2016

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Recommended Citation

Cloern, James E.; Robinson, April; (...); Canuel, Elizabeth A.; and et al, Primary Production in the Delta: Then and Now (2016). *San Francisco Estuary & Watershed Science*, 14(3).
doi: 10.15447/sfews.2016v14iss3art1

Title
Primary Production in the Delta: Then and Now

Journal
San Francisco Estuary and Watershed Science, 14(3)

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Publication Date
2016

DOI
https://doi.org/10.15447/sfews.2016v14iss3art1

OCTOBER 2016

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Sponsored by the Delta Science Program and the UC Davis John Muir Institute of the Environment

ESSAY

Primary Production in the Delta: Then and Now

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Volume 14, Issue 3 | Article 1
doi: http://dx.doi.org/10.15447/sfews.2016v14iss3art1

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ABSTRACT

To evaluate the role of restoration in the recovery of the Delta ecosystem, we need to have clear targets and performance measures that directly assess ecosystem function. Primary production is a crucial ecosystem process, which directly limits the quality and quantity of food available for secondary consumers such as invertebrates and fish. The Delta has a low rate of primary production, but it is unclear whether this was always the case. Recent analyses from the Historical Ecology Team and Delta Landscapes Project provide quantitative comparisons of the areal extent of 14 habitat types in the modern Delta versus the historical Delta (pre-1850). Here we describe an approach for using these metrics of land use change to: (1) produce the first quantitative estimates of how Delta primary production and the relative contributions from five different producer groups have been altered by large-scale drainage and conversion to agriculture; (2) convert these production estimates into a common currency so the contributions of each producer group reflect their food quality and efficiency of transfer to consumers; and (3) use simple models to discover how tidal exchange between marshes and open water influences primary production and its consumption. Application of this approach could inform Delta management in two ways. First, it would provide a quantitative estimate of how large-scale conversion to agriculture has altered the Delta's capacity to produce food for native biota. Second, it would provide restoration practitioners with a new approach—based on ecosystem function—to evaluate the success of restoration projects and gauge the trajectory of ecological recovery in the Delta region.

KEY WORDS

Sacramento–San Joaquin Delta, ecosystem restoration, primary production, historical ecology, food quality, habitat connectivity, land-use change

INTRODUCTION

The Sacramento–San Joaquin Delta is a highly disturbed ecosystem bearing little resemblance to the habitat mosaic, hydrological system, and biological communities that existed in the mid-19th century. Continuing losses of native plants, mammals, resident and migratory birds, fish, and their invertebrate prey motivated California's Delta Reform Act that established a goal of protecting, restoring, and enhancing the Delta ecosystem. This goal is challenging because of the magnitude and diversity of human disturbances that have reduced the Delta's capacity to support native plant and animal communities. Meeting this goal will require actions grounded in scientific understanding of how each human disturbance alters the ecosystem processes that sustain native biota.

We outline here a science-based approach to measure the effects of one human disturbance—land-use change—on the ecosystem process of primary production. The capacity of ecosystems to support consumer populations is determined in part by the quantity and quality of primary production—the supply of food energy and biochemicals required to produce animal biomass. An inventory of organic–carbon sources revealed that the Delta is a low-productivity ecosystem (Jassby and Cloern 2000). One consequence of low productivity is limited availability of high-quality food for consumers such as fish and invertebrates. Ultimately, this food limitation constrains the ability of managers to meet biological recovery goals for the Delta. But is low productivity an inherent attribute of the Delta, or is it largely a consequence of human disturbances such as land-use change? How much has primary production changed over time, and how much would it be enhanced through different restoration actions? What are the rates and food value of production by non-native aquatic plants in today's Delta?

These questions are relevant to EcoRestore, California's recovery plan for the Delta, to restore over 17,500 acres of floodplain habitat, 3,500 acres of managed wetlands, and 9,000 acres of tidal and sub-tidal habitat (*http://resources.ca.gov/ecorestore/*). This and other recovery plans are built from an expectation that habitat restoration will lead to recovery of lost ecosystem functions that result from land-use change. This expectation is largely based on qualitative "guiding images" (Palmer et al. 2005) of the undisturbed Delta. However, the Historical Ecology Team (Whipple et al. 2012) and Delta Landscapes Project (Grossinger et al. 2014) have recently produced spatially explicit comparisons of the Delta's historical and contemporary habitat mosaics. These provide, for the first time, opportunities to (1) quantify the effects of land-use change on Delta primary production, and (2) compare anticipated increases of primary production from planned habitat restoration actions against a baseline of historic primary production in the Delta.

A HYPOTHESIS

In October 2015, we met in a workshop sponsored by the Delta Science Program and the U.S. Geological Survey to discuss approaches for exploring this new opportunity. Discussions centered on a conceptual model of the Delta's primary producer groups, factors that regulate their productivity, routing of their production through food webs, and approaches that could be used to convert the new metrics of habitat change into metrics of altered primary production. A detailed workshop report (Robinson et al. 2016) is available online: *http://www.sfei.org/sites/default/files/biblio_files/Primary Production in the Sacramento-San Joaquin Delta 3-31-2016.pdf*. This essay is a synopsis of that report.

The workshop was inspired by a few simple calculations that used measures of land-use change in the Delta since the mid-19th century (Table 1). Coverage of freshwater emergent (tule and scrub–shrub) wetlands decreased from 193,224 to 4,253 ha while open-water habitats increased from 13,772 to 26,530 ha (Grossinger et al. 2014). Annual production of tules in managed marshes is about 2000 $\mathrm{g\,C\,m^{-2}}$ (Miller and Fuji 2010) compared to phytoplankton production of about 100 $\mathrm{g\,C\,m^{-2}}$ (Jassby et al. 2002). Therefore, annual tidal marsh production has decreased from about 3,800 to 85 kilotons of carbon while phytoplankton production has increased from about 14 to 27 kilotons of carbon. This calculation suggests a hypothesis (depicted in Figure 1) that can now be tested.

Hypothesis

The Delta has been transformed from
a high-productivity ecosystem largely
dependent upon marsh-based production to a
low-productivity ecosystem dependent upon
production of aquatic plants and algae.

TESTING THE HYPOTHESIS

The calculations above are suggestive of large-scale change but they are not sufficient to test the hypothesis because: (1) the primary producer community is diverse and occupies all habitat types listed in Table 1—for example, marsh-based production includes production by micro-algae not considered above, and the extent of riparian habitat in the historical Delta suggests that litterfall was once an important energy source to aquatic food webs; (2) the quality and accessibility of primary production to consumers varies across producer types; (3) primary production and its consumption are not static processes; and (4) transport processes influence production and its routing to aquatic food webs. Workshop participants considered each of these complicating factors and how information could be gathered to measure the effects of land-use changes on primary production.

Diversity of Primary Producers. Three groups of vascular plants occupy different habitat types: submerged and floating aquatic vegetation (SAV/FAV), marsh plants, and riparian vegetation along shorelines. Two microalgal groups include phytoplankton suspended in water and benthic/epiphytic species living in sediments and attached to surfaces. For each group we considered that a combination of models, measurements, and professional judgments could be used to assign a characteristic rate of primary production and identify sources and magnitudes of uncertainty. These rates could then be applied across past and present habitat areas (Table 1) to compare annual production of the five producer groups in the historical and modern Delta.

Food Quality and Transfer Efficiency to Aquatic Consumers. Primary producers have different food values to consumers because they have widely ranging elemental and biochemical compositions (Hessen et al. 2013). Microalgae such as diatoms have high nutritional value because they are rich

Table 1 Changes in the areal extent of 14 habitat types in the Delta since the mid 19th century. Source: Grossinger et al. (2014).

		Area (ha)		
	Habitat Type	***Historical***	***Modern***	***% Change***
🟦	Managed wetlands	0	9,454	∞
⬜	Urban/Barren	0	35,517	∞
⬜	Agriculture/Non-native/Ruderal	0	216,085	∞
🟫	Stabilized interior dune veg.	1,032	4	-99
🟩	Willow riparian scrub/shrub	1,637	2,878	+76
🟩	Willow thicket	3,567	132	-96
🟨	Grassland	9,108	11,800	+30
▨	Alkali seasonal wetland complex	9,193	238	-97
▨	Vernal pool complex	11,262	3,007	-73
🟦	Water	13,772	26,530	+93
🟩	Valley foothill riparian	15,608	4,010	-74
🟨	Oak woodland/savanna	20,460	0	-100
🟩	Wet meadow/Seasonal wetland	37,561	2,445	-93
🟦	Freshwater emergent wetland	193,224	4,253	-98

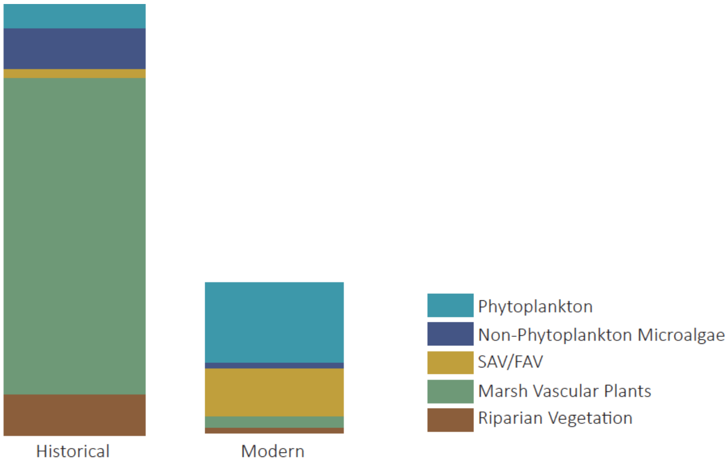

Figure 1 Hypothesized changes in Delta primary production (height of bars) and the relative contributions of five primary producer groups, based on changes in the areal extent of 14 habitat types since the mid-19th century (see also Table 1). The hypothesis is based on assumptions that: phytoplankton production tracked the >60% increase of open-water habitat and production by marsh vascular plants, riparian vegetation, and non-phytoplankton microalgae likely tracked the 98% loss of marsh habitat. Today's Delta waterways include large areas of submerged and floating aquatic vegetation (SAV/FAV), but the record contains little evidence of this producer group in the historical Delta.

in nitrogen (high protein and nucleic acid content) and lipids including fatty acids essential for animals (Brett and Müller–Navarra 1997). Vascular plants, and especially woody plants, have lower food value because much of their biomass is in structural compounds such as lignin and cellulose (Emerson and Hedges 2008). Therefore, the quantity of organic matter produced by each plant group does not directly reflect its availability to the food web. There are several approaches for converting primary production of each group into a common currency (carbon or energy units) that accounts for these differences in food quality. One approach is to weight primary production using its biochemical composition and corresponding calories of energy for each biochemical (Figure 2), giving high weights to those rich in proteins or lipids and low weights to those enriched in lower-quality polysaccharides and lignin. This step converts primary production into units of biologically available food (calories), which can be compared across the different primary producer groups.

The routing (trophic transfer) of energy from primary producers to aquatic consumers is also highly variable across producer groups. Microalgae are generally consumed directly by consumers, resulting in high trophic transfer efficiencies (~ 15% to 30%; Likens 2010). Macrophytes have lower trophic transfer efficiencies because their biomass must first enter the detrital pool by undergoing decomposition before becoming available to macroconsumers. During this process, macrophyte litter is colonized by fungi and bacteria, increasing its nitrogen content and nutritional value. Only about half of macrophyte production enters the detrital pool; the rest is lost to burial or export (Sherwood et al. 1990). The transfer efficiency from detritus to consumers is ~ 10%. Therefore, a second step (Figure 1) is required to convert the bioavailable fraction of production by each producer group into a quantity of carbon or energy available to primary consumers such as rotifers, amphipods, copepods, and insect larvae.

Hydrology as a Source of Variability. The historical Delta was a vast wetland region. Approximately 2,450 km^2 of its surface was inundated at high tide, and an additional 1,000 to 1,300 km^2 was seasonally inundated by flood waters during wet years (Grossinger et al. 2014). Fluvial inundation of marsh plains and floodplains expands the habitat for microalgal production that is either exported

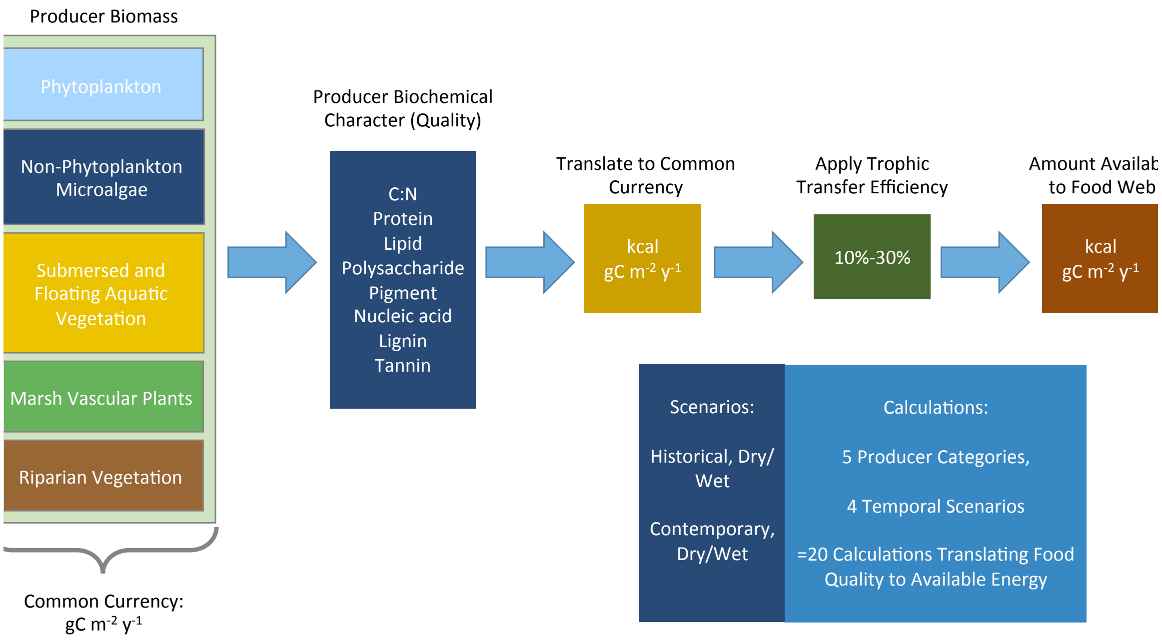

Figure 2 A process for (1) converting annual production of five primary producer groups into a common currency that accounts for differences in their food quality (biochemical composition), and (2) measuring the amount of that bioavailable production available to consumer organisms. (Source: Robinson et al. [2016], Figure 7.)

to channel habitats or consumed locally to support production of invertebrates and their predators such as juvenile Chinook Salmon and Splittail (Sommer et al. 2004). From maps of the historical and modern Delta (Figure 3) we can measure minimum and maximum extents of inundation during wet and dry years. From the steps above, we can estimate annual primary production both in the historical and modern eras and under wet- and dry-year conditions. This would then compare the effects of hydrologic variability and lost connectivity between land and water on Delta primary production. It would also provide one measure of the variability of annual primary production, recognizing that freshwater inflow is a key driver of that variability.

A Simple Model of Tidal Exchange. All calculations described above depict individual habitat types in isolation from the others. However, primary production and its use by consumers are strongly influenced by connectivity across habitats (Cloern 2007) and, in particular, by tidal water exchanges of sediments, nutrients, detritus, and small consumers among aquatic, floodplain, and marsh plain habitats. Levees now block this connectivity: the historical Delta had over 3,000 km of edge habitat connecting large marshes to water, but only 31 km remain (Grossinger et al. 2014).

This loss of connectivity between marshes and water might be as important to overall Delta ecosystem

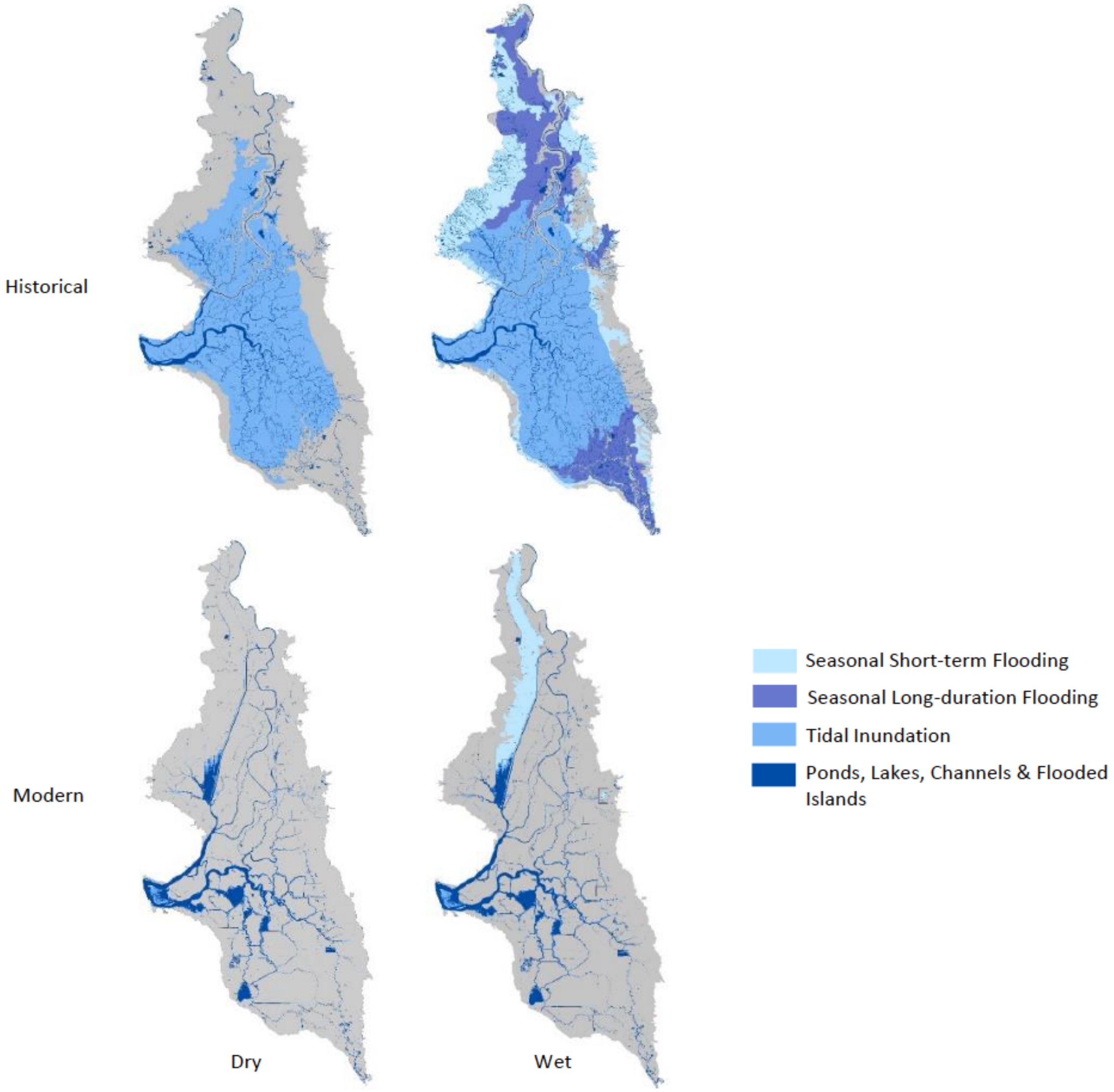

Figure 3 Flooding patterns as maximum extent of inundation in the historical and modern Delta during dry (left) and wet (right) years. Modified from Grossinger et al. (2014).

productivity as habitat losses. Testing this hypothesis requires coupling of a tidal hydrodynamics model with a production–consumption model. This is a major undertaking, but simple models can be used to begin exploring the ecological significance of lost habitats and their connectivity. An existing nutrient–phytoplankton–zooplankton model (Cloern 2007) can be coupled to a two-box model that represents tidal exchanges of water and sediments between a marsh and tidal channel (Figure 4). This tool could be used to address first-order questions, such as: (1) Does the movement of water onto marsh plains create shallow aquatic habitat that substantially increases microalgal production relative to the static calculations described above? (2) Did marsh habitats in the historical Delta trap sediment to clear its waters and increase primary production in aquatic habitats?

Expected Outcomes. The October 2015 workshop identified a science-based approach to: (1) produce the first quantitative estimates of how land use change has altered Delta primary production and contributions from different producer groups; (2) convert these production estimates into a common currency so the contributions of each producer group reflects its food quality and transfer efficiency to consumers; and (3) use simple models to explore the ecological significance of lost habitat connectivity within the Delta. These outcomes could help shape a larger research and modeling agenda that addresses specific questions about how management and restoration could best support the recovery of essential ecosystem processes, such as primary production, across the Delta region.

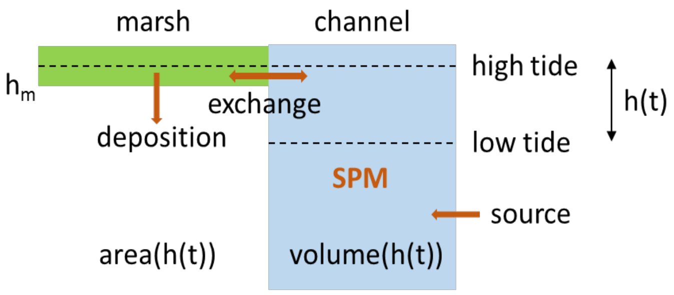

Figure 4 A two-box model of marsh and channel interaction. h(t) represents tidally-variable water elevation at time *t*; h_m is marsh elevation; SPM is suspended particulate matter. The model could simulate tidal transports of SPM, nutrients, phytoplankton, and zooplankton between marsh and water, and compute primary and consumer production. (Source: Robinson et al. [2016], Figure D.8.)

WHY IS THIS INFORMATION IMPORTANT?

Resource managers face a dizzying array of decisions about how to protect, restore, and enhance the Delta ecosystem while also providing reliable water supplies for human uses. These decisions address wide-ranging topics such as contaminant inputs, freshwater inflow, water exports, sewage treatment, invasive species, and habitat restoration. The Delta Stewardship Council's *Delta Plan* recognizes that strategies to meet goals of the Delta Reform Act must be strongly grounded in scientific understanding of the Delta as an ecosystem (*http://deltacouncil.ca.gov/sites/default/files/documents/files/DeltaPlan_2013_CHAPTERS_COMBINED.pdf*). The Delta Science Program (DSP) identified 17 action areas to address critical knowledge gaps (*http://deltacouncil.ca.gov/sites/default/files/2014/11/ISAA_final_110714.pdf*), and the science-based approach described here addresses two of these: habitat restoration and lower aquatic food webs. Restoration targets in the *Delta Plan* are provided as total areas of each habitat type including floodplain, tidal and subtidal, emergent wetland, and riparian forest. However, the biological outcomes of these restoration actions cannot be estimated, partly because the ecological functions provided by each habitat type have yet to be quantified. We present an approach for measuring how the life-sustaining process of primary production has changed across the altered habitat mosaics of the Delta.

This approach could inform Delta management in two ways. First, it would measure historical losses in the Delta's capacity to produce food for native biota. This information would provide a quantitative basis for understanding the consequences of land-use change as one component of a complex, multi-stressor problem. Second, it would identify those restoration actions most likely to increase ecosystem production and, thus, provide an objective basis to prioritize restoration actions and locations. This strategy would lead to a more accountable approach for planning and gauging the trajectory of ecological recovery in the Delta region.

ACKNOWLEDGEMENT

The Delta Science Program and the U.S. Geological Survey provided funding for the workshop summarized in this essay.

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