced does not directly reflect availability to the food web. Calculating total availability requires first translating the biochemical character of available primary producer groups into a common currency for entrance into the food web. We describe here an approach for estimating the potential energy available (i.e. the bioavailability) to consumers in a common currency for Phase 2 of this project. Both caloric content (kcal) and g C m^{-2} yr^{-1} are acceptable currencies and will be calculated. Phase 2 will examine four scenarios: Historical (wet and dry years) and contemporary (wet and dry years). For each scenario, we will use the production estimate for each producer group (20 total estimates), and determine the caloric value of each group based on literature values. In order to do this, we will determine the biochemical character for each of the five producer groups, then translate the composition into a common currency. This value will be multiplied by the fraction of total biomass for each group that enters into the detrital pool (e.g., ~45% for emergent marsh macrophytes), and by trophic transfer efficiency rates for each source and scenario.

The diagram below (Figure 7) outlines the process by which we propose to translate producer biomass to amount of available food to the aquatic food web. This effort will involve reviewing the literature on the biochemical composition of different primary producers and (in Phase 3) making measurements where gaps exist (see boxes 1-3 in Figure 7). For Phase 2, information about the caloric value of different biochemicals in our five producer groups will be obtained from the literature.

Estimating Trophic Transfer Efficiencies

The last step in estimating the energy provided by primary producers to the food web is to apply trophic transfer efficiencies to their estimated caloric value (see last two boxes in Figure 7). In general, algal sources are more labile than macrophytes and, as a result, can be more readily assimilated. Algal sources are generally consumed directly by grazers with a trophic transfer efficiency between 15-30% (Likens 2010). Macrophytes exhibit lower trophic transfer efficiencies (~10%), and must first enter the detrital pool for microbial and fungal conditioning before becoming available to macroconsumers. Only a fraction of macrophyte production enters the detrital pool (~47%) (Sherwood et al. 1990). Of that fraction, only ~10% is considered labile. Bacterial biomass has a low C:N ratio (~3 to 5); as a result, terrestrial organic matter tends to gain nitrogen during decomposition as lignins and polysaccharides are degraded and leave behind microbial metabolites and remains (Burdige 2008). This so-called "bacterial conditioning" of detritus is thought to increase the lability of the detrital pool (Sosik and Simenstad 2013). Primary production also contributes to the dissolved OM pool in the form of leachates from phytoplankton and macrophytes. Roughly 10-15% of the DOC pool in the Delta is considered bioavailable (Stepanauskas et al. 2005; Sobczak et al. 2002) while 20-30% of particulate organic carbon (POC) is bioavailable (Sobscak et al. 2002). These estimates from the literature will be applied to the caloric estimates for each primary producer group to determine the amount of energy available to the food web.
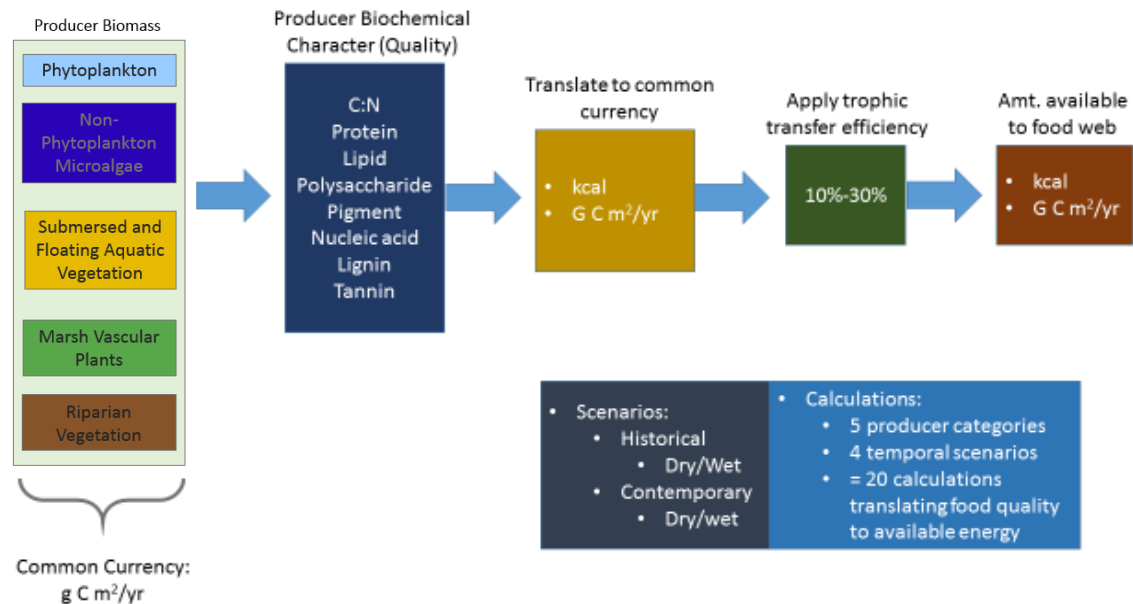

Figure 7. Process for Estimating Bioavailability and Trophic Transfer Efficiencies for 5 Producer Groups.

Estimating What Consumers Eat

The method for estimating the routing of OM sources through the food web as described above is a bottom-up approach based on empirical rates of (1) primary production, (2) consumption of primary producers by consumers (direct consumption and detrital pathway), and (3) assimilation efficiencies between trophic levels.

An alternative method for estimating food web pathways would be a top down approach using geochemical biomarkers. While this approach would not be possible in Phase 2 of this project it is presented here for contrast with the approach outlined above. Using stable isotopes of carbon, nitrogen, and sulfur, in combination with Bayesian stable isotope mixing models (Ward et al. 2010), it is possible to trace food web linkages between primary producers and consumers. These techniques allow us to estimate the proportional contribution of different organic matter sources to consumer diets. In this way, we can unravel which primary producer ecosystem components of the Delta constitute food web support for different types of consumers. This top-down approach for quantitatively estimating food web routing is an effective means of partitioning specific types of food web support among ecosystem components.

Once we know the proportional contribution of different OM sources to consumers, we can use a budgeting approach to translate OM sources into the biomass they support for upper trophic level organisms such as fish. First, a fairly simple calculation multiplying the biomass of sampled organisms (e.g., 7,500 g of a specific fish taxa at Liberty Island) by the mean percent contribution of each OM group (e.g., phytoplankton, SAV, emergent marsh vegetation), provides an estimate of the amount of biomass supported by particular OM sources in particular locations. Ideally, we would obtain biomass density estimates at the Delta scale for different consumer groups (i.e., zooplankton, amphipods, fish) under flood and normal conditions, allowing us to understand the level of biomass change that results from increasing inundation of floodplains such as the Yolo Bypass. We can also apply the same methodology to the historical Delta, which will present increased area for invertebrate and fish habitat. In the absence of fish and invertebrate surveys from the 1850s, we will use scaling relationships between consumer density and habitat areas to address historical density conditions.

CHAPTER 5: PHYSICAL TRANSPORT

In Phase 2 of this Science Strategy we plan to estimate primary production in a way that considers habitat types in a "static" way, not accounting for fluxes between wetland and aquatic areas or local transports between different areas of the Delta. While this is a necessary simplification for Phase 2, it ignores many key processes that affect both the magnitude and fate of primary production. These key components of physical transport could potentially be incorporated into more detailed integrative models in Phase 3, and are discussed in more detail in Appendix D.

As a first attempt to integrate physical transports into our production estimates, we outline a simple model that would describe exchanges between marsh and channel habitats as a part of Phase 2. The simple model can help us quantify abiotic factors affecting primary production such as sediment and light dynamics. This model will help address uncertainties in the Delta system around the relationship between marsh and channel habitats in food web processes (e.g., Do marshes provide food subsidies to channels? Are marshes food sinks or sources depending on tides and morphology? Does the majority of marsh production's contribution to the food web consist of mobile organisms visiting the marsh during certain life stages, then transferring to channel habitats?). Lessons learned from this simple model can be applied to more complex integrative modeling in Phase 3.

Exploratory Modeling of Exchanges Across Habitats

Consideration of transport between habitat types is needed to answer basic questions such as how marsh habitat alters pelagic habitat in the historic and modern Deltas. In Phase 2, each habitat type will be considered in isolation, with the exception of a numerical experiment, described here, where channel phytoplankton are tidally transported to the marsh surface where their production changes due to shallower depth.

In Phase 2 we will use a simple two box model of a marsh and channel and the Cloern (2007) pelagic nutrient-phytoplankton-zooplankton (NPZ) model to investigate how transport between habitats affects production. In addition to pelagic phytoplankton spending some time on the marsh plain, the marsh can act as a source or sink for heat, suspended particulate matter (SPM), N, P, and zooplankton (Z) which determine phytoplankton primary production. For formerly independent variables SPM and heat, introducing the marsh as a source or sink requires at least one additional source or sink to prevent unrealistic values. An example hypothesis to test is that greater marsh habitat in the historical delta trapped more sediment, thus clearing delta waters and increasing phytoplankton primary production. To test this hypothesis, the following would be needed in a two box model for both historical and modern conditions: area and elevation of marsh, channel volume, a time step that discretizes tidal inundation of the marsh plain, tidal elevations, a sediment trapping efficiency of the marsh, assumptions that the marsh and channel are each well-mixed and additional water at high tide has the same SPM as at low tide (Figure D.8). Such a model would eventually completely clear SPM from the channel because there is no input of sediment to the channel. Two examples of adding a realistic source

are either river and Bay input and exchange terms or simulating erosion with a channel equilibrium SPM and accompanying first order rate coefficient need to be added. In general, other constituents, habitats, and primary producers would require a similar model. For many constituents that determine primary production, however, quantification of their behavior in and between different habitats is lacking.
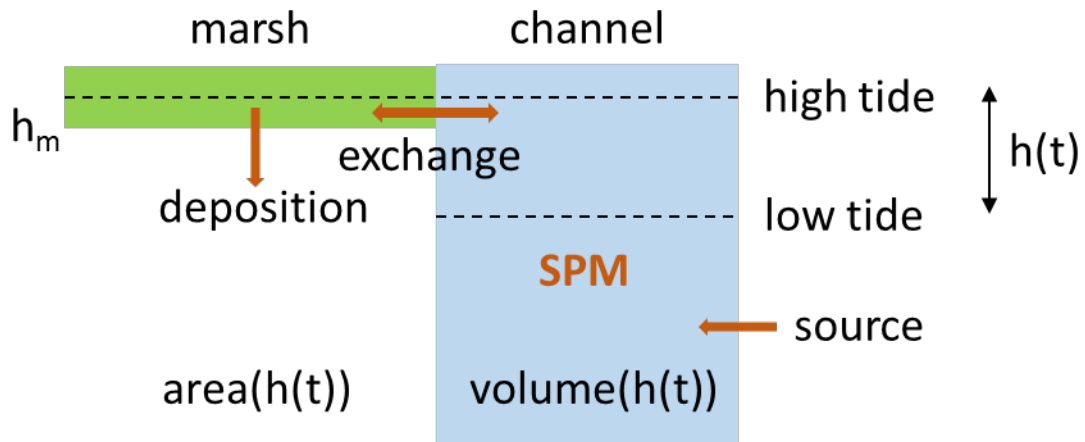

Figure D.8. A two-box model of marsh and channel interaction. h(t) is water level as a function of time t, h_m is the marsh elevation, and SPM is suspended particulate matter.

CHAPTER 6: CONCLUSION

Photo Credit: Amy Richey

Management Implications

Resource managers face a dizzying array of decisions to protect, restore and enhance the Delta ecosystem. Those decisions address contaminant inputs, freshwater inflow, water exports, sewage treatment, the introduction and spread of invasive species, and strategies of habitat restoration. The Delta Stewardship Council (DSC) recognizes that strategies to meet goals of the Delta Reform Act must be strongly grounded in scientific understanding of the Delta ecosystem. The Delta Science Program has identified 17 science action areas to address critical knowledge gaps (DSC 2014). The study plan developed here addresses two of those priority science action areas: habitat restoration and lower aquatic food webs. The Delta Plan (DSC 2012) includes restoration targets expressed as area of habitat types to expand such as floodplain, tidal and subtidal, emergent wetland, and riparian forest. The biological outcomes of these restoration actions are uncertain, partly because the ecological *functions* provided by each habitat type have not been quantified.

We present a strategy for estimating how the life-sustaining *function* of primary production has changed across the altered habitat mosaics of the Delta. Outputs from this study will inform Delta management in two ways. First, it will measure losses in the Delta's capacity to produce food for its native biota. Resource managers need to know the relative importance of individual stressors on the

ecosystem, and this information will provide a quantitative basis for understanding the consequences of landscape change as one component of a multi-stressor problem. Second, results from this study will provide restoration practitioners a new approach for establishing targets and performance measures based on the ecosystem functions that will be amplified by different restoration actions. Knowledge of which functions have been most lost can be useful for deciding which functions to prioritize for restoration.

The Science Strategy for Phase 2, described in this report, will provide us for the first time with first-order estimates of Delta primary production. This is an important first step in understanding the food web dynamics that form the basis for the Delta's carrying capacity. Many producer groups comprise the total primary production in our system, and this study includes them in a systematic way, providing a perspective beyond phytoplankton-centric version of food web dynamics. Because Phase 2 is an initial effort prior to new data collection and modeling (Phase 3), we will need to make simplifying assumptions about how the system works. Subsequent phases of this project would refine our approach by collecting information about these assumptions, thus adding to our understanding of the Delta ecosystem, and ultimately helping to guide restoration actions in the Delta.

The estimates we generate for Phase 2 will test our hypotheses about the magnitude and relative contribution of primary production among five major producer groups, historically and today, and will provide us with estimates of the energy provided by these various groups. Our conceptual model will help us explore the mechanisms through which primary production is transferred through the food web. We will consider how primary consumers utilize these food resources. And our simple transport model will not only help us answer first-order questions about how exchanges among habitats affect primary production, it will also serve as the first step in creating a more refined transport model that can include more nuanced information in the future.

Information acquired in Phase 2 will help us develop testable hypotheses and design research projects to further understand the spatial and temporal patterns of primary production in the Delta. We envision Phase 3 as a larger research program that will support new data collection and modeling to test the hypotheses and research questions generated from Phase 2.

The proportion of primary production in today's Delta is likely very different from the historical patterns that supported the wildlife and functions we are hoping to restore in the future Delta. By learning more about the proportion of the five groups of Delta primary producers historically, and linking these groups to primary consumers, we can discover key components of the mosaic of habitat types and connectivity that are needed to support desirable consumers. Shifting a portion of agricultural production to wetland/aquatic production is at the heart of many proposed restoration efforts, whose aim is to benefit fish. In Phase 3 of the project we will be able to address the key management questions to help inform restoration projects. Potential questions this effort could inform include:

What do changes in primary production mean for secondary production and higher trophic levels? What primary productivity resources for specific aquatic species have changed or been lost? These questions link primary production to the consumers we are most concerned about in the Delta.

What are the linkages between habitat attributes and responses by important producer and consumer groups? For example, we can use a model to explore which habitat attributes contribute to the types of primary production we are most interested in promoting. The model will explore attributes such as water depth, flows and residence time, salinity, temperature, landscape connectivity and complexity. In other words, with such a model, we can explore the habitat attributes that we can potentially manage.

What approaches can be taken to maximize recovery of lost production and transfer to higher trophic levels? By comparing historical primary production patterns with today's, we can more clearly see how much we have gained, for example dense SAV/FAV beds, and what we have lost, for example marsh-derived production. We can use this information to inform hypotheses about the link between these production types to outcomes for consumers and guide our efforts toward creating or encouraging habitat conditions that favor the outcomes we desire.

Next steps

This section provides a list of science products for Phase 2 and describes possible directions for Phase 3.

Science Products of Phase 2. Phase 2 would provide our first ever estimates of aquatic primary production for the Delta, allowing us to compare historical and contemporary conditions that will also inform where the system can go in the future. The outcome of Phase 2 would be a journal manuscript that includes the following information:

- Production estimates for five producer groups in the historical and modern Delta for wet and dry years
- Calculations of the energy produced by each of these groups that is available to primary consumers in a common currency (bioavailability estimates)
- A two-box transport model that explores the importance of tidal hydrodynamics for transport of primary production between marsh and channel habitats
- Discussion of the implications of these findings for consumers and the carrying capacity of native wildlife in the Delta
- Discussion of how these findings may be relevant to restoration options (see Phase 3 below for more).

Possible Directions for Phase 3. The questions we ask in Phase 3 will be guided in part by the outcomes of Phase 2, and in part by collaborating with other scientists and managers. The goal of Phase 3 is to provide guidance for future science, management, and restoration in the Delta through a targeted research program. Elements of Phase 3 might include:

- Incorporating a more detailed transport model to explore the role of landscape change in carrying capacity

- Developing a multidisciplinary model that explores hypotheses about the mechanisms through which food energy is transferred through the Delta ecosystem. For example, the model could link food web pathways with landscape configuration to explore the implications of increasing historical sources of primary productivity through restoration

- Conducting additional field or laboratory research to fill in knowledge gaps identified in Phases 1 and 2, including characterizing consumer diets using geochemical biomarkers.

Photo Credits: Sarah Pearce

APPENDIX A: FULL CONCEPTUAL MODEL

Introduction

Hindcasting the pre-development biotic production of the Sacramento-San Joaquin Delta presents a multitude of challenges in the absence of empirical data on the disparate production components, the abiotic and biotic factors regulating that production, and a utilitarian understanding of the ecosystem dynamics that once pervaded the Delta's landscape and food web. Developing a conceptual model of the factors regulating and distributing pre-development production into the Delta's, and ultimately the Bay's, food webs is essential to achieving a realistic estimate of how the ecological role of the Delta has changed in the Anthropocene. A conceptual model of the productive capacity of the pre-development Delta is a required precursor to understanding how restoration of different ecosystems and landscapes in the contemporary Delta could achieve renewed ecological benefits in the future. The nexus of this conceptual framework is assembling sufficient scientific understanding of not only the pre-development structure of the Delta, but also how abiotic and biotic regulating factors and ecosystem dynamics are predicted to change under future scenarios of ecosystem restoration and climate change.

The following describes a conceptual model that emerged through the process of assembling and conducting the Delta Primary Production Workshop. Our fundamental objective was to assemble a conceptual framework of the "ecological energetics"—net primary production and trophic pathways to primary consumers—that most likely characterized the foundation of the pre-development Delta food web. The factors that were considered included:

- The ~1,500 km^2 of tidal Dominant primary producer components
- Primary production rates and abiotic factors regulating those rates
- Spatial and temporal distribution of total organic matter production
- Direct and indirect consumption by primary consumers
- Transport of production to, through, and out of the Delta
- Exchanges between habitats.

We subsequently attempted to capture as much detail as possible for the freshwater wetlands and ~111 km^2 of channels in the pre-development Delta (Whipple et al. 2012). And, while it may be derived from our estimate of production within the Delta, it is not within the scope of our assessment to estimate exports to or production within San Francisco Bay.

Primary Production and Transport at the Delta Scale

Accounting for autochthonous production internal to the Delta is best reviewed at two scales: (1) the Delta landscape as a system, including allochthonous watershed inputs; and, (2) among habitat type-

exchanges within the Delta. In a system-scale view, allochthonous living and dead (detrital) organic matter and consumer organisms imported into the Delta from the watershed, contribute to the total autochthonous production (Figure A.1). Suspended phytoplankton and organic matter, as well as some consumers such as planktonic zooplankton and neustonic insects, are the primary inputs to and from the Delta. The total amount of detrital organic matter entering the contemporary Delta from surrounding watersheds is not a trivial source to the food web, and is considerably greater from the Sacramento and its tributaries (e.g., 39,000±12,000 Mg year^{-1} DOC) than from the San Joaquin watershed (9,000±5,000 Mg year^{-1} DOC) (Chow et al. 2007); Jassby and Cloern (2000) estimated input from Sacramento tributaries to be 270±50 Mg day^{-1} TOC including phytoplankton. Some consumer organisms also move passively into the Delta (from fluvial inflow and with tidal transport) or actively move across both ecotones, such as anadromous fishes. Although they do not contribute directly to primary production, nutrient inputs from watersheds (specifically nitrogen, phosphorus and silica) and suspended sediments strongly influence several factors that regulate primary production within the Delta, most notably the influence of light on turbidity.
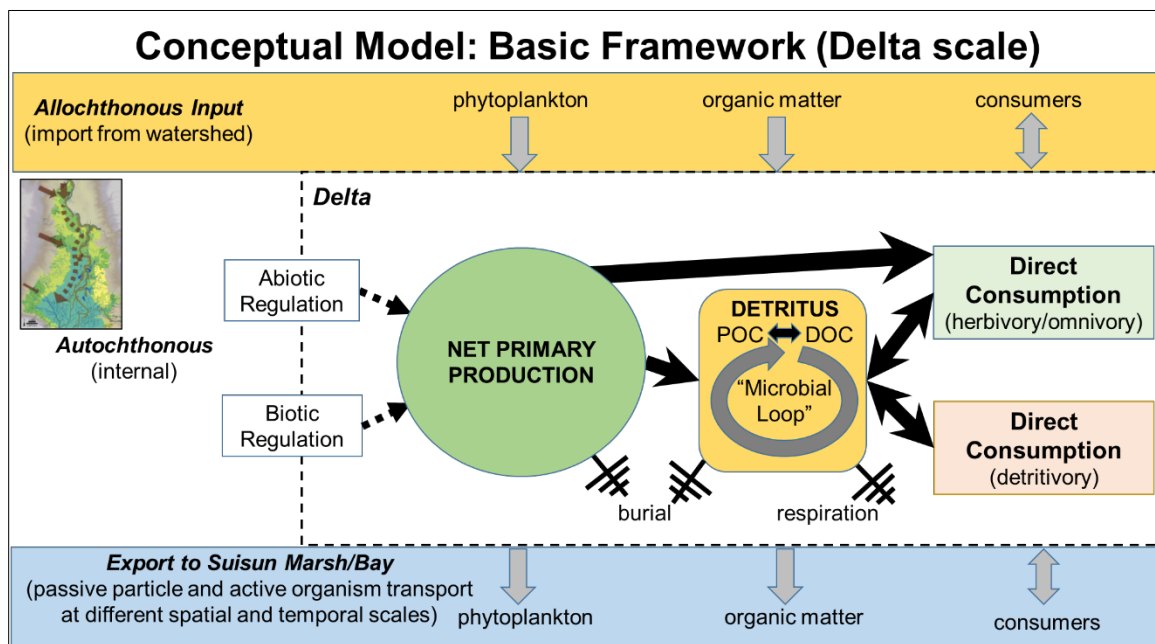

Figure A.1 Basic conceptual model framework of primary production at Delta scale.

In addition to the spatial area or volume available to the different primary producers, factors regulating the rate of production and the standing stock of biomass are both abiotic (such as light, nutrients, temperature, etc.) and biotic (e.g., direct consumption). The relative importance of different factors vary among the five different primary producer assemblages, which includes phytoplankton, emergent marsh macrophytes, submersed and floating aquatic vegetation, riparian vegetation, and benthic and epiphytic microalgae. These producer assemblages are distributed in different proportions among the

various biomes (habitat types) that have been mapped for the pre-development Delta landscape (SFEI-ASC 2014), although the area of a 'mud flat' habitat type is not explicitly mapped and will have to be estimated as a proportion of other habitat types (Figure A.2). For instance, the net primary production rate of phytoplankton is regulated principally by the volume of the water column, light (*vis a vis* turbidity and water depth), temperature and nutrients, and the standing stock as delimited by zooplankton and other suspension feeding invertebrates (especially the non-indigenous clam, *Corbula fluminea*) consumers (see Cloern section on *Phytoplankton*). The net primary production rate of emergent marsh macrophytes (such as the dominant tules, *Schoenoplectus* spp.), on the other hand, is affected less by light variability and more by nutrients and below-ground sediment chemistry, as well as consumptive losses by macrograzers (invertebrates and small herbivorous mammals). All primary producer assemblages, including phytoplankton, lose some proportion of their standing stock to sinking and burial of senescent organic matter in sediments, which has been has been assumed to be 20% in one mass balance calculation for the contemporary Delta (Jassby et al. 2002) but much is routed to the food web through a benthic "microbial loop" (Deming and Baross 1993).
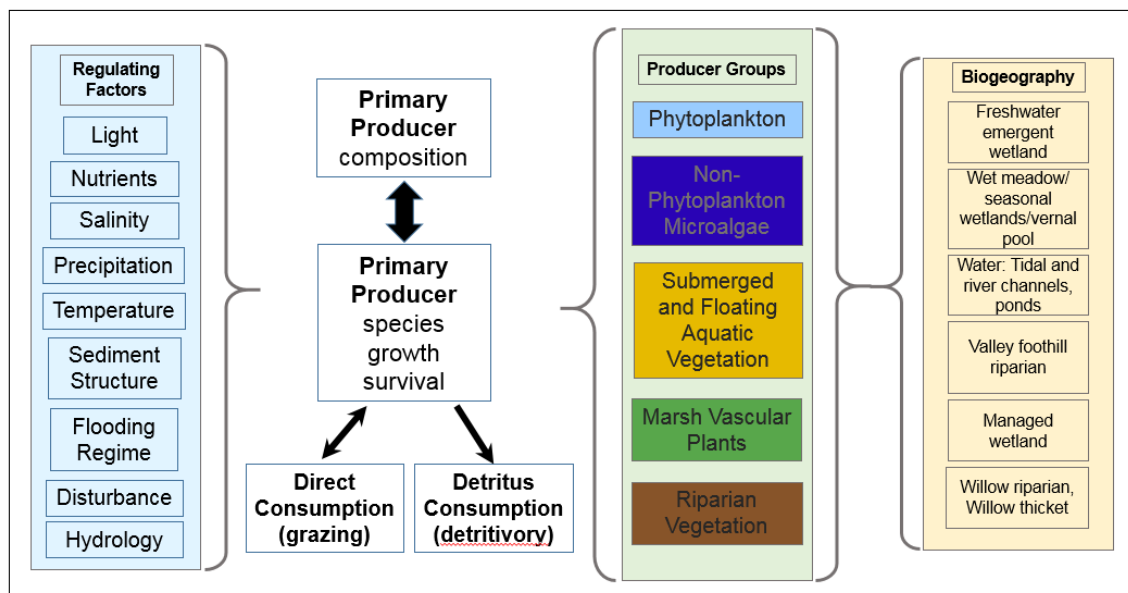

Figure A.2 Basic conceptual model of components and factors regulating the composition, growth, survival and trophic output of different primary producer assemblages occurring in different biomes (Biogeography).

While direct consumption by consumers is the most obvious and more computable pathway of available primary production into the metazoan food web, a potentially large component of net primary production enters the food web through a heterotrophic "microbial loop," the process whereby dead organic matter (POM "detritus") and dissolved organics (DOM) are utilized by bacteria and fungi that are in turn consumed by flagellates and ciliates (Figure A.3). There are complex

feedback processes around and within the microbial loop that supply the organic matter energy source in dissolved and particulate states. Most important may be the often extensive leaching of DOM from rapidly photosynthesizing or senescing primary producers and becomes the energy substrate for both free-living and attached microbes. Organic matter sources "feeding" the microbial loop are both allochthonous DOM and POM of different origins, and internal sources of production with proportions likely varying as a function of habitat type and position in the Delta landscape (see below). Microbial loop processes are confusingly dynamic, with transformations between dissolved and particulate states of organic matter, release of organic matter by microbes, and microbes switching from being attached to particles or free-living. Much of the organic matter processed in the microbial loop is lost through respiration, but microbes are still arguably the primary energy source of most estuarine consumers that feed on detritus albeit with differing nutritional value (Phillips 1984; Shin et al. 2012).
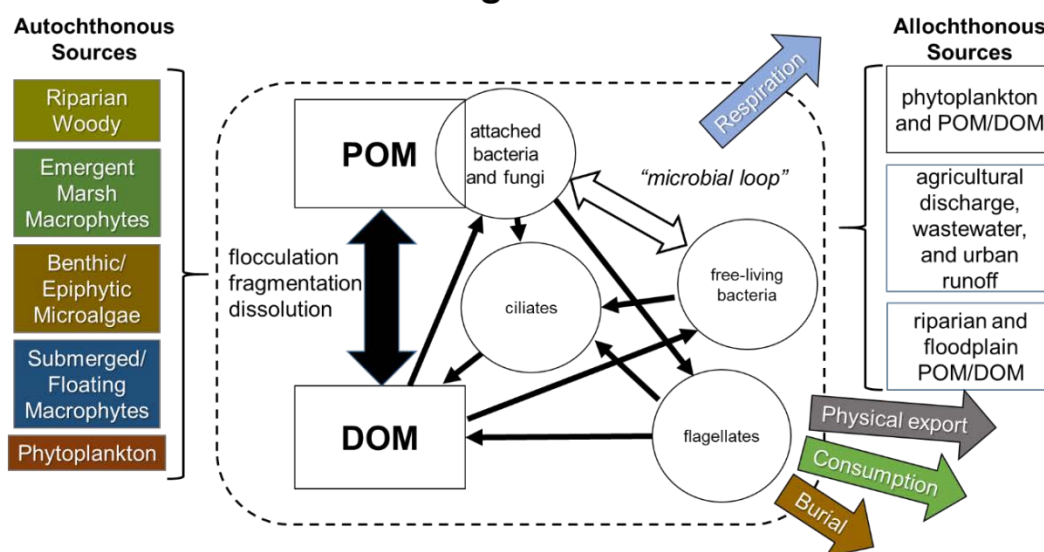

Figure A.3 Basic conceptual model of export and transformation of organic matter to the Delta food web.

The overall allochthonous input and autochthonous production in the Delta will vary over multiple, integrated spatial and temporal scales. During dry years, water volume available for phytoplankton production and exchanges between distributary channels and tidal channel networks in adjacent marsh plains are confined primarily to tidal inundation cycles (Figure A.4). Under these conditions, only the production of marsh plain wetlands and their low-order channel networks are connected on a neap-spring tidal cycle variability. Thus, detritus from primary production generated in other higher elevation features such as riparian forests isolated lakes and ponds, and other seasonal wetlands would seldom be exported to the delta except under minor fluvial flooding. Conversely, lower suspended sediment transport during dry years would produce lower water turbidity, resulting in higher net phytoplankton and benthic/epiphytic microalgae production. Even under dry year conditions, the gradient in habitat types from head of tide to the seaward terminus of the Delta will result in different contributions and channel-marsh plain exchanges of production and detrital organic matter from the valley foothill riparian dominated landscape in up-estuary reaches to the tidal freshwater emergent wetland landscape at the seaward margins.
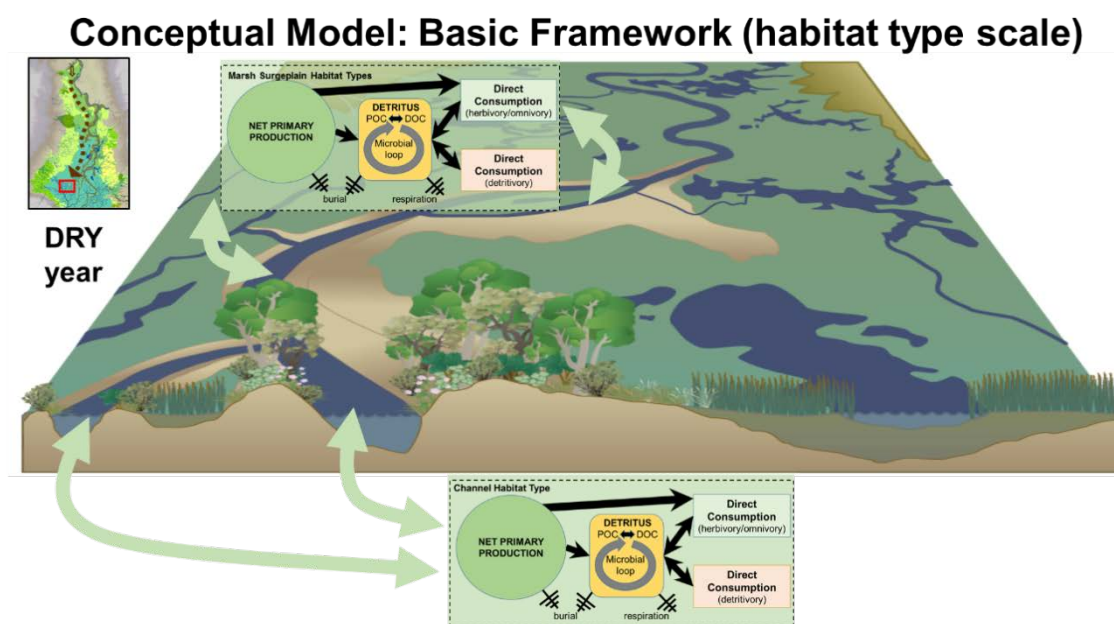

Figure A.4   Basic conceptual model framework of primary production within the Delta at habitat type scale during dry years.

Under wet year conditions, both watershed floodplains and the Delta marsh plains are activated during flood events, and even higher elevation habitat types such as willow thickets, willow riparian scrub or shrub, and grassland may be inundated during extreme events (Figure A.5). Landscape connectivity is increased among all the habitat types across the Delta, exchanges among the marsh plain habitat types and distributary channels is enhanced by combined fluvial and tidal flows, and fluvial contributions from a diversity of tributaries and higher elevation habitat types. Although the habitat types, areas and

elevations will vary considerably under wet year flood conditions, the approximately ~2,450 km^2 of tidal wetlands and channels that contribute primary production and detrital processing to the Delta food web under dry conditions may expand to ~3,500 to ~3,800 km^2 in wet years.

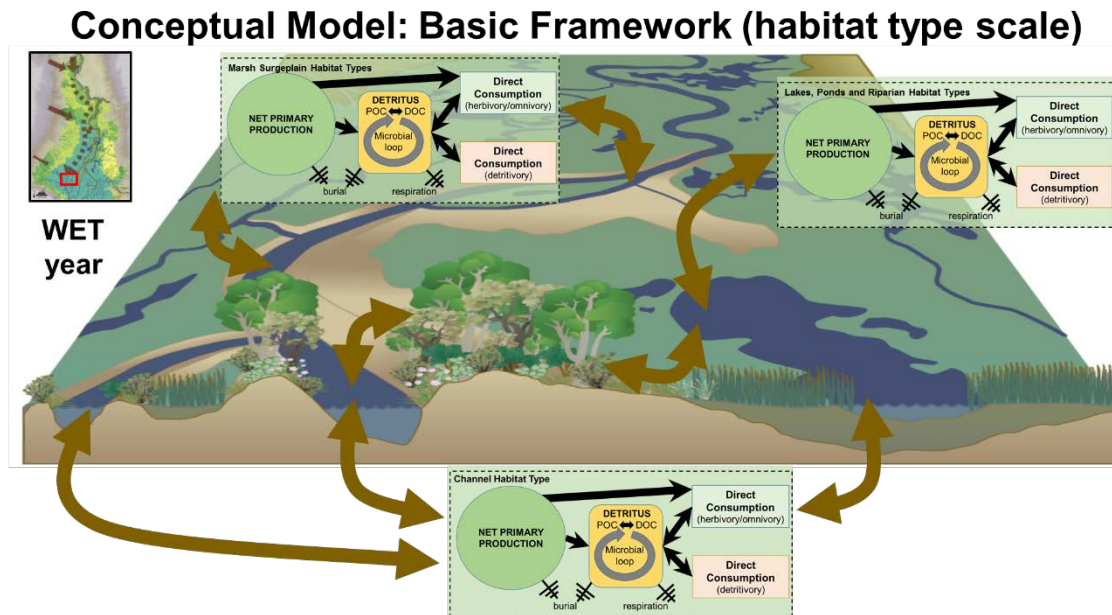## Conceptual Model: Basic Framework (habitat type scale)

Figure A.5   Basic conceptual model framework of primary production within the Delta at habitat type scale during wet years.

While serial discontinuity (Ward and Stanford 1983) across the Delta gradient is diminished in wet years, the effects of pulsed floods (Hitchcock and Mitrovic 2015) expand the moderate effect of regular tidal pulses to periodically inundate floodplains and marsh plains, expanding the area, magnitude and diversity of primary production in both tidal and non-tidal/seasonal habitat-types. This pulsing recharges nutrients and organic matter, increases rates of geochemical cycling within flood plains and marsh plains, and expands exchanges of both production and consumers to distributary channels and progressively through the Delta. Increased fluvial inflow will also modify the factors regulating primary production of many of the primary producers as well; phytoplankton will be particularly modified along several axes, including diminished light from increased water turbidity but increased water volume as well. As the best contemporary example from the Delta, flood inundation of the agriculturally modified Yolo Bypass floodplain has been documented to increase phytoplankton biomass and export downstream to the estuary and enhances zooplankton and fish production (Schemel et al. 2004; Grosholz and Gallo 2006; Opperman 2012; Sommer et al. 2014).

As the different primary producers and their organization among the different habitat types varies spatially along the Delta gradient, their primary productivity rates, accumulated standing stock and availability to consumers, also vary temporally (Figure A.6). While the production of phytoplankton and

most other primary producers is maximal and available for direct consumption in early spring through mid-summer (Jassby and Cloern 2000), the accumulation of detritus sources and their microbial decomposition is protracted through the other seasons. This is hypothesized to increase resilience in estuarine ecosystems by spreading out macrophyte production of detritus and microbial processing, thus ensuring prolonged food supply for consumers (McLusky and Elliott 2012). With tidal and flood pulsing of varying frequency and duration, and the resulting variation in detritus retention time, detritus availability to the Delta food web likely spirals over varying temporal and spatial scales along the estuarine gradient, as conceived for carbon spiraling in rivers (Newbold et al. 1982).
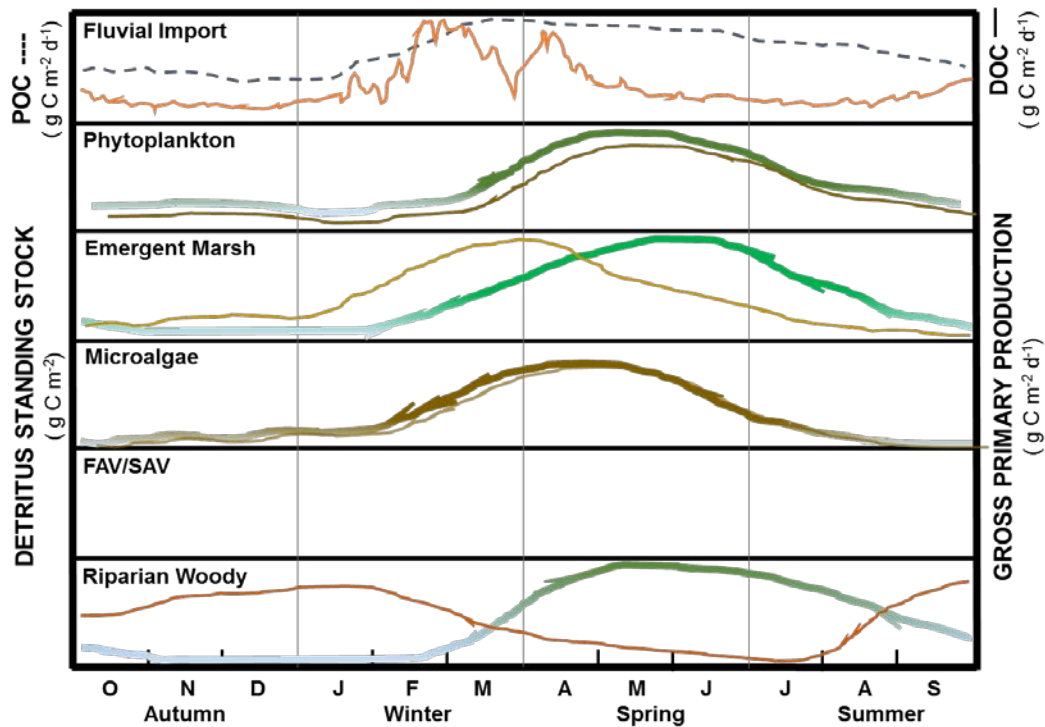

Figure A.6   Conceptual patterns in seasonal availability of primary production sources to Delta food web over the hydrologic year. Thick lines are gross primary production and thin lines are standing crop of detrital organic matter for phytoplankton, emergent marsh, microalgae, FAV/SAV and riparian woody organic matter.

APPENDIX B: CRITICAL DRIVERS CHANGING OVER TIME

Quantifying primary production estimates based on landscape changes is the focus of this Science Strategy, but there are other major drivers of change that influence primary production in the Delta that are not explicitly accounted for in Phase 2. Several important drivers of primary production processes in the Delta were discussed during the Workshop, and short summaries of those drivers are listed below to capture those discussions. These drivers include hydrodynamcis and transport, sediment dynamics, nutrient concentrations, effects of species invasions, multi-decadal tidal trends, reservoir and water operations, and effects of climate change. Incorporating these major drivers will likely be part of Phase 3 of this project.

Sediment Supply

Sediment supply to the Delta from the watershed has been greatly altered since the 1800s by hydraulic mining, dams, land use changes, and channelization (Schoellhamer et al. 2013). Suspended-sediment concentrations in the Delta have also been affected by marsh loss and expanding aquatic vegetation. At present, the hydraulic mining sediment pulse appears to have waned, and floods larger than experienced since hydraulic mining may be needed to exceed geomorphic thresholds and deliver large quantities of sediment. Between large floods are periods of equilibrium. Contemporary measurements of suspended-sediment concentration and turbidity are plentiful while no measurements prior to the Gold Rush exist. The following factors support the hypothesis that the historical Delta received more sediment and was more turbid than the contemporary Delta: the hydraulic mining sediment pulse has waned, dams trap sediment, flood bypasses trap sediment, river meandering is now prevented by levee stabilization, the historical delta had more backwater sloughs which trap sediment and increase turbidity, and aquatic vegetation traps sediment in the modern Delta (Hestir et al. 2013; Morgan-King and Schoellhamer 2013; Schoellhamer et al. 2013; Wright and Schoellhamer 2004). Agriculturalization and marsh loss are factors that would oppose this hypothesis. The time periods for this project are before and after the hydraulic mining sediment pulse, which fortunately eliminates having to consider the dynamics of this disturbance which determined sediment supply from about 1862 to the late 1900s (Moftakhari et al. 2015; Schoellhamer et al. 2013).

Nutrients

Nutrient enrichment reflects another landscape change—agriculturalization and urbanization of the Central Valley—that paralleled landscape transformations of the Delta. Nutrient inputs to the Delta from the Sacramento and San Joaquin Rivers today are high and, as a result, nitrogen and phosphorus rarely limit plant growth and primary productivity (Jassby et al. 2002). Nutrient concentrations in the historical Delta were certainly much smaller and potentially limiting to the growth of aquatic producers,

but we don't know how much smaller because the first measurements of nutrient concentrations were not made until the 20th century. Several different approaches can be taken to estimate historical nutrient concentrations and, from these, primary production across a range of nutrient-limitation scenarios of the past. First, we can use measurements of dissolved inorganic N and P in headwater tributaries of the Sacramento and San Joaquin Rivers (Kratzer et al. 2011) as proxies for nutrient levels in stream waters before they are enriched by agricultural and urban runoff. Second, we can hindcast nutrient concentrations from trajectories of increase measured in the Sacramento and San Joaquin Rivers during the 20th century (Kratzer et al. 2011). Lastly, we can use global measurements of increasing nitrogen and phosphorus yields from lands as crop and livestock production increased the past two centuries (Bouwman et al. 2013). Nutrient loadings are strongly tied to runoff and this is one motivation for comparing annual primary production between wet and dry years.

Invasive species

Invasive species are introduced organisms that disrupt native species and ecosystem functions. In the absence of natural predators or controls on population growth, these species in their novel settings displace native species, and can cause cascading changes to ecosystem structure and function, including impacts at the species, community, and ecosystem levels (Grosholz 2002). Alteration of species composition and function in the primary producer community is likely a key driver of foodweb processes in the modern Delta. The Delta is a highly invaded estuarine system, where most communities are dominated in both numbers and biomass by invasive species (Light et al. 2005). For some producer groups, species invasion may be the dominant driver of changes historically versus today. Two groups are considered here: phytoplankton and floating and submerged aquatic vegetation.

A restructuring of the planktonic food web followed the introduction of the non-native clams (Cloern and Jassby 2012). Filter-feeding by the non-native clams *Corbula fluminea* (Lopez et al., 2006) and *Potamocorbula amurensis* (Alpine & Cloern, 1992) has greatly reduced phytoplankton biomass and production in the Delta. Preliminary calculations with a nutrient-phytoplankton-zooplankton model (Cloern 2007) suggest that annual phytoplankton production in today's Delta would be nearly twice as high (~ 40,000 tons C) if these alien species had not been introduced.

Major shifts in species composition and ecosystem function are associated with invasions of floating and submerged aquatic macrophytes in the Delta (Hestir et al. 2008, 2015). About 12% of the surface area of the Delta is covered by invasive submersed and floating aquatic vegetation in the summer months, and these species can act as ecosystem engineers by reducing local water velocities and providing new substrates for additional spread of other submersed and floating species (Santos et al 2009). These invasive plants compete with native plants, alter water quality, and cause problems for recreation and aquaculture (Santos 2009; see review by Boyer and Sutula 2015).

Landscape changes affecting hydrodynamic processes

Landscape transformation in the Delta as a result of agricultural 'reclamation' changed the hydrology of the Delta in at least three fundamental ways: (1) levees now limit exchange between habitats, (2) channel networks are structured differently, and (3) flooded islands have been created.

Levees were constructed that isolated pelagic from terrestrial habitats. Historically, tidal exchanges into and out of marshes displayed an extraordinary degree of temporal and spatial heterogeneity over contemporary leveed marshes. Due to spring-neap tidal cycles, coupled with historical Delta geomorphology, it is very likely that pelagic environments throughout the historical Delta must have changed enormously at fortnightly timescales. Pelagic and terrestrial environments were essentially decoupled for 8-10 days during neap tide cycles, then were strongly coupled for a period about 4-6 days during spring tides throughout the entire Delta. The consequences of this periodic fortnightly decoupling/coupling of pelagic and habitats, individually and together, on the biogeochemistry, primary producers and on both the pelagic and marsh plain ecosystems is unknown. However, the implications of small-scale studies suggest a radically different ecosystem existed in the historical Delta compared to the ecosystem that exists today, particularly at the primary producer level.

The Delta's historical dendritic "tree-like" geomorphology was transformed into a web-like system of canals. The transformation of the landscape from a dendritic marsh system into a web of conveyance canals changed the Delta in two fundamental ways: (1) new channels were cut to improve access to farmland and for conveyance, which transformed a patchwork of adjacent nested dead-end channel systems into a highly interconnected web of canals within the range of a single tidal excursion; and (2) the intense spring tide pelagic/terrestrial coupling was abruptly ended.

Flooded islands exist in the contemporary Delta where there were none historically. The geomorphology of the historical open water areas bear little resemblance to the modern day flooded islands. Flooded islands, given their size and depth, create a huge hydrodynamic footprint in the contemporary Delta. For example, Franks Tract dominates the hydrodynamic landscape in the Central Delta. Dispersive mixing from the San Joaquin River through False River into Franks tract is so large that a $25M barrier was installed for 3 months in 2015 to keep salinity intrusion from incapacitating the export facilities in the South Delta. Flooded islands also affect turbidity in various ways. For example, Liberty Island is a source of turbidity all summer long, whereas turbidity in Franks Tract is source of suspended sediment during wind events and a sink otherwise.

Phase Shift in the Tidal Diurnal Cycle

The phase relationship between the diurnal (day/night) cycle and the tidal cycle can be an important ecosystem driver. This consistent seasonal relationship between the phase of the semi-diurnal tide extremes and the diurnal (day/night) cycle is caused by differences in the principal partial (M2) tide

(period of 12.42 h) and the tropical fortnightly cycle (period of 11.45 h). This seasonal scale phase relation between tide extremes and the diurnal cycle changes slowly, by approximately 1.09 days/year, or with a period of 335 years (Malamud-Roam 2000). Thus, ~170 years ago, in the historical Delta, the phase relation between the semi-diurnal tidal extremes and the diurnal cycle would have been completely flip-flopped. There are physical, biochemical, and ecological implications to these cycles.

For example, today, mean higher high water (MHHW) occurs in Suisun Marsh at night, when the summertime sea breeze cools the thin sheet of water advecting over the marsh plain, thus cooling the water temperatures during marsh inundation events. If water is confined to channels during MHHW (as is the case for many of the modern Delta's channels), a drastically reduced surface area is exposed to the air, and the drop in water temperature is correspondingly less (see Appendix D for more details). Because of the phase shift in tidal diurnal cycle, high tides in the historical Suisun Marsh would have flooded over the marsh plain during the day, elevating water temperatures in the marsh and within pelagic habitats during spring tides.

Some modern ecological responses to tidal/diurnal cycles have been quantified. For example, mudflat exposure to sunlight depends on when low tide occurs during the diurnal cycle; Malamud-Roam (2000) found large differences in biochemical process rates on mudflats when the mudflats were exposed to sunlight during low tides. In Mildred Island, Lucas et.al. 2006 found that thermal stratification occurred at slack tide during mid-day on a very warm day, causing conditions conducive to a phytoplankton bloom. Slack water occurring any other diurnal phase would not have produced this physical, then biological response. Night time occurrences of the peak ebb tides during November to January allow out-migrating salmon to move through the system faster by simply seeking refuge during the day (Chapman et.al. 2012; Plumb et.al. 2015) when the peak flood tides occur. It is uncertain how these phase shifts will impact ecological responses in the future.

Reservoirs and changes in water management

Modern addition of reservoirs and basin scale water management changed the hydrology of the Delta. Reservoirs increase dry season low flows but do not reduce peak flood flows in the lower Sacramento River (Singer 2007). They also tend to capture snow runoff, contributing to a shift in the peak flow from May to January-March and a ~10% reduction in the peak (Moftakhari et al. 2013, figure already used).

Water use and exports contribute to a ~35% decrease in freshwater flow since the 1800s (Moftakhari et al. 2015). Four percent of Delta inflow is consumed in the Delta (table already used). Monsen et al. (2007) found that: (1) the reduction of export pumping decreases the proportion of Sacramento- to San Joaquin-derived fresh water in the Central Delta, leading to increases in salinity; (2) Delta Cross Channel gate operations affect salinity in the western Delta and alter the freshwater source distribution in the Central Delta; and (3) the removal of the head of Old River barrier, in autumn, increases the flushing time of the Stockton Ship Channel from days to weeks, contributing to a depletion of dissolved oxygen.

When freshwater inflow is typically low, water exports from the Southern Delta reverse tidally-averaged flows in Old River, Middle River, and parts of the San Joaquin River (Arthur et al. 1996).

Climate change

In the Workshop we discussed climate change primarily with regard to future change. Increasing air and water temperatures, changes in the timing and amount of freshwater inputs from the watershed, and rising sea levels will impact primary producer habitats and growth rates. However, there are many uncertainties around exactly how these factors will influence primary production in the Delta. It is worth noting that changes in climate between 1850 and today have likely also affected primary production in the Delta. These factors should be looked at in more detail in Phase 3.

APPENDIX C: FURTHER CONSIDERATIONS FOR BIOAVAILABILITY AND BIOTIC TRANSFER

Much discussion at the Workshop revolved around the fate of primary production within Delta food webs. The following captures the ideas we discussed during the Workshop and highlights avenues for future research that could be incorporated into Phase 3.

In Chapter 4, we outlined an approach for estimating the energy available to primary consumers from the five producer groups that would be carried out in Phase 2. In this Appendix, we explore the pathways through which primary production could be routed through the food web, and include a discussion of primary consumption. In the first section, we propose hypothetical pathways of energy flowing from the primary producer groups through the Delta food web. We then seek to untangle the relative contribution of the various primary producer groups to aquatic consumers in the Delta food web so we can get a better picture of the portfolio of food resources available historically and in today's Delta.

Trophic Transfers: how energy is routed through the food web

Primary production, whether originating from phytoplankton, benthic algae or vascular plants, is either stored, consumed within local food webs, or translocated through a number of different biological and physical processes (Polis et al. 1996). Much of the production in ecosystems goes to respiration and other metabolic heat losses (Calow 1998). Some production is exported through physical processes (e.g., downstream flows; flushing by tides; seasonal rainstorms; see Appendix D). However, other potentially important mechanisms of translocation involve animal migrations (Polis et al. 1996) or trophic relays in which size- or species-specific predator-prey interactions result in a chain of transfers that moves production across the landscape from shallow to deeper portions of aquatic systems (e.g., Kneib 2000).

Trophic transformations of energy and biomass are inefficient for a number of reasons, including the fact that only a portion of production is consumed with the balance senescing and decomposing, stored via burial (e.g., peat accumulation), or incorporated into the refractory portions of plant cell walls (e.g. lignin). Consumption of the remaining production occurs at considerable energetic cost associated with metabolic processes, which limit the number of transfers (i.e., trophic levels) that can occur in an ecosystem (Pimm 1982). A "10% rule" of ecological (trophic) efficiency—the transfer efficiency from one trophic level to the next—traces its origin to the early work of Lindeman (1942). When detailed energetic information is lacking for a specific ecosystem, 10% ecological efficiency is often used as the

default value. However, subsequent research has shown this figure can vary considerably due to relationships between species- and size-specific food conversion efficiencies (e.g., Kneib and Parker 1991), seasonal changes in species composition (e.g., Winemiller 1996), the effects of consumers feeding at multiple trophic levels (e,g, Persson et al. 1996) and a variety of indirect or cascading effects that occur in food webs (e.g., Abrams et al. 1996). At the extremes, ecological efficiencies range from 1% in some terrestrial food webs to as much as 70% in some marine plankton communities (Calow 1998).

Smaller organisms (e.g., bacteria or micro-plankton) tend to have higher rates of production but are also likely to senesce and die before being consumed, with much of their assimilated energy expended in respiration during their short lifespans. While productivity in such groups may be relatively large, standing stocks available for instantaneous consumption may be relatively low and inaccessible to many larger consumers.

Most of the primary production in semi-terrestrial estuarine systems (e.g., tidal marshes) is not consumed directly by herbivores, but rather enters the food web as detritus (e.g. refractory plant material undergoing decomposition by microbes, including bacteria and fungi). Few large consumers (e.g., fishes) can assimilate much energy from detritus but rather depend on smaller consumers— primarily small crustaceans—to capture the energy and biomass from the decomposition process (microbial loop) before it is respired (Kneib 2003). In terrestrial and semi-terrestrial ecosystems, such as tidal marshes, fungi can be very efficient in capturing production (Newell and Porter 2000), often outcompeting bacteria in the initial stages of decomposition and efficiently (55%) accumulating production that persists long enough to be consumed by macroinvertebrates such as snails and amphipods (Kneib et al. 1997; Graça et al. 2000). A similar scenario may occur in mats of floating wetland vegetation, the roots of which harbor high densities of insects and amphipods that are common in the diets of many fish species (Toft et al. 2003).

Benthic (algal) production can be more efficiently transferred to higher level consumers such as fishes than pelagic (phytoplankton) production in aquatic systems even when ecological efficiencies between primary production and primary consumers are greater in pelagic than benthic pathways. Vander Zanden et al. (2006) found that pelagic production in Castle Lake, California was less efficiently transferred to secondary consumers (fish) than benthic production because much of the phytoplankton production was consumed as detritus by smaller primary consumers (zooplankton) and fish fed primarily (>60%) on larger benthic and terrestrial prey species instead of zooplankton. Consequently, some pathways may be considered nearly dead-ends in the aquatic food webs.

Bioavailability of Primary Production Types

Stable isotope biomarkers indicate that detritus emanating from marsh, riparian, and submersed aquatic macrophytes contributes to consumer diets, as do benthic microalgae, epiphytic algae, and phytoplankton. These sources of food at the base of the aquatic food web reflect different levels of bioavailability due to: (1) the physical presence, structure, and accessibility to each primary producer

type, and, (2) the biochemical composition, and nutritional value of the different sources. In this section, we focus on biochemical bioavailability, which is influenced by both the biochemical composition of the producer and environmental conditions.

Bioavailability is a measure of the amount of organic matter (OM) that can be utilized by microorganisms and consumers at time frames ranging from hours to weeks to months. OM is defined as "labile" when its turnover occurs at timescales of minutes to days, "semilabile" when its turnover occurs on timescales of months to years, and "refractory" at longer turnover times (Carlson 2002). Bioavailability is determined by the intrinsic properties of the OM, including its chemical composition; environmental factors like temperature, light and presence of abiotic sources of nutrients; and interactions among microorganisms in the food web (del Giorgio and Davis 2002). It can be very difficult to tease apart the relative contribution of these intrinsic and extrinsic factors. Bioavailability is often measured in terms of the metabolized fraction of dissolved organic carbon (DOC) and particulate organic carbon (POC) (Sobczak et al 2002).

Biochemical controls on bioavailability

The bioavailability of different primary producers is influenced in part by their biochemical composition, which in turn controls elemental composition and stoichiometry. To some extent, it is possible to distinguish broadly among primary producers (e.g., microalgae vs. vascular plants) based on biochemical ratios. Phytoplankton, for example, are rich in nitrogen (N) due to high proportions of nucleic acids and protein, while woody vegetation is rich in carbon (C) due to high contributions from structural components such as lignin and cellulose (Table C.1). As a result, phytoplankton have low C:N ratios (~7) while vascular plants and woody tissues have considerably higher C:N ratios ($\geq$20).

Mineral nutrients (N and P) are also important components of food quality because relative to carbon, N and P are less available to herbivores in many aquatic and terrestrial ecosystems (Hessen 1992; Elser and Hassett 1994; Sterner et al 1997; Elser et al. 2000). Additionally, a number of specific biochemicals are essential for animals including fatty acids, sterols, amino acids, and proteins (Hassett 2004; Crockett and Hassett 2005; Boechat and Adrian 2005). Many of these biochemicals cannot be biosynthesized by animals and must be obtained from their diets.

Material	Protein	Polysac.	Lipid	Pigment	Nucleic acid	Lignin	Tannin
Bacteria	55-70	3-10	5-20	2-5	20	0	0
Phytoplankton	25-50	5-50	5-20	3-20	20	0	0
Zooplankton	45-70	3-5	5-20	1-5	20	0	0
Vascular plant	2-5	37-55	<3	5-20	<1	15-40	<20
Wood	<1	40-80	<3	0	<1	20-35	<45

Table C.1 Major biochemical compositions by % carbon for common organisms (from Emerson and Hedges, 2008)

Environmental Controls of Bioavailability

For sources of OM production that are not directly consumed, but instead route through the detrital food web, environmental conditions such as light, oxygen, salinity, temperature and nutrient availability also play an important role in influencing the bioavailability of different sources of OM to microbial decomposition, the conditioning phase prior to the detrital food web. OM bioavailability changes as materials are exchanged (sorbed-desorbed) between dissolved and particulate forms, move across different light regimes, and as conditions for different decomposer organisms are altered (Lehmann and Kleber 2015). Salinity, oxygen and nutrient concentrations influence the dominant communities of decomposer microbes as well as the enzymatic capabilities available in the environment (e.g., nitrogen availability to lignin-degrading microorganisms; aerobic vs. anaerobic metabolisms, etc.). Temperature is a "master" environmental variable and influences the rates of these decomposition processes. Because these parameters change temporally (e.g., in response to river flow, which controls inundation and residence time), estimates of bioavailability should include comparison of wet and dry periods.

What Consumers Eat: Estimation of Consumption of Primary Production

Diversity of consumers and food web pathways

The mosaic of ecosystems within the Sacramento-San Joaquin Delta hosts a diversity of aquatic consumers that span the gradient from terrestrial to aquatic systems (Herbold and Moyle 1989). Tidal ecosystems, such as marsh channels, sloughs, and flooded islands, are inhabited by aquatic species, including benthic and epibenthic invertebrates, zooplankton, fishes, muskrats, and birds. In contrast, riparian, marsh plains, and floodplain ecosystems primarily support terrestrial consumers (e.g., insects, shrews, mice, bats, voles, beavers, mink, river otters, and song birds), except under very high flow conditions when these ecosystems and lakes and ponds are activated and utilized by aquatic consumers such as Sacramento splittail and juvenile Chinook salmon (Sommer et al. 2001). Emergent marsh ecosystems play the role of intermediary, hosting primarily aquatic species during high tides and flood conditions, and more terrestrial species during low tides and drought conditions. The emergent marsh ecotone thus integrates aquatic and terrestrial ecosystems within the Delta (Grenier 2004; Robinson et al. 2011).

Within the tidal freshwater portions of the Delta, invertebrate communities likely play a critical role in concentrating and transferring photosynthetic energy from living plants and detritus particles to higher trophic levels. Invertebrate primary consumers are capable of concentrating the nutrient content of their food by 10 to 100 fold, and transforming detrital material into a food source for fish, birds, and other higher order consumers (Ortega-Cisneros and Scharler 2015).

The Delta's invertebrate community represents a wide diversity of life history patterns and feeding guilds, each of which translates energy via a different pathway. Energy can move into the food web via direct grazing (herbivory) or via more indirect detritus processing (detritivory); see Conceptual Model.

Herbivorous organisms directly graze upon phytoplankton, benthic and epiphytic microalgae, aquatic macrophytes, or emergent marsh vegetation. For detritivores, however, decaying organic material is first processed by microbes before entering the detrital food web. Feeding guilds can be used to partition consumers by the way in which they obtain food. Important feeding guilds within invertebrate assemblages include suspension-feeders, deposit feeders, browsers, scavengers, scrapers, collector-gatherers, omnivores and predators.

A Portfolio of Food Resources: An aquatic food web example from the Delta's tidal marsh ecosystems

Emerging-stable-isotope-diet studies of the Delta's fish and invertebrate assemblages suggests that consumers are rarely dependent upon a single food source (Howe and Young in prep). Rather, primary and secondary consumers draw upon a portfolio of energy sources available in vegetated shallow water ecosystems, either by directly consuming a suite of primary producers and detritus, or by consuming a suite of invertebrates which in turn represent different feeding pathways. In a study of consumers in Liberty Island, we used Bayesian mixing models to interpret stable isotope data of both OM sources and consumers, and found that primary consumers were utilizing a variety of food sources, including phytoplankton, emergent marsh detritus, SAV, benthic diatoms, and green filamentous algae (see Figure C.1) in varying proportions. Isotopic studies of fish indicate that the ultimate sources of energy parallel the diets of invertebrate consumers. One of the more striking results from this approach to food web routing is that fish considered to be pelagic zooplanktivores (i.e.,Delta Smelt) were found to derive only 50% of their ultimate diet from phytoplankton.
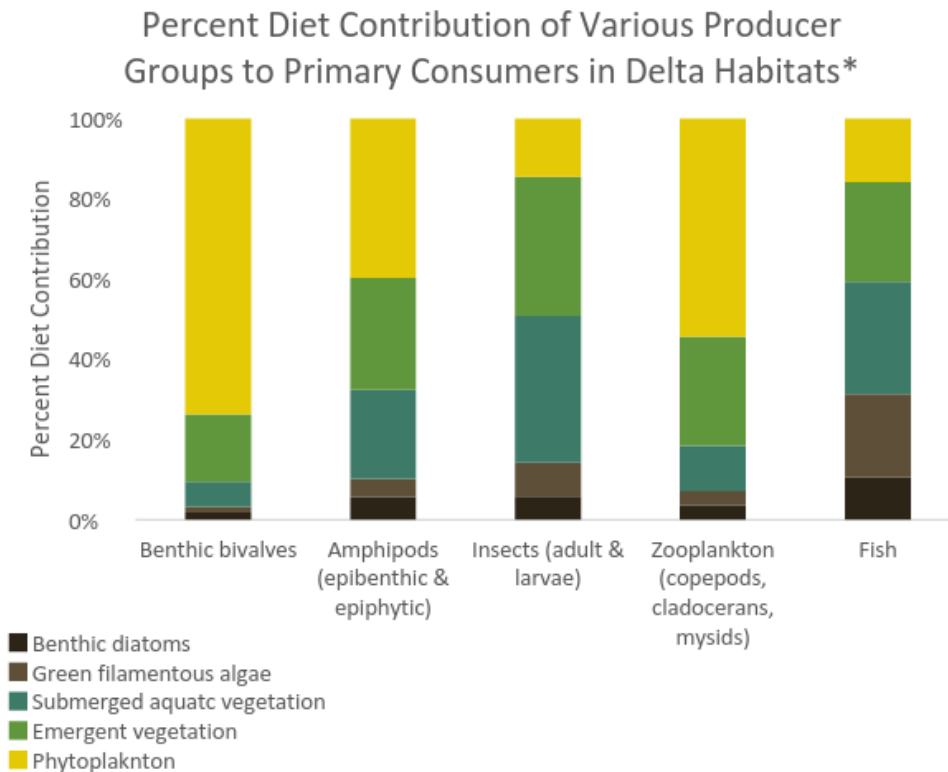
Percent Diet Contribution of Various Producer Groups to Primary Consumers in Delta Habitats*

Legend:
- Benthic diatoms
- Green filamentous algae
- Submerged aquatc vegetation
- Emergent vegetation
- Phytoplaknton

Figure C.1   Percent Diet Contribution of Various Producer Groups to Primary Consumers in Delta Habitats*

*Note: Fish data is taken from Lindsey Slough, all others are a snapshot from Liberty Island.

Caveats, uncertainties, and knowledge gaps

The emerging data on OM contributions to the Delta's aquatic food web are restricted to vegetated shallow water ecosystems in the North Delta, and do not necessarily reflect food web pathways in portions of the Delta with different landscape units (i.e., marshes, ponds, channels), configurations, and levels of connectivity between units. We assume different landscape configurations would reflect variation in detrital inputs and consumer access. Spatial differences in food web support thus present a challenging framework to tackle as we move to scale up the food web relationships described by Howe and Young (in review) to the scale of the entire Delta. In Phase 3, we would combine SFEI's vegetation mapping techniques with hydrodynamic models of particle transport and field measurements of particulate organic matter, allowing us to describe spatial and temporal variations in the availability of different types of OM across the Delta. We can use such a tool to link food web pathways with landscape configuration and the implications of increasing historical sources of organic matter through restoration.

Invasive species and a changing invertebrate assemblage present a challenge in terms of comparing the contemporary food web with the historical Delta. San Francisco Bay and Delta is one of the most

invaded estuaries in the world, with non-native species outnumbering native species in many cases (Cohen and Carlton 1995). As such, we acknowledge that feeding behavior at the community level may differ significantly between current and historical conditions. However, emerging results from Howe and Young (in prep.), coupled with work from other estuarine systems (Ortega-Cisneros and Scharler 2015), suggest that strong similarities exist among organisms within a feeding guild. By grouping species by feeding category, we will be able to make defendable comparisons between the historical and contemporary food web of the Delta.

APPENDIX D: FURTHER CONSIDERATIONS FOR PHYSICAL TRANSPORT

Integrating physical transport into our thinking about primary production was a lively topic of discussion during the Workshop. Physical transport shapes the processes in the Delta, and a discussion of these and their importance follows. These processes could be described in an integrative model during Phase 3 of this project.

In this section we discuss a series of changes in the landscape identified in *A Delta Transformed* (SFEI-ASC 2014) that we believe had a large impact on the hydrodynamics of the Delta. We then discuss the hydrodynamic implications of each of these changes, and finish with possible ecological consequences. Most of the material presented in this section is based on a scaling up of insights gained from a handful of targeted small-scale site-specific field experiments (Enright et al. 2013; Lucas et al. 2006) and nearly 30 years of experience with numerical models of the system. The concepts presented here could be further refined and quantified by comparing numerical model runs of the historical and contemporary Delta. The magnitude of the differences in the fundamental hydrodynamics processes could then be quantified using bulk metrics that encapsulate the processes we expect to change, then related to biological productivity in the Delta. Impact assessments based on the scaling up of results from small-scale experiments is, of course, fraught with danger, because a seemingly small change in a small region multiplied by a large region can have a large impact. Nevertheless, since to date there are no experiments conducted at a large scale—one of our recommendations for future work—upscaling small-scale experiments is all we have.

Changes in Delta Hydrodynamics due to Agricultural Reclamation

The greatest change in the hydrodynamics of the Delta occurred during the period of agricultural reclamation, when levees were created along existing Delta channels to create farmable regions (the so-called Delta islands). Also, over time, new channels were cut to improve conveyance and access. Agricultural reclamation changed the landscape in three fundamental ways (given in order of descending influence on the hydrodynamics): (1) levees were constructed that isolated pelagic from terrestrial habitats, (2) the Delta's historical dendritic "tree-like" geomorphology was transformed into a web-like system of canals, (3) flooded islands exist in the contemporary Delta where there were none historically (Liberty, Franks Tract, Mildred Island, Big Break).

Mediation of Contemporary and Historical Hydrodynamics by Landscape Morphology (Including Levees)

There are a handful of channel/marsh systems that exist in the contemporary Delta, yet these systems dominated the historical Delta (SFEI-ASC 2014) in much the same way as levees now dominate the land/water interface in the contemporary Delta. There are several such near-natural marsh systems in Rush Ranch, preserved by the Solano Land Trust; First Mallard Branch being one of them. Enright et al. (2013) placed devices to monitor discharge and water quality fluxes at the mouths of two channels in Suisun Marsh—First Mallard Branch and Sheldrake Slough—to study the influence of levees on marsh exchange processes (Figure D.1). First Mallard Branch is one of the few contemporary examples of a historical dendritic marsh system (though small when compared to the marsh systems that existed in the historical Delta). Sheldrake is an example of a typical leveed-off channel in the Delta. Given their proximity, these two channels receive roughly the same tidal forcing and, remarkably, have similar within-channel tidal prisms: tidal discharges on the order 300-400 cfs, (Figure D.2). Yet, for a few days during every spring tide, the discharge in First Mallard Branch roughly doubles when compared to Sheldrake Slough. This large increase in tidal discharge during spring tides happens virtually nowhere in the contemporary Delta, yet must have been a ubiquitous and defining feature of the historical marsh.

The source of the significant difference in exchange between these systems is the lack of a levee in First Mallard Branch. Whereas the increase in water levels that occur during spring tides are confined to the channel in Sheldrake Slough by levees (Figure D.3), the water entering First Mallard Branch has a sudden and almost unlimited access to the tidal prism in the marsh plain (Figure D.4) when water levels exceed Mean Higher High Water (MHHW; Figure D.1). The consequence: flood tides increase from 400 cfs to over 10000 cfs for a few tidal cycles in First Mallard Branch during spring tides when the tide height exceeds MHHW (Figure D.2).
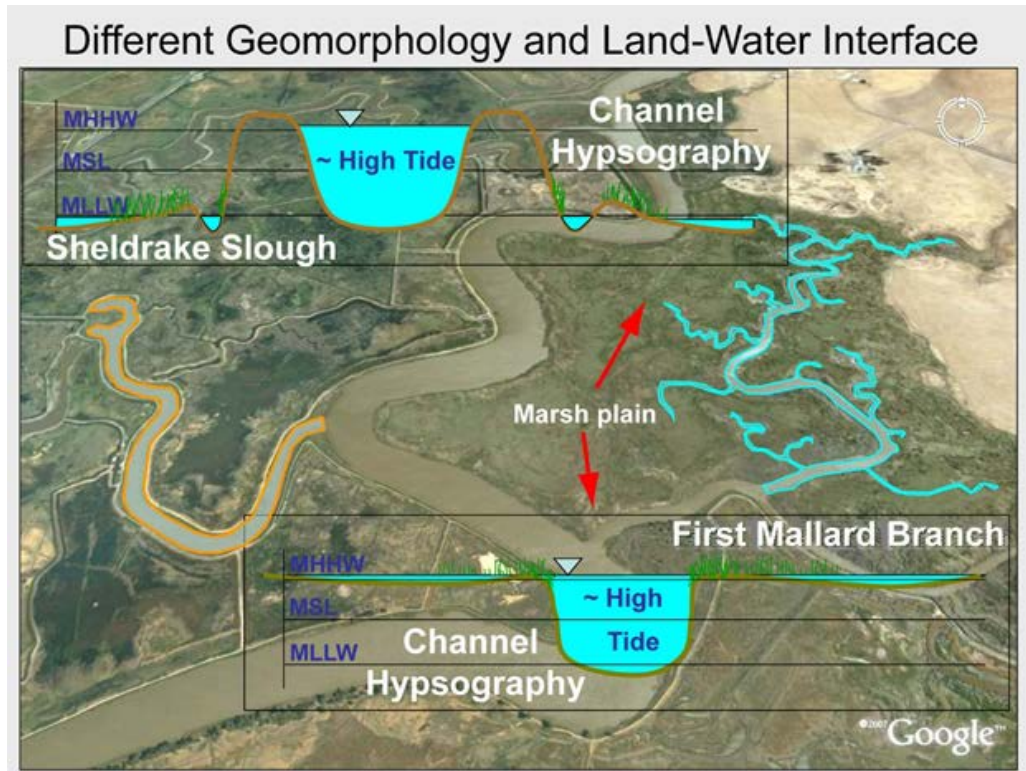
Figure D.1 A comparison between two channel systems in Suisun Marsh: (1) Sheldrake Slough (shown in the upper left), a typical Delta channel system where the channel has been separated from marsh by a levee, (2) First Mallard Branch which maintains a natural low berm at Mean Higher High Water (MHHW) that separates the channel from marsh. MSL = mean sea level, MLLW = mean lower low water (After Enright et al. 2013).
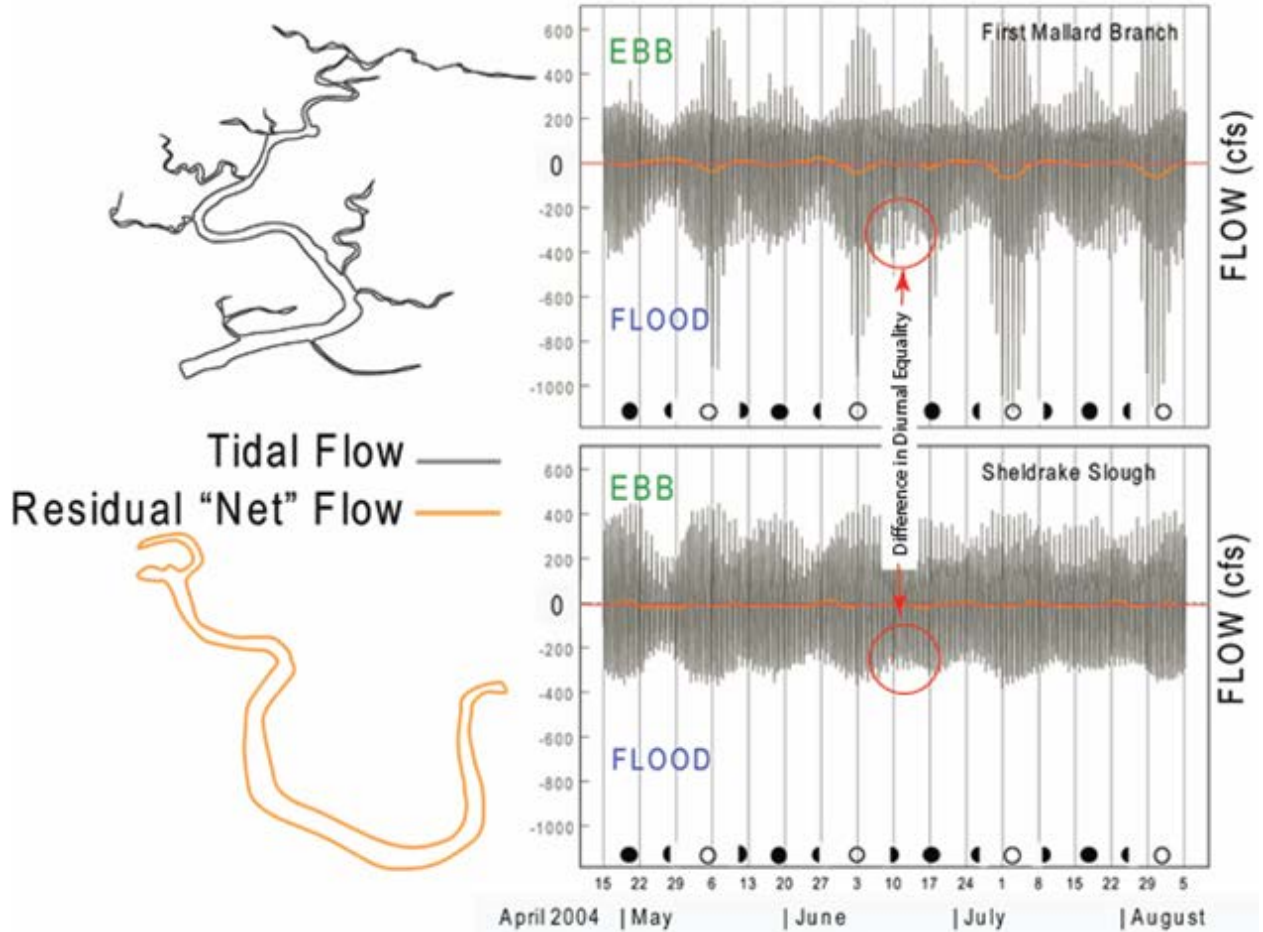
Figure D.2 Time series plots of tidal (black) and tidally averaged (or net) discharge (orange) and in First Mallard Branch (top panel) and Sheldrake Slough (bottom panel) from April to August 2004. Spring tides correspond to new and full moons, whereas neap tides occur when the sun and moon are in quadrature (half moon) (After Enright et al. 2013).
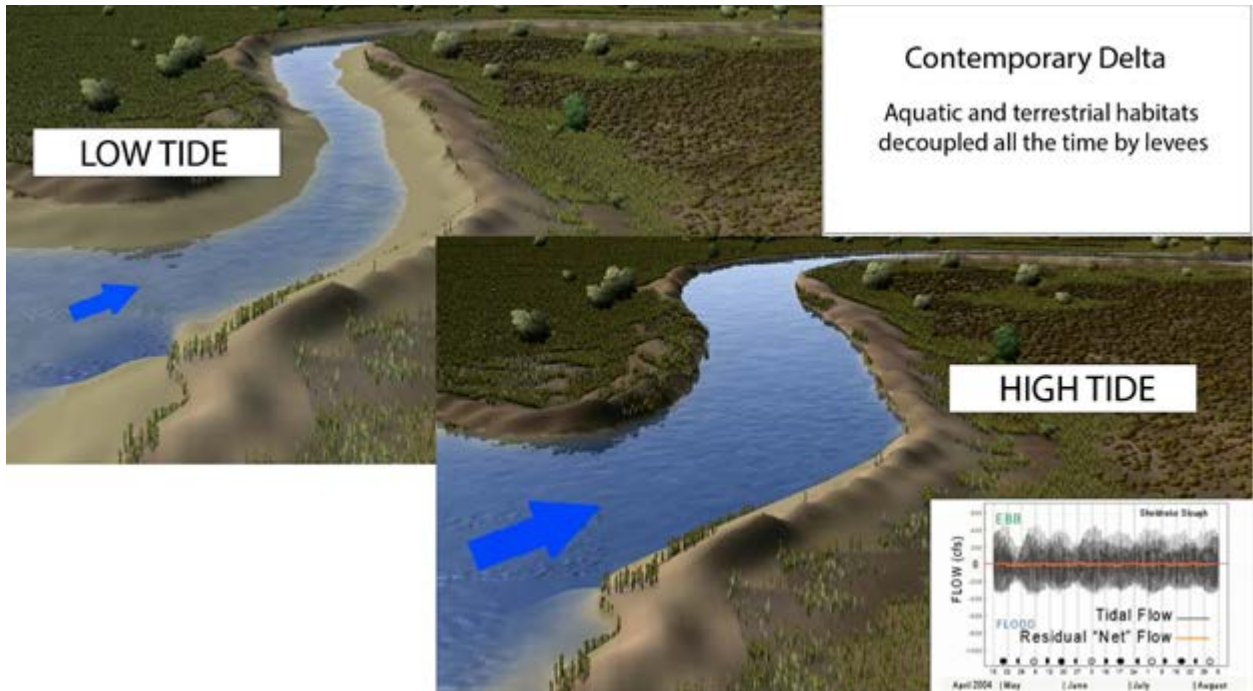
Figure D.3 Tidal exchange in a typically leveed-off Delta channel (e.g. Sheldrake Slough). Aquatic and terrestrial habitats separated by levees. Tidal exchange is confined to the channel (Courtesy of 34north).
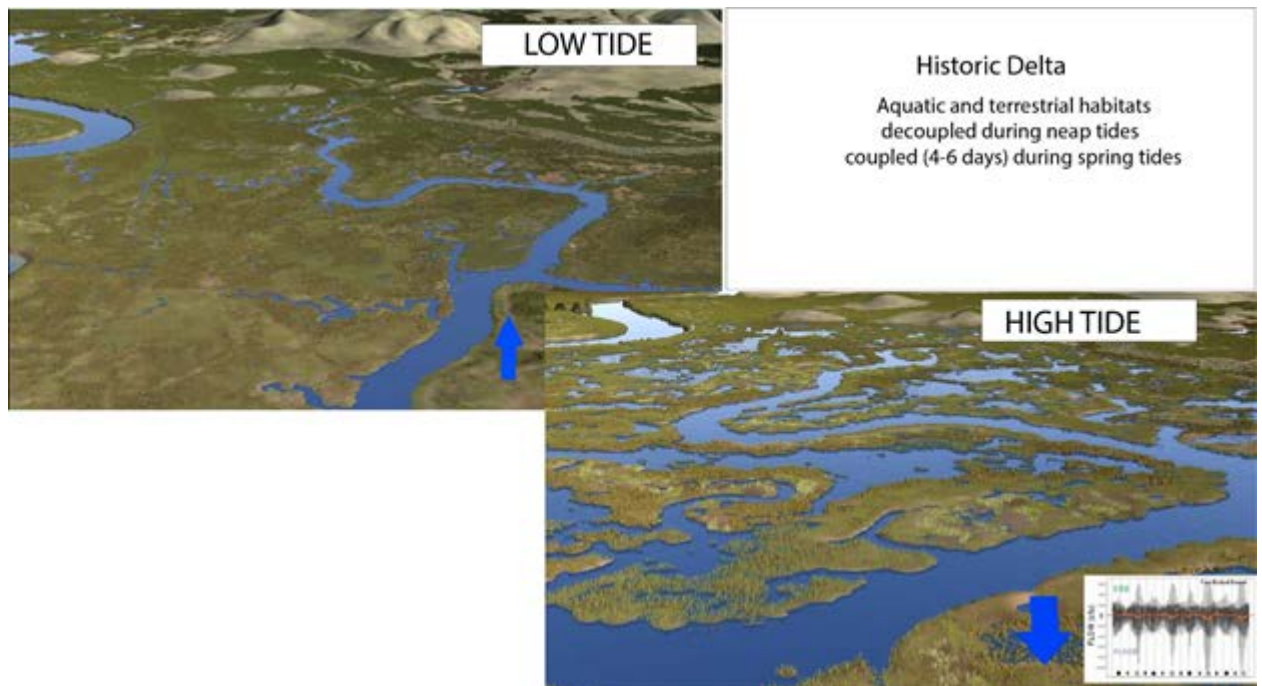
Figure D.4 Tidal exchange in a typical historic channel (e.g. First Mallard Branch). Aquatic and terrestrial habitats function independently for approximately 10 days, but for about 4 days, during spring tides, when water levels exceed MHHW, a large exchange between the channel and the marsh occurs. In the case of First Mallard Branch the discharge doubles. Tidal exchange is confined to the channels for approximately 10 days out of 14 (Courtesy of 34north).

These systems could not be more hydrodynamically different—the exchanges into and out of First Mallard Branch suggest an extraordinary degree of temporal and spatial heterogeneity over Sheldrake Slough. Firstly, both systems act similarly but not identically when the tides are below MHHW. For example, the spring/neap variability in the diurnal inequality in the flood tides in Sheldrake Slough are virtually non-existent due to Sheldrake Slough's shorter length of channel and a lack of secondary channels compared to First Mallard Branch. Sheldrake is a shorter (1.8 km), single, leveed-off channel, whereas First Mallard Branch is a longer (2.4 km), dendritic branching network of channels, which responds in a more complex and nuanced way to tidal forcing even when the stages are below MHHW (Figure D.2). The enhanced flood tide variability associated with the diurnal inequality means there is greater every-other-tide variability in exchange in First Mallard Branch over Sheldrake and, by extension, increased variability in spatial exchange within First Mallard Branch's channel network system. By contrast, less flood tide variability at spring/neap time scales as shown in Sheldrake Slough (Figure D.2) is typical of the Delta, except within the Cache Slough Complex, also a dead-end channel system. The consequence of a balance in ebb and flood tide variability at spring/neap timescales in dead-end channel systems is unknown, yet this was undoubtedly a salient feature of the historical marsh. Variability in flow at the mouth of the channel equates to changes in the influence of the tides in space through temporal changes in the distribution of the tidal excursions on the landscape (Figure D.5). Changes in the distribution of the tidal excursions on the landscape, in turn, create distinct pelagic habitats that vary in time and space and thus control the temporal evolution of pelagic habitat variability overall.
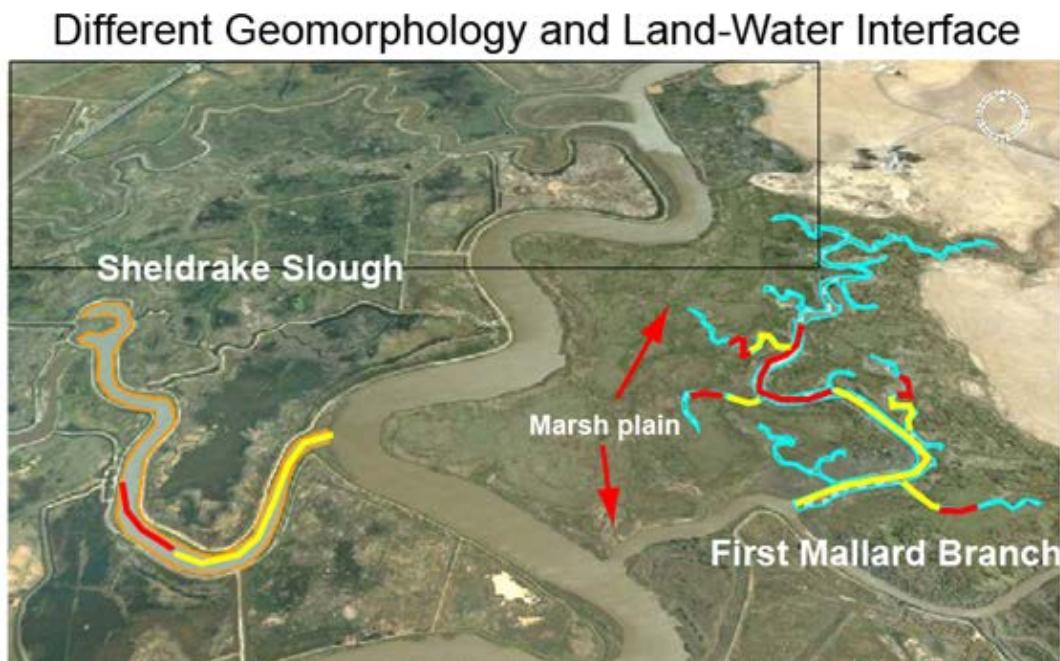

Figure D.5 Tidal excursion estimates from the mouth of each channel indicated in Sheldrake Slough and First Mallard Branch. Maximum neap tide (yellow), spring tide maximum (red).

In Sheldrake Slough there are two distinct habitats that evolve over a fortnightly period, delineated by the maximum neap and spring tidal excursions respectively. Distinct habitats are created in these narrow (25 m) and long channel (2.4 km) dead-end channel systems because longitudinal mixing is weak. These distinct pelagic habitats shift their positions along the channel within the Slough, where the Suisun Slough water progressively intrudes into Sheldrake Slough over a ~7 day period when the tides transition from neap to spring. The water in the yellow region in Sheldrake Slough in Figure D.5 is basically water of Suisun Slough origin, whereas the red water maintains longer residence times that are distinct to Sheldrake Slough because this water minimally exchanges with Suisun Slough, and importantly, the marsh plain during neap tides. In contrast, in First Mallard Branch, every side channel has a region that exchanges with the main channel but also may have a hydrodynamically separate high residence time region at the upstream boundary of the side channel, depending on the local tidal prism (e.g., some small channels completely dewater during spring tides).

The tidal excursion relative to the channel length (or basin dimension) is an essential driver of pelagic habitat extent and exchange, including in the contemporary Delta. Many of the temporal gradients observed at sensors deployed at fixed sites within marsh systems are simply tidal advection of water that was at one time at the tidal excursion interface between water bodies that had differing residence times. Tidal excursions within the contemporary Delta can be quite long relative to the channel length (Figure D.6). For example, the tidal excursion from the mouth of Liberty Island extends past Rio Vista on the Sacramento River a distance of over ~14 km (~8 miles). These extraordinarily long tidal excursions relative to the channel lengths in the contemporary Delta create homogeneous pelagic habitats that likely extend over much longer spatial scales than occurred in the historical Delta. Finally, during the transition from spring to neap, the water that was exchanged into Sheldrake from Suisun Slough during

Figure D.6 Tidal excursion estimates in the Liberty Island Cache Slough region.

the neap to spring transition will be successively exchanged from Sheldrake Slough back into Suisun Slough during the spring to neap transition. This process is effectively how dead-end channels (and flooded Islands with a single breach) exchange the production that occurs within dead-end channels into the surrounding environment. Importantly, most of the production in dead-end channels is exchanged during the neap-to-spring transition and the extent of the subsidy is related to the difference between the spring and neap tidal excursions.

During the peak spring tides, the pelagic habitats between the two channels could not be more different: Sheldrake Slough maintains a persistent long-residence time pelagic habitat at the back of the slough. Whereas the entire pelagic habitat that exists in First Mallard Branch for a period of roughly 10 days is likely completely advected out of the channel onto the marsh plain once the stage exceeds MHHW. Moreover, a significant portion of the water that enters the marsh during the really large spring tides does not exit the main opening but rather is absorbed by the vegetation in the marsh or exchanges with adjacent dendritic marsh systems, as can be seen by the increase in the net flow into the marsh (full moons on July 1 and Aug 1 in Figure D.2). Thus, pelagic habitats that develop over about an 8-10 day period within the channels in a dendritic marsh system during neap tides are massively exchanged with the terrestrial habitats of the marsh plain on the subsequent flood tide. In a similar fashion, the marsh plain is effectively isolated from the adjacent aquatic habitats during this same 8-10 day period. Then, during spring tides the two habitats—aquatic and terrestrial—are intimately coupled for a period of 4-6 days.

If we scale up the differences in the hydrodynamic processes between these channel systems to the scale of the Delta we can only conclude that pelagic environments throughout the historical Delta must have changed enormously at fortnightly timescales: pelagic and terrestrial environments where essentially decoupled for 8-10 days then were strongly coupled for a period about 4-6 days during spring tides throughout the entire Delta!

However, it is unclear how tidal propagation in the historical Delta compares with the contemporary Delta and how tidal energy was redistributed between the spring and neap tidal phases in the historical Delta. Nevertheless, because Carquinez Strait is a hydraulic control, it places a cap on tidal exchanges in the Delta: the overall amount of tidal energy between the historical and contemporary marsh were very likely nearly identical. Therefore, the difference in transport processes in the Delta between historical and contemporary Delta amount to an unknown redistribution of tidal energy, not a change in overall tidal energy. Fortunately, this redistribution process is something that can be quantified with numerical models.

The consequences of this periodic fortnightly decoupling/coupling of pelagic and habitats individually and together on the biogeochemistry, primary producers and on both the pelagic and marsh plain ecosystems is unknown. However, the implications of this small scale study suggests a radically different ecosystem existed in the historical Delta compared to the ecosystem that exists today, particularly at the primary producer level.

Field studies like those just described that looked purely at the physical differences between those places that represent historical systems with contemporary systems need to be expanded to include the study of ecological functioning in these systems. Numerical modeling at the simplistic conceptual model level (1 and 2D models) and renderings of detailed 3D model results into simplified bulk metrics that can be used to understand the implications of scaling up the small-scale experiment just described. Finally, the designs of proposed marsh restoration efforts should take the physical observations described above into consideration, especially with regard to land surface elevations relative to MHHW that could allow for the fortnightly variation in tidal exchange observed in First Mallard Branch, one of best existing representations of the historical marsh.

The Transformation of a Dendritic Marsh System into a Web of Conveyance Canals

The transformation of the landscape from a dendritic marsh system into a web of conveyance canals changed the Delta in two fundamental ways: (1) new channels were cut to improve access to farmland and for conveyance (Figure D.8) which transformed a patchwork of adjacent nested dead-end channel systems into a highly interconnected within-a-tidal excursion web of canals, and (2) the intense spring tide pelagic/terrestrial coupling was abruptly ended.

The historical marsh was made up of a patchwork of adjacent nested dead-end channel systems like First Mallard Branch. These dead-end channel subsystems likely acted like independent watersheds for ~8-10 days, then were coupled during the peak in the spring tides. This network of adjacent nested dead-end channel systems likely created an incredibly dynamic diversity of habitats at tidal (a diversity of tidal excursion length scales within a channel network) (Figure D.5) and at fortnightly timescales when the pelagic environments exchanged with the marsh plain *and* between adjacent dead-end channel sub-systems.

In contrast, the combination of long tidal excursions relative to the channel lengths and the persistence of relatively strong net flows within the channels of the contemporary Delta tend to homogenize pelagic habitats at both the tidal, fortnightly period and tidally averaged time scales.

Firstly, long tidal excursions relative to the channel lengths (or basin dimension) means relatively few unique habitats exist. For example, roughly 2/3 of Liberty Island exchanges with Cache slough every six hours (Figure D.6). The pelagic habitat that is unique to Liberty Island represents only the upper 1/3 of the Island. Similarly, water that enters Franks Tract from False River through breaches on its western border completely transits this flooded Island every single tide (Figure D.7).

Secondly, tidal excursions in the web-like structure in the contemporary Delta typically exceed the channel length (Figure D.8) and thus these exchanges also tend to homogenize (and mix out) pelagic habitats.

In addition, persistent relatively short residence times exist in the contemporary Delta overall because it is essentially a flow-through system. For example, in the historical Delta, relatively few big channels conveyed the river flows to the bay with a bunch of connected smaller branches that were primarily involved in off-channel storage. Thus, longer residence time pelagic environments likely existed in the larger dead-end channel systems in the historical Delta, at least during neap tides. The possibility of longer residence times, coupled with the possibility of short periods (say a couple hours) of relatively quiescent water near slack water also suggest vertical temperature stratification could have been a prominent feature in the historical Delta. Whereas, because of the strength of the tidal and net current speeds in the contemporary Delta, vertical temperature stratification is rare, with a few notable exceptions: Mildred Island (Lucas et al. 2006), the Deep Water Ship Channel and some of the dead-end sloughs in the Cache/Liberty Island complex. Vertical temperature stratification is known to enhance phytoplankton production by keeping phytoplankton in the photic zone and isolating phytoplankton from the benthos.

Ironically, even though the contemporary dead-end channel sub-systems are highly engineered, they are some of the most productive in the contemporary Delta (Feyrer et al. 2017). For example, the North Bay Aqueduct (NBA) maintains the highest organic carbon content of any of major export withdrawal. The high organic carbon content suggests that Lindsey Slough is trying very hard to function as a marsh, yet its primary production is exported from the system. The NBA is not alone: agricultural withdrawals create landward net flows into the Liberty Cache Slough region, so whatever primary production is created in this region is ultimately spread on farm fields and never makes it into the balance of the Delta.
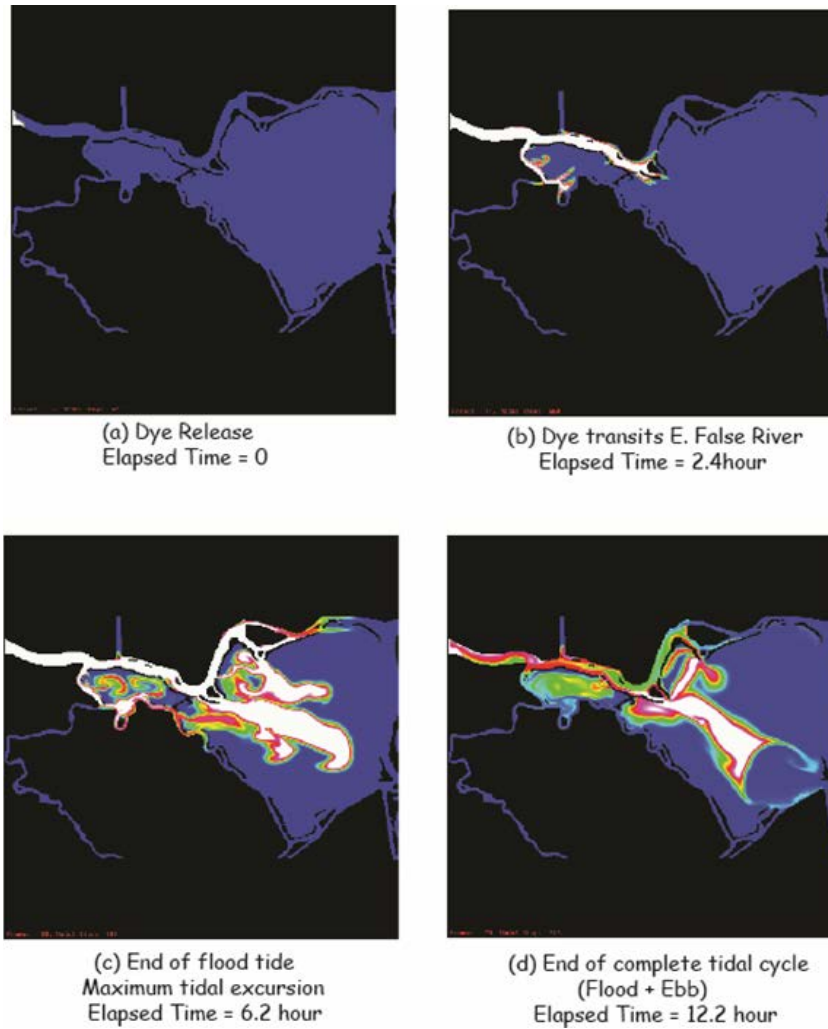
(a) Dye Release
Elapsed Time = 0

(b) Dye transits E. False River
Elapsed Time = 2.4hour

(c) End of flood tide
Maximum tidal excursion
Elapsed Time = 6.2 hour

(d) End of complete tidal cycle
(Flood + Ebb)
Elapsed Time = 12.2 hour

Figure D.7 Numerical model simulation of dye released at the False River/San Joaquin River confluence over a complete tidal cycle. Flooded Islands like Franks Tract are incredibly good at creating dispersive mixing and thus tend to homogenize pelagic habitats.

Network Dispersion
Conceptual Model

Tidal Currents

L_u

L_c

L_u
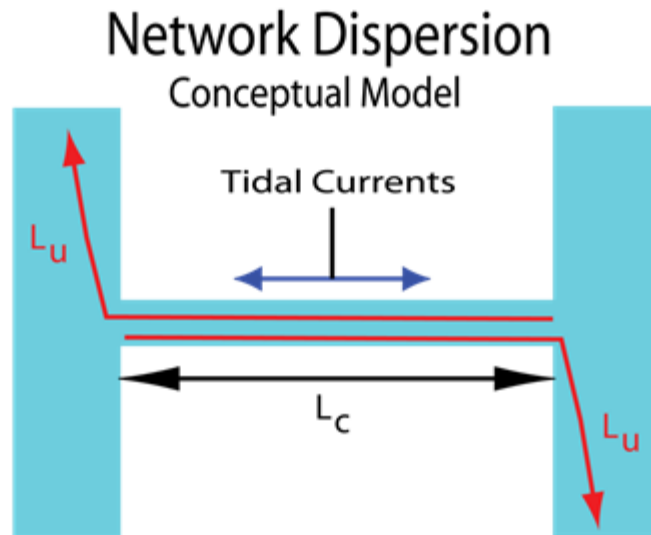
If $\gamma = \dfrac{L_u}{L_c} > 1$:   system is dispersive

If $\gamma = \dfrac{L_u}{L_c} < 1$: system is advection dominated

L_c = Channel Length

L_u = Tidal excursion

$L_u \sim \dfrac{U*P}{\pi}$

U = Tidal current amplitude

P = Tidal Period (12.42 hrs)

Figure D.8 Conceptual model of network dispersion.

Flooded Islands

The geomorphology of the historical open water areas bear little resemblance to the modern-day flooded Islands. Flooded Islands, given their size and depth, create a huge hydrodynamic footprint in the contemporary Delta. For example, Franks Tract, dominates the hydrodynamic landscape in the Central Delta. Dispersive mixing from the San Joaquin River through False River into Franks tract is so large (Figure D.7) that a $25M barrier was installed for 3 months in 2015 to keep salinity intrusion from incapacitating the export facilities in the South Delta. Moreover, Liberty Island is a source of turbidity all summer long, whereas Franks Tract can be a source of suspended sediment during wind events and a sink otherwise.

Changes in Delta Hydrodynamics Associated with Flood Protection

The channels in the contemporary Delta were engineered for conveyance, primarily to protect human assets, both farmland and cities, and secondarily to move water through the Delta to (1) repel salinity intrusion, (2) export water from the Delta, and (3) for navigation. Flood protection became a priority as the value of off-channel human assets grew, so that levees originally built for reclamation of the marsh for agriculture were eventually raised and covered with rock to prevent levee failure from erosion due to flood flows, wind-waves and boat wakes.

There were four fundamental changes in the landscape associated with optimization of Delta channels for conveyance. The channels alternatively were: (1) initially deepened through the creation of borrow ditches that were used to build levees, (2) made into narrow, prismatic, canals bordered by steep-sided rocked-levees (particularly in the upland fringes of the Delta), or, (3) massively widened in the western Delta to accommodate Sacramento River peak flood flows of ~400k cfs, and (4) straightened from their historical alignments.

Narrow, Prismatic, Steep-sided, Rocked Canals

Channels in the Delta that were initially deepened through borrow ditches of material that was used to build levees were eventually rocked to protect the levees from wind wave resuspension, and later, boat wakes. In the North Delta, in particular, the channels were engineered to be narrow, steep-sided, rocked prismatic canals to make sure the huge load of hydraulic mining debris in the Sierras would not adversely affect their flood conveyance capacity and navigation. The North Delta channels were constructed narrow to maintain high velocities so bed sediment would not accumulate. The geomorphologic consequence of this narrow design is the channels in the North Delta are unnaturally deep, the currents are strong, and these channels maintain very little if any bathymetric complexity.

The consequence of making the channels narrow on the ecosystem is multifold: (1) since the channels run deep, fast and turbid, phytoplankton, on average, are out likely out of photic zone a greater percentage of the time than they would have been in the historical Delta, (2) because there is no bathymetric variability, there is virtually no lateral variation in the velocity distributions in these channels, except in the immediate vicinity of the bank, (3) the principal land-water interface in the contemporary Delta is rock—neither sediment, nor vegetation.

The lack of bathymetric variability creates a pelagic habitat wasteland. For example, natural geomorphologic features, such as point bars, cut banks, deep areas and shallow create spatial variability in the velocity distributions in natural river channels that pelagic fish use for foraging, resting, out-migrating. These features do not exist in much of the contemporary North Delta. As a consequence, for example, survival of juvenile salmon emigrating from the North Delta is low (~20% from the city of Sacramento to Chipps Island (Perry at.al. 2013, 2015) and near zero in the San Joaquin (Buchanan et al. 2012, 2013) due to predation.

Dredging of Sacramento River as part of the Central Valley Flood Control System

The conveyance capacity of the Cache Slough/Western Sacramento River was massively increased to handle peak discharges from the Yolo Bypass of ~400k cfs (Figure D.10). According to Kelley (1998), more material was removed from this stretch of river than was removed in the making of the Panama Canal (Figure D.10). A pair of clamshell dredges worked 24/7, 365 days a year between 1913 and 1933. This creates a tidal exchange superhighway into the Cache Slough/Liberty Island region. Roughly 90% of the tidal volume that passes the City of Rio Vista travels into the Cache Slough/Liberty Island region, making it an ideal location for tidal marsh restoration since the tidal conveyance is there courtesy of this massive flood control project. This dredging operation is therefore responsible for the unusually long tidal excursions in this region, and a corresponding lack of pelagic habitat diversity. Except for a few small blooms, the channel between Liberty and Chain Island typically has very near zero Chl-a concentrations.
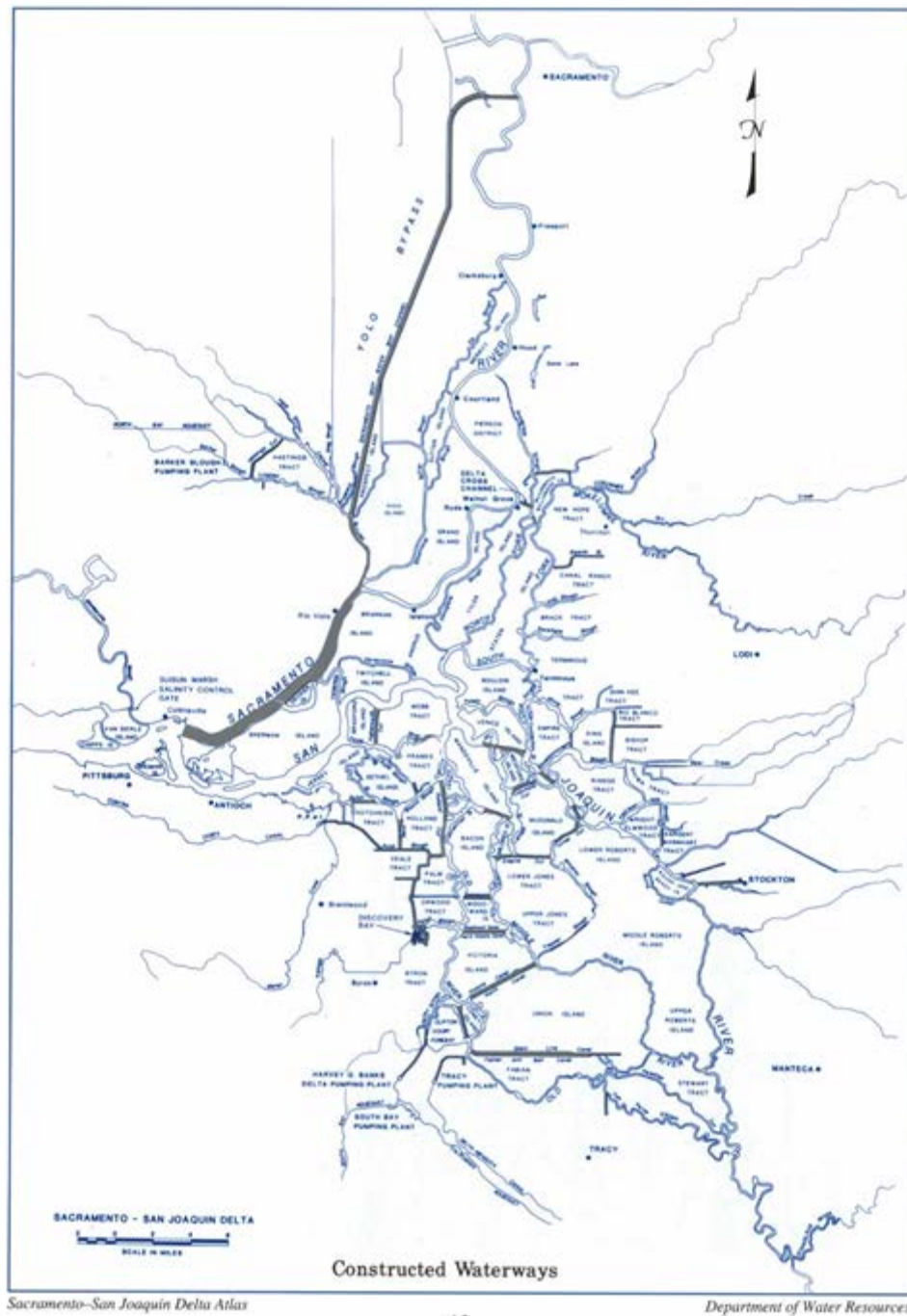
Constructed Waterways

12

Figure D.10 Delta Map showing constructed waterways in grey based on DWR's Delta Atlas, with one addition. The Cache Slough/Western Sacramento River is shown as a constructed waterway because it was massively dredged to accommodate Sacramento River Flood flows through the Yolo Bypass.

Conveyance of Flood Waters: dendritic vs. web of canals

The conveyance of river flows and flood waters through the historical Delta were accommodated primarily by a limited number of main channels (Sacramento, Mokelumne and San Joaquin River channels) and overbank flows. The majority of the Delta's web of secondary and tertiary channels were likely not engaged in the conveyance of flood flows, except in attenuating the flood wave by enhancing off-channel storage on the marsh plain. The web of secondary and tertiary channels likely acted like a flood flow dampener, serving the same function as our bypasses do in the contemporary Delta, except with appreciably longer residence times in the historical marsh.

In contrast, almost all of the channels in the contemporary Delta are engaged in conveying flood waters to the bay, especially in the North Delta. Because the contemporary Delta is a conveyance system, flood waters are designed to move through the system quickly, so the duration of the effect of flooding is short in the contemporary Delta relative to the historical Delta. So even at flood stages, the historical Delta provided longer and a more spatially diverse palette of water residence times when compared to the contemporary Delta, which has relatively short water residence times and little variability in residence time because the contemporary Delta was engineered to move water quickly through the system under flooding conditions.

Changes in Delta Hydrodynamics due to Exports

With few exceptions, there is a significant net (tidally averaged) flow in most of the channels in the contemporary Delta at all times. The Delta is a conveyance system in the summer too. Water, primarily from the Sacramento River, moves through the North Delta and into the Central Delta through Georgiana Slough and the manmade Delta Cross Channel into the Central Delta where it either moves into the South Delta for export or toward the bay where it is used to maintain salinity standards during low flow periods. Except during extremely high flow events, the entire San Joaquin River flow, including water quality constituents from the San Joaquin River drainage, is exported to Southern California. Water is withdrawn from the Delta (and sometimes returned) for farming, a quantity known as Delta Island Consumptive Use, DICU, which is computed on a yearly basis. During droughts, DCIU can significantly exceed exports.

None of the net flow patterns resulting from the maintenance of salinity standards in the San Joaquin and the removal of water from the Delta occurred in the historical Delta.

As was discussed previously, water exported from the North Bay Aqueduct removes a significant amount of the organic carbon from Lindsey Slough (part of the Cache/Liberty Island complex), and, along with agricultural withdrawals create a tidally averaged net flow in Cache Slough into the Cache/Liberty Island complex, depriving the greater Delta of any of the primary production generated in the Cache/Liberty Island complex.

71

The Delta Cross Channel

While the construction of the Delta Cross Channel (DCC) in the 1950s is a seemingly insignificant change in the landscape because it is only 1.2 km (0.75 miles) long and 110m (350 feet) wide, it has an outsized influence on water supplies south of the Delta and on the hydrodynamics of the Mokelumne system. Water that flows through the Delta Cross Channel is used for export and to meet water quality standards at Jersey Point (e.g. repel salinity intrusion). A gate was built on the DCC that was initially closed in the winter/spring to protect Mokelumne River levees from Sacramento River Flood waters, but it is now also closed to protect Sacramento River salmon outmigrants.

When the DCC is closed, the Sacramento River and Mokelumne systems are separate, as they were historically. With the DCC gates closed the Mokelumne system is strongly tidally forced, with minimal net flows from the local watershed in the summer. However, when the gate is opened—in effect, a dramatic change in geometry that connects two historically separate tidal basins—the Mokelumne system completely switches its hydrodynamic character from a system that is tidally dominated to a riverine system.

Transports in the Modern Delta

Watershed Inputs and Exports

Rivers transport water, sediment, nutrients, detritus, organisms, contaminants, and other constituents from the watershed to the Delta. The Sacramento River is the primary source of freshwater to the Delta (DSC 2012, Table D.1). Hydraulic mining greatly increased sediment supply in the late 1800s (Gilbert 1917, Moftakhari et al. 2015) and sediment supply as well as the amount of suspended sediment captured by Delta wetlands beforehand is not known.

River	Delta inflow, percent of total
Sacramento River	74%
San Joaquin River	14%
Yolo Bypass	8%
Eastside tributaries	4%

Table D.1 Long-term average contributions of rivers to Delta inflow (DSC, 2012)

At the seaward or western boundary of the Delta at Chipps and Mallard Islands, bidirectional tides exchange water between Suisun Bay and the Delta and the tidally-averaged net flow is seaward. Most water that exits the Delta flows into Suisun Bay (DSC 2012, Table D.2). The flow rate due to tides can be

two orders of magnitude greater than the freshwater discharge (Smith 1969). Freshwater flow to San Francisco Bay has decreased about 35% since the 1800s (Moftakhari et al. 2015). Before 1900, a snowmelt-driven peak flow of ~1850 m³/s typically occurred in early May (Moftakhari et al. 2013; Figure D.11). From 1968-2008 the peak flow is ~10% smaller (1700 m³/s) and normally occurs between January and March, roughly coincident with peak precipitation. Hydrographs vary tremendously from year to year due to variable precipitation. These temporal observations qualitatively apply to Delta inflow. Contemporary sediment outflow from the Delta is episodically driven (McKee et al. 2013) as is sediment supply. About one-third of the sediment that enters the modern Delta leaves it (Wright and Schoellhamer 2005) and this value is likely less for the historic Delta because tidal marshes were common and they trap sediment (Ganju et al. 2005).

Sink	Delta outflow, percent of total
San Francisco Bay	73%
Exports	23%
In-Delta use	4%

Table D.2 Long-term average modern Delta outflows (DSC, 2012)
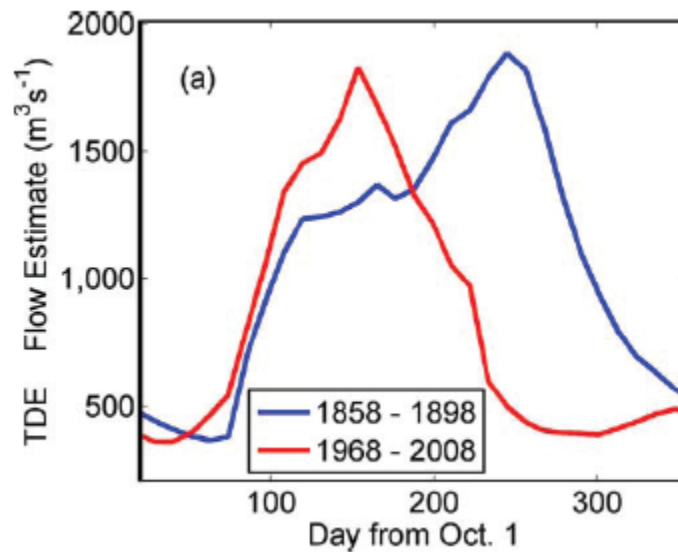

Figure D.11 Flow to San Francisco Bay estimated from measured Bay water levels, from Moftakhari et al. (2013)

Regional Transport

The Sacramento – San Joaquin Delta is an inland estuary where regional physical transport of dissolved and suspended material is driven by tidal flow and by the balance of river inflows and in-Delta losses or diversions (net flow). The contemporary Delta includes over 1000 km (622 mi) of interconnected channels. During low flow periods, tidal flow dominates many of the channels, and in-particular the deep water ship channels leading to the ports in West Sacramento and Stockton. Tidal excursion in the Western Delta can be on the order of 14 km (9 mi). The movement of tidal flows over varied bathymetry, in and out of embayments, and through channel connections gives rise to significant dispersion of dissolved and suspended material (which is the primary mechanism that moves ocean salt into the Central Delta). Net, or riverine, flow typically dominates in the Sacramento River near Sacramento and San Joaquin River near Vernalis. During periods of high inflow, the portion of the Delta dominated by riverine flow expands significantly. During periods of high pumping for the Central Valley Project (CVP) and State Water Project (SWP), net flows in the South Delta are strongly affected, reversing the normal net flow direction in Old and Middle River (Figure D.12).
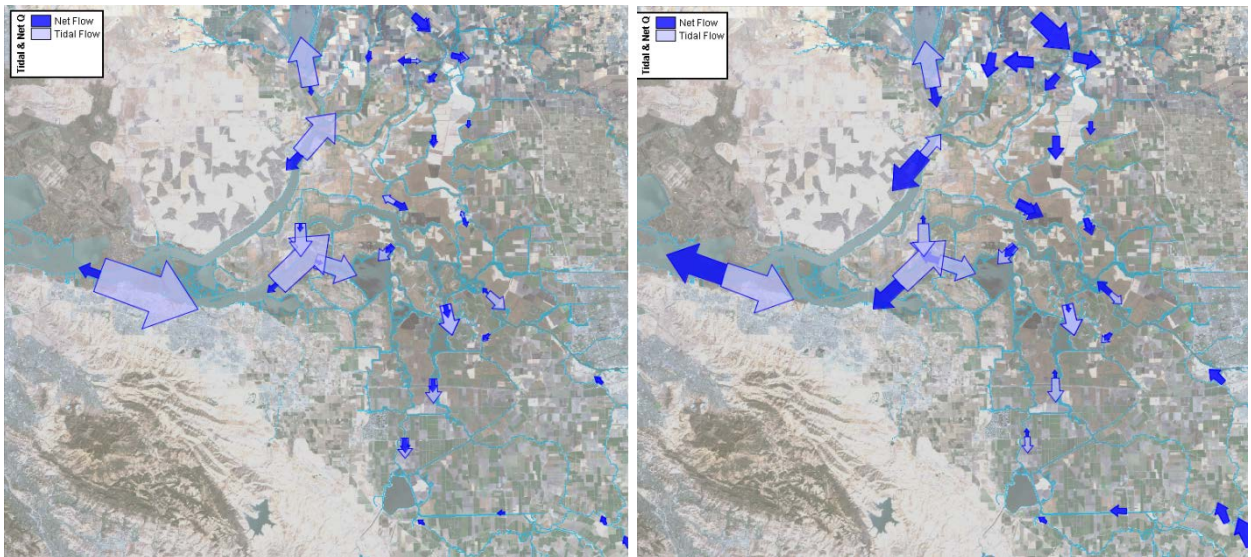

Figure D.12   Representative comparison of tidal and net flow during periods of low inflow (left) and high inflow (right), note that tidal flow is shown for peak flood flow (RMA model demonstration result).

SWP and CVP export pumping has a very strong effect on the distribution of source water throughout the Delta (Figure D.13). With no export pumping the inflows from the Sacramento, San Joaquin, and Mokelumne Rivers all flow out through the Suisun Bay and into San Francisco Bay. During periods of moderate inflow, export pumping can exceed the sum of the San Joaquin and Mokelumne inflows so that nearly all of the Mokelumne and San Joaquin River inflows are captured in the South Delta.
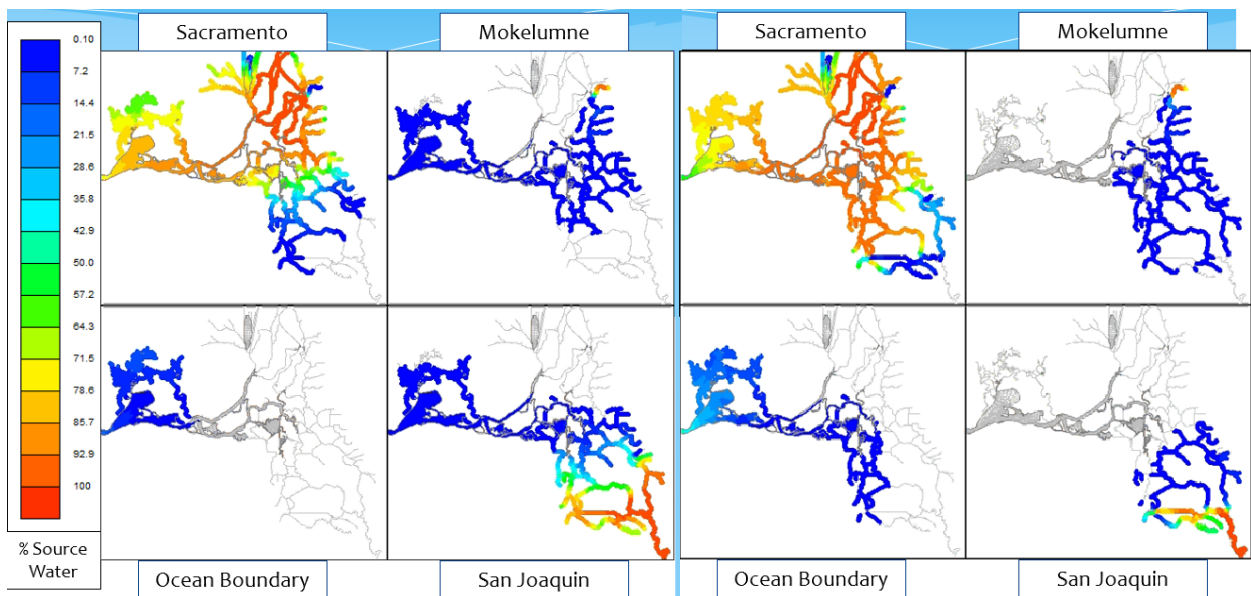
Figure D.13   Comparison of the distribution of source water (fingerprinting) during periods of no export pumping (left) and high export pumping exceeding the sum of the San Joaquin and Mokelumne inflows (right) (RMA demonstration model result).

The rate of transport through and residence time within regions of the Delta (or put another way, the time water is exposed to regions within Delta) varies strongly with both river inflow and export pumping. The rate of transport is related to productivity and food web by affecting exposure to favorable (or unfavorable) habitats as well as the connectivity between habitats. Phytoplankton production is concentration dependent and typically longer residence times in favorable habitat will lead to higher productivity. Rapid Transport between connected habitats may be able to move material and organisms from regions of higher productivity to regions of lower productivity. Figure D.14 presents two views of "exposure time" (RMA 2005) within the Delta based on historical simulation for 1989. Under most conditions, water passes through the North Delta channels within a few days. The major exception is the Sacramento Ship Channel north of Cache Slough and Elkhorn Slough where residence time is much longer as there is little or no direct inflow to those channels. During low flow periods, the Cache Slough region is on the order of a month or more, but during high flow periods with the Yolo Bypass is flowing, exposure time is reduced dramatically. With moderate export pumping, exposure time in the Old and Middle river corridor is actually greater during high flow events because most of the San Joaquin inflow is taken up by CVP and SWP exports leaving the net flow in the Old and Middle River corridors very low.
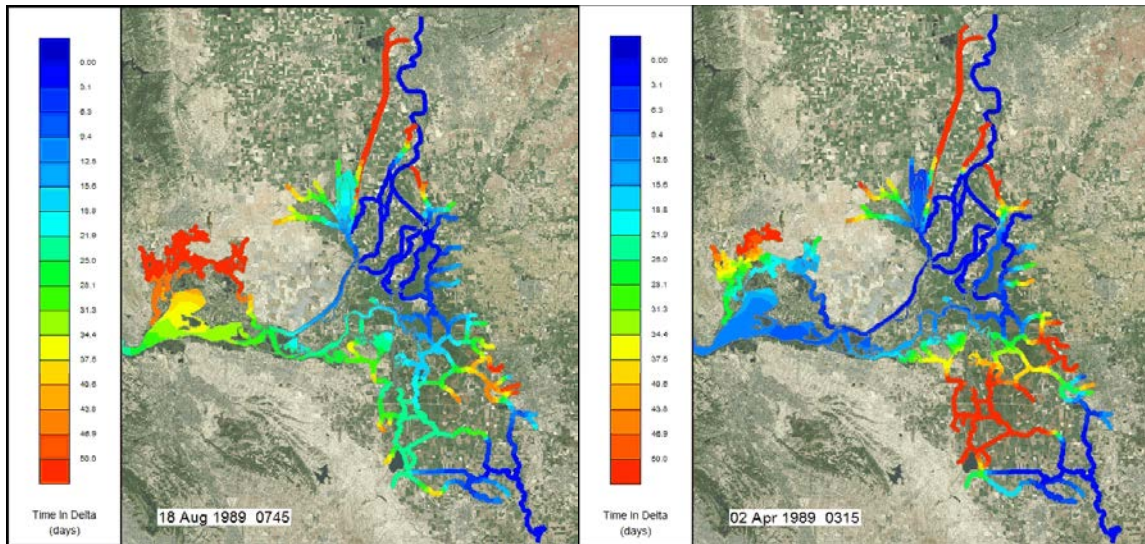
Figure D.14 Comparison of time water has been in the Delta during periods of low inflow (left) and high inflow (right) (RMA historical simulation for 1989 flow conditions).

Local Transport

Some regions in the Delta will be more productive for phytoplankton based on light availability in the water column (related to turbidity and depth of water), flow velocity and dispersion (affecting residence time), and nutrient availability (watershed inflow, substrate). In general, longer time spent in a productive region (residence time) allows higher production. Exchange with neighboring habitats distributes the production, but the region of influence of a zone of primary production will be affected by the rate of transport, the production rate, and the consumption rate. If the consumption rate is very high, then all production is consumed locally and regional-scale transport processes will be less important (or not important at all). If the local consumption rate is low relative to the rate of production and the local transport rate, then production in one area may influence distant areas of the Delta.

Mixing, or dispersion, is a very important transport process in the Delta, widely distributing dissolved or suspended material and generally reducing concentration peaks. One of the key sources of mixing in the Delta occurs at flow splits between channels. Because the contemporary Delta has many more interconnected channels—a web-like structure—than the historical Delta, which had a more dendritic channel arrangement, this form of mixing is more important in the contemporary Delta.

Tidal trapping in embayments along the main channels of the estuary like Honker Bay and Big Break is another important cause of mixing. Along the main channels of the estuary, peak tide level is reached while the channels are still in flood flow (progressive wave). Embayments adjacent to the channel will fill early during flood tide. Water in the channel will continue moving upstream, separating the previously adjacent parcels of water (some in the embayment and some in the channel), and enhancing mixing.

Marshes at the ends of tidal sloughs or areas where the conveyance capacity is tuned to the tidal period would experience a standing wave characteristic where water would move off the channel into the marsh and then back without enhancing mixing. The remaining marshes in the contemporary Delta tend to be of this kind. In the historical Delta for some tidal marsh areas adjacent to the larger channels, flooding over low natural levees is likely to have occurred during flood tide, and then drained during ebb tide through marsh channels creating a net transport across the marsh plain (Figure D.15).
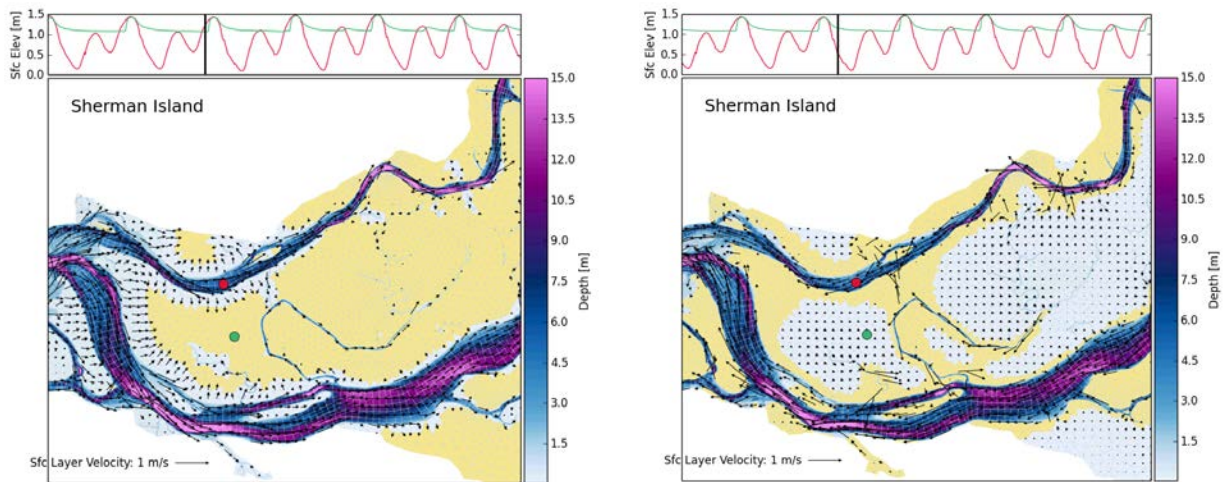

Figure D.15 Marsh flooding over natural levees and draining through higher order channels leading to ebb- dominant transport in some tidal marshes of the Historical Delta (Historical Delta Model Hydrodynamic Model, paper in preparation).

Burial

Burial is the permanent immobilization of inorganic and organic matter on the marsh plain and in channel beds, which leads to the accumulation of carbon and inorganic sediment (Canuel et al. 2009; Drexler et al. 2009). Here we are using the term "permanent" to mean longer than other transport time scales being considered such as tidal, river flood, anthropogenic, or sea level change. It is important to note that burial is the *net* amount of material that remains after processes such as scour, dissolution, and decomposition have acted on the deposited material (Reed 1995; Canuel et al. 2009). In marshes, burial is part of a process called vertical accretion, which serves to increase the elevation of the marsh plain in order to keep pace with sea-level rise (Turner 2001). In Delta marshes, permanent burial of organic matter and inorganic sediment have led to the formation of peat soils up to 6,800 years old (Drexler et al. 2009).

The current Delta is a depositional environment—Wright and Schoellhamer (2005) found that during water years 1999-2002 approximately 2/3 of the sediment supplied to the Delta remained there. Tidal marshes and backwater sloughs, which were once prevalent in the Delta, are efficient sediment traps

(Wang et al. 1993; Leonard et al. 1995; Ganju et al. 2005; Morgan-King and Schoellhamer 2013), so it is likely that the historical Delta trapped an even greater fraction of both organic and inorganic matter that was suspended in the water column.

Phase Relation between Tidal and Diurnal Cycles

The phase relationship between the diurnal (day/night) cycle and the tidal cycle can be an important ecosystem driver. For example, in the case of the Sheldrake Slough/First Mallard Branch experiment, MHHW occurred at night, when the summertime sea breeze cooled the thin sheet of water advecting over the marsh plain. Thus, the water temperature exiting first Mallard Branch dropped a full 6 °C, during the marsh inundation events (Figure D.16). Because the water was confined to the channel in Sheldrake Slough with a drastically reduced surface area exposed to the air, the drop in temperature was orders of magnitude less than in First Mallard Branch (Figure D.16).

This temperature drop is not the only instance of the importance of the phasing of the tidal cycle with the diurnal cycle. For example, Malamud-Roam (2000) found large differences in biochemical process rates on mudflats when the mudflats were exposed to sunlight which depend on when low tide occurred during the diurnal cycle. Lucas et al. 2006 found the timing of slack (quiescent) water relative to the diurnal cycle was relevant in the creation of phytoplankton blooms in Mildred Island, a deep, flooded island in the Central Delta. For example, when slack water occurred at mid-day in Mildred Island on an especially hot summer day, thermal stratification occurred, which lead to a bloom. Slack water occurring any other time of the day would not have produced this physical, then biological response. Finally, the timing of the peak ebb tides occur during the night in the November to January salmon out-migration season allows salmon to move through the system faster by simply seeking refuge during the day (Chapman et al. 2012; Plumb et al. 2015) when the peak flood tides occur.

This consistent seasonal relationship between the phase of the semi-diurnal tide extremes and the diurnal (day/night) cycle is caused by differences in the principal partial (M2) tide (period of 12.42 h) and the tropical fortnightly cycle (period of 11.45 h). This seasonal time-scale phase relation between tide extremes and the diurnal cycle changes slowly, by approximately 1.09 days/year, or with a period of 335 years (Malamud-Roam 2000). Thus, ~170 years ago, in the historical Delta, the phase relation between the semi-diurnal tidal extremes and the diurnal cycle would have been completely flip-flopped, where the water in Suisun Marsh would have flooded over the marsh plain during the day, elevating water temperatures in the marsh and within pelagic habitats during spring tides.
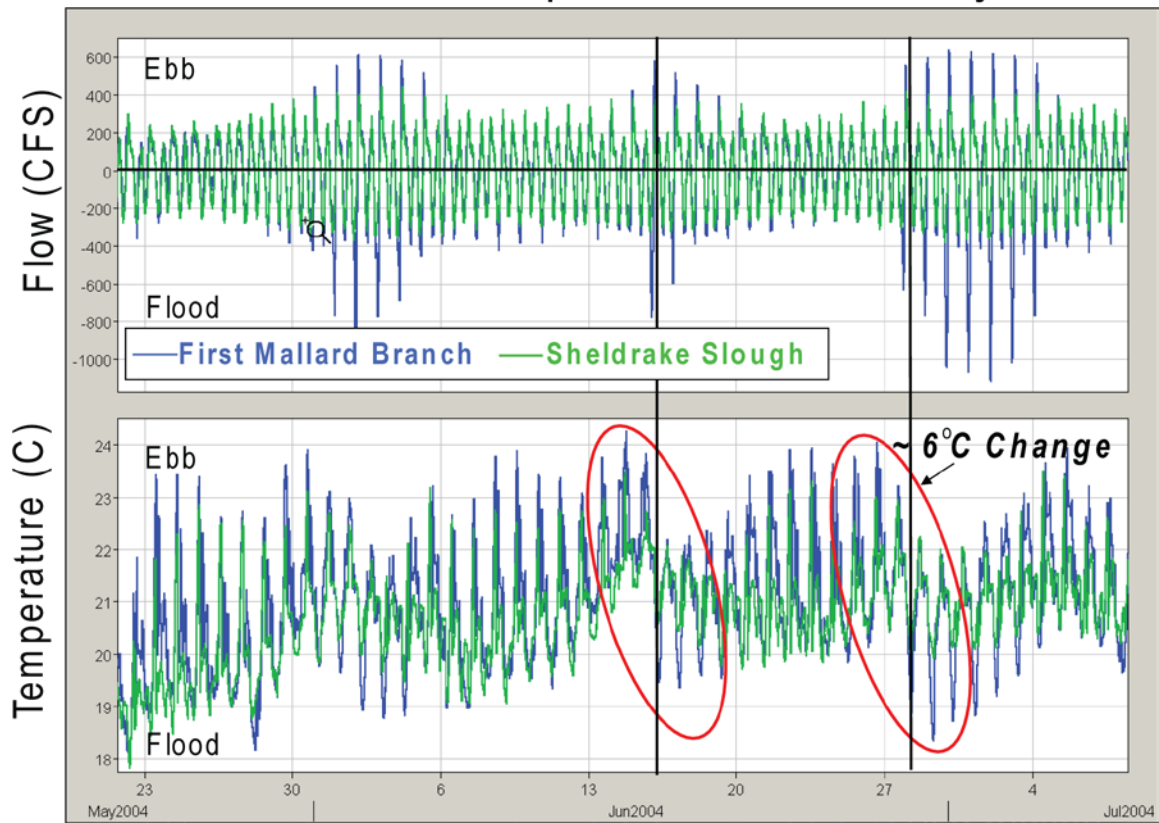
Figure D.16 Time series of discharge (top panel) and water temperature (bottom panel) in First Mallard Branch (blue) and in Sheldrake Slough (green). The Red ellipses indicate an ~6 °C drop in water temperature exiting First Mallard Branch during spring tides compared to a much lower ~2 °C drop in water temperature in Sheldrake Slough.

APPENDIX E: WORKSHOP DETAILS AND PROCESS

Workshop Details/Process

During a three-day technical Workshop, SFEI hosted a diverse array of experts recruited for their knowledge of primary production and related key processes. The Workshop participants presented knowledge about primary production and transport in the Delta, communicating with the group the important controls on the primary producer group, as well as identifying key habitat attributes, and major uncertainties and knowledge gaps. The team discussed a draft conceptual model of primary production in the historical and modern Delta, and laid out assignments for individual scientists to develop a quantitative approach for estimating primary production. Four questions formed the basis of the discussions during the three days:

1. What approach can we use to estimate the **magnitude** of primary production for this producer group in the (1) modern and (2) historical Delta?

2. Which habitat **conditions/factors** likely exert the most influence on the amount of primary production? How can we account for spatial, seasonal, and inter-annual variation in estimating primary production?

3. What can we say about the **transport and connectivity** of this production to areas where it would be available to primary consumers of interest, historically, and today? Describe the fluxes across habitat types.

4. What is the **bioavailability** of this production? How much of this production is routed through the food web?

Ideas were discussed in plenary, and in small groups. The end of each of the days provided time to discuss management implications, broader picture analysis, and opportunities to cross-pollinate.

High Priority Knowledge and Data Gaps Identified in Phase 1

The following data and knowledge gaps were identified for Phase 2 calculations:

- Uncertainty around nutrient concentrations/levels in the historical Delta
- Uncertainty around sediment loads and suspended sediment concentrations in the historical Delta

- Lack of productivity and distribution data for non-phytoplankton microalgae in the modern Delta
- Above and below-ground biomass studies in emergent and scrub-shrub wetland communities in the Delta
- Linkage of above studies with remote sensing approaches
- Uncertainty around inter-annual variation in SAV/FAV abundance, and how well average production can be estimated
- Relative contributions of organic matter from riparian forests as compared to OM contributions from other Delta sources
- Aquatic habitat and productivity losses from removal of dead wood from channels
- Site specific characteristics of riparian vegetation from multiple Delta locations
- Changes in bioavailability of riparian-derived OM caused by widespread invasive species

Additional data gaps and uncertainties surround the controls on spatial and temporal variability in production, food web pathways, and physical transfers within the Delta. These gaps will be identified and addressed in Phase 3.

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