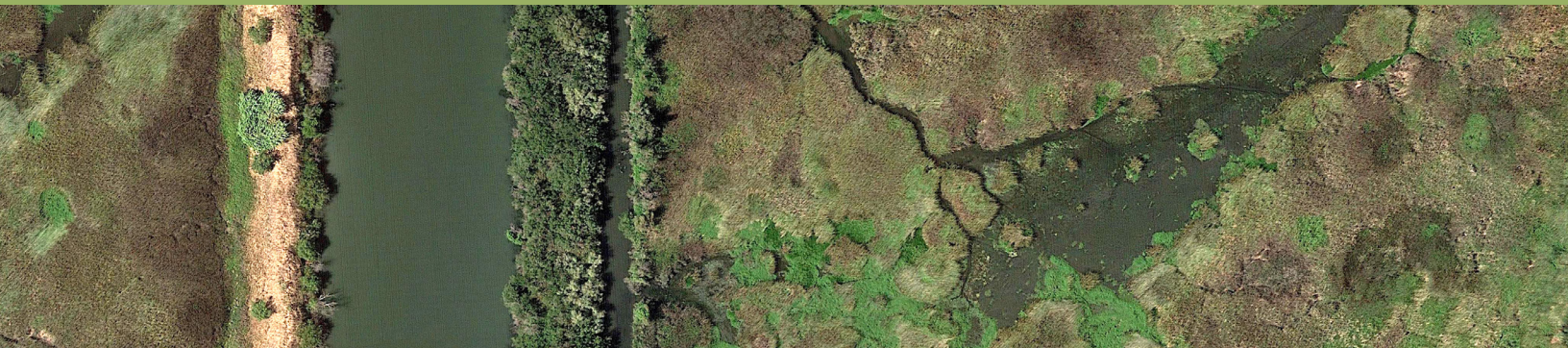


**DELTA LANDSCAPES  
PRIMARY  
PRODUCTION**

Past,  
Present,  
Future







# DELTA LANDSCAPES PRIMARY PRODUCTION

Past,  
Present,  
Future



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Delta Stewardship Council



**Delta  
Science  
Program**

DELTA STEWARDSHIP COUNCIL

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*SUMMARY OF*  
**Delta  
Landscapes  
Primary  
Production:**

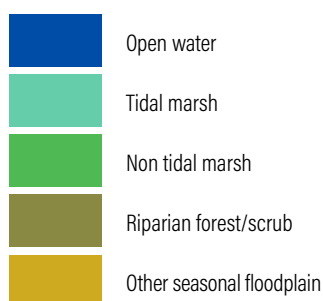
*PAST, PRESENT, FUTURE*

The historical Sacramento-San Joaquin Delta was a highly productive freshwater estuary, dominated by tidal marsh. Primary production by algae and plants provided year-round food and structural habitat for aquatic consumers. Today, only a small fraction remains of the historical “hydrologically connected Delta,” defined as open water, wetlands, and other seasonally flooded habitats that are linked by surface flows. This area is the food-producing engine for the Delta’s aquatic invertebrates, fish, mammals and birds. As this area has shrunk, so has the system’s capacity to feed its aquatic consumers.

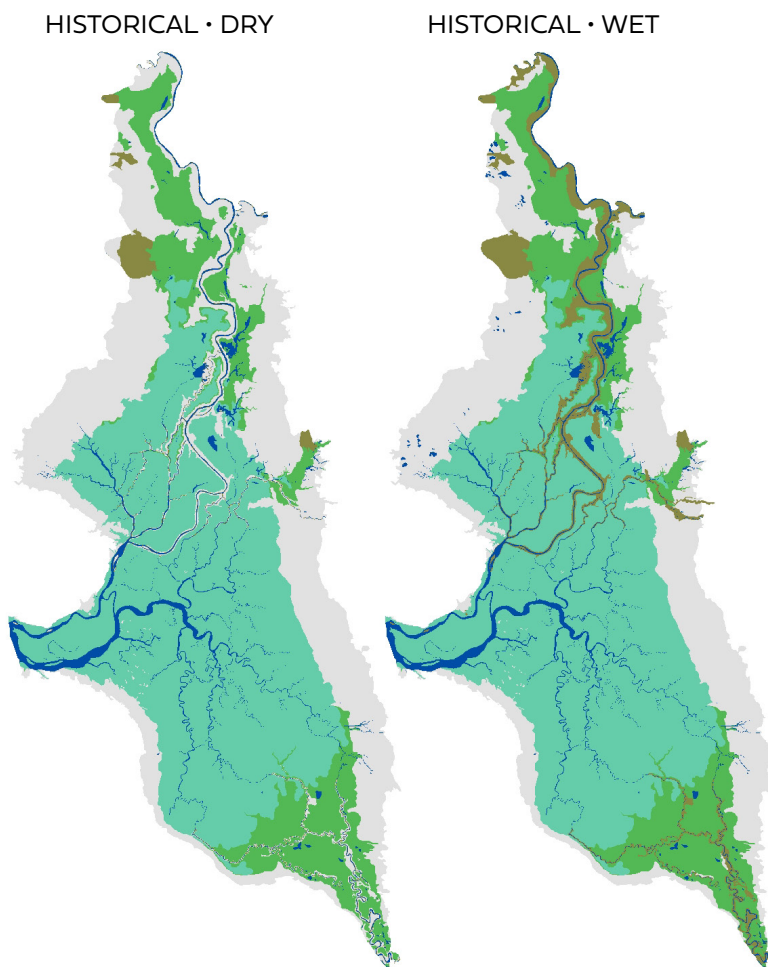
This report describes the Delta Landscapes Primary Production project, which quantifies how landscape change in the Delta has altered the quantity and character of primary production. Combining historical and modern maps with simple models of production for five dominant plant and algae groups, we estimate primary production across the hydrologically connected Delta. We evaluate changes in primary production over time (between the early 1800s and early 2000s), between wet and dry years, and with future targets for landscape-scale restoration.

For managers in the Delta, restoring historical patterns of primary productivity is a means to better support native fish and other wildlife. To better equip decision makers in managing for improved primary production, this study offers historical context and the best available science on the relative production value of habitat types and their configurations.



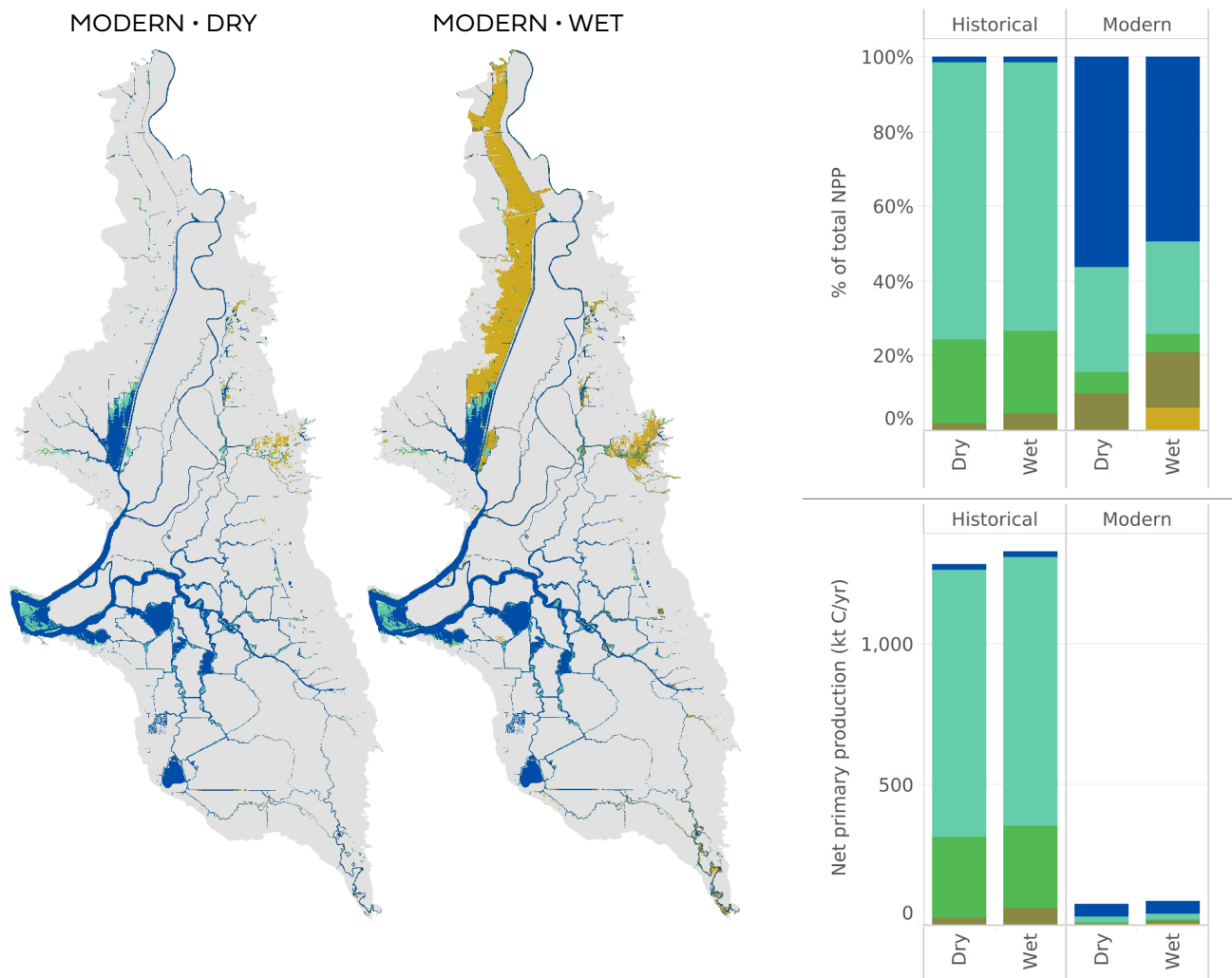


Since the early 1800s, landscape change has decreased primary production in the hydrologically connected Delta by more than 90%. Primary production has shifted from wetland-based sources (marsh plants and microalgae) to open-water based sources (phytoplankton and invasive aquatic vegetation).



## Key findings

- Since the early 1800s, **landscape change in the Delta has decreased primary production by more than 90%** within the hydrologically connected region, from over 1000 kilograms of carbon (kg C) per year to less than 100 kg C per year.
- The portfolio of production in the modern hydrologically connected Delta bears little resemblance to its historical counterpart. **Primary production has shifted from marsh plants and algae (wetland-based sources) to phytoplankton and invasive aquatic vegetation (open-water based sources).** Restoring the historical portfolio of habitat types and primary producers in the Delta may help native fish populations recover.
- **In the historical Delta, over 95% of the total primary production was generated in marshes.** In addition to vascular plant material, these historical marshes produced nearly all of the Delta's attached microalgae and over half of the phytoplankton. In stark contrast, around half of all primary production in the modern hydrologically connected Delta comes from open-water areas.
- Marshes are highly productive on a per-area basis. **Even with dramatic losses (98%) in their historical extent, tidal and non-tidal marsh remain an important source of food for fish and their invertebrate prey.**



- In the modern Delta, the extent, depth, and duration of flooding in seasonal floodplain areas exert strong controls on the growth of phytoplankton and attached microalgae. **By prioritizing flooding in these agricultural fields, managed wetlands, and grasslands, water managers in the Delta may increase contributions to total primary production.**
- **In the historical Delta, marsh primary production potentially supported 10 times as much primary consumer biomass as all the other habitat types combined.** In the modern Delta as well, stable isotope data indicate that **marsh plants are the dominant source of primary production in the diets of aquatic consumers.**
- **Delta Plan targets for wetland restoration could nearly triple primary production in the hydrologically connected Delta,** with a 7-fold increase in marsh plant production and a 4-fold increase in attached microalgae. Marsh restoration at this scale would feed grazing invertebrates, the detrital food web, and ultimately fish, while shifting the balance of the aquatic food web to more wetland-based sources of primary production.

## *Opportunity for Action*

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Restoration matters for primary production. By restoring wetlands in the Delta, managers have the opportunity to rebuild and rebalance the primary production at the base of the aquatic food web. Tidal marshes in the Delta have high rates of primary production, diverse types of primary producers, and varied food-web pathways. Restoring marshes that are hydrologically connected is an efficient way to increase year-round food web support and provide important co-benefits, such as habitat structure and carbon sequestration. In the years when they are inundated, seasonal floodplains also produce food that benefits fish. Future management and restoration of floodplains in the Delta could increase valuable phytoplankton resources.



Eastside Bypass on the San Joaquin River. Photo courtesy of USFWS





Riparian vegetation in the Delta. Photo by Amy Richey, SFEI

## Acknowledgments

The Delta Landscapes Primary Production project was funded by the Delta Stewardship Council as a follow up to the Delta Primary Production Workshop and ensuing science plan. We are grateful for this financial support and for the Stewardship Council's guidance and feedback through all stages of the work, particularly from Karen Kayfetz, Eva Bush, John Callaway, Cliff Dahm, and Jessica Law. This project benefited greatly from input from our scientific advisors and reviewers, David Schoellhamer, Si Simenstad, Ron Kneib, and Liz Canuel. We also thank the attendees of a January 7, 2020 workshop, whose input helped steer this project toward the primary concerns of managers in the Delta.

## *Primary production in context*

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Estuaries and freshwater wetlands are some of the most productive ecosystems on Earth. These systems support a diverse array of plants, algae, invertebrates, fish, and other aquatic consumers, in turn providing resources for birds, humans, and other connected ecosystems. At the base of the estuarine food web, algae and plants in wetlands and open water fix carbon from the atmosphere into biomass through photosynthesis. This primary production is a first-order control on the carrying capacity for fish and other aquatic consumers.

The historical Sacramento-San Joaquin Delta was a highly productive freshwater estuary. As the largest tidal marsh on the North American Pacific coast, the extensive wetlands of the historical Delta provided habitat and year-round food for fish and other wildlife. Primary production in the historical Delta supported California's largest salmon runs, bird migrations on the Pacific Flyway, now-threatened, endemic species such as Delta smelt, hundreds of other wildlife species, and many people in the Native American communities of the region.

**In the modern Delta, humans have appropriated much of the historical productivity.**

Wetland conversion to agriculture has led to a near-complete loss of tidal and non-tidal marshes, eliminated many small tidal channels and straightened large ones, and reduced hydrological connectivity between land and water. The Delta of today remains highly productive as an agricultural region, but at great cost to the native aquatic ecosystem. While Delta phytoplankton production is known to be low relative to other estuaries (Jassby et al., 2002), the impacts of wetland loss on primary production across a suite of producers has received little study.

Although these habitat losses have profoundly altered Delta ecosystems, the modern Delta supports many ecological functions and services. The Delta is home to a range of invertebrates, fish, birds, and other aquatic organisms. However, it is well recognized that changes to the status quo are necessary to maintain and improve ecological health, as well as water supply reliability and the resilience of the Delta's landforms relative to earthquakes and flooding. Management actions to improve primary productivity, such as habitat restoration, enable managers to support desired ecological communities, particularly when and where they are limited by food availability. Managing effectively for primary productivity requires empirical information on the relative production value of habitat types and configurations (such as marsh size and channel network structure).

## *Project goals and scope*

---

The Delta Landscapes Primary Production project addresses the question: **How has landscape change in the Delta altered the quantity and character of primary production that is potentially available for the aquatic food web?** To evaluate historical changes in primary production, we estimated primary production in the historical (early 1800s)





Cosumnes River Preserve. Photo by Bob Wick, courtesy of Bureau of Land Management

and modern Delta (early 2000s) for wet and dry years, as a result of changes in the extent of hydrologically connected habitats. We quantified changes in Delta-wide production from major producer groups and habitat types, which translate to changes in the portfolio of production entering the aquatic food web.

Humans have modified Delta ecosystems in a multitude of ways over the last 200 years. In this highly altered system that faces multiple stressors, this project isolated the effects of one broad change, wetland habitat loss, on one key metric of ecological function: primary production available to the aquatic food web. Other variables related to human impacts were held constant, including nutrient loads, sediment supply, hydrology (e.g., flow regime and precipitation), and the presence of invasive clams. This simplified approach offered a straightforward framework to link estimates of primary production to metrics of change in the spatial extent of habitat types. Key examples of landscape change include freshwater tidal marsh loss and fragmentation; increased channel volume due to channel cuts, widening, and deepening; and the creation of novel habitat types, such as flooded islands.

This project was designed with decision makers in mind. Metrics of primary production in the historical Delta—the magnitude and composition of primary production entering the historical food web—provide meaningful context for restoration and management decisions. By comparing production rates in wet vs. dry years, we can identify habitat types in the Delta where primary production is responsive to water-availability variations. Finally, our framework and areal productivity rates can be used to estimate the effect of restoration targets on Delta-wide primary production.



In the modern Delta, humans have appropriated much of the historical productivity.



The area studied includes the full extent of the Delta's historical tidal wetlands, connected non-tidal freshwater wetlands, and upland transitional areas, as mapped in the SFEI-ASC *Sacramento-San Joaquin Delta Historical Ecology Investigation* (Whipple et al., 2012). More specifically, it is the contiguous lands and waters lying below 25 feet in elevation, which covers approximately 8000,000 acres in Sacramento, Yolo, Solano, Contra Costa, and San Joaquin counties. Note that this area differs slightly from the legal Delta, as defined by the state.

Within the larger study region, **we identified the “hydrologically connected Delta,” which we define as the region of open water, wetlands, and other seasonally flooded habitats that are connected via surface flows. This highly productive region contributes plant and algal biomass to the aquatic ecosystem.** Production originating outside the hydrologically connected Delta, such as riverine inputs from upstream, were not considered in this analysis.

To delineate the historical hydrologically connected Delta, we used the mapped historical extent of four dominant habitat types: *open water*, *tidal marsh*, *non-tidal marsh*, and *riparian forest/scrub*. For the modern Delta, we used the same habitat types, but only the subset with a possible surface water connection to the aquatic ecosystem (those not located behind a levee). We also included a fifth habitat type in the modern Delta, which we refer to as *other seasonal floodplain*. This habitat type denotes other areas (like agricultural fields, managed wetlands, and grasslands) not located behind a levee and shown via satellite image analysis to be periodically inundated (Pekel et al., 2016).

We evaluated changes in the hydrologically connected Delta by mapping its historical (early 1800s) and modern (early 2000s) extent for wet and dry years. Historically, freshwater inflows to the Delta were driven by the natural flow regimes of the Sacramento and San Joaquin Rivers and other rivers flowing into the Delta. Today, water management, including large upstream dams, regulate how much and when freshwater flows into the Delta. We identified wet and dry years as the upper (wet) or lower (dry) 20th percentiles of total annual Delta outflow within the modern managed period (CDWR, 2019). The estimated number of days and associated area of flooding for the wet and dry years (or “water year types”) were used in our analysis. Given the high year-to-year variability of inundation extent in other seasonal floodplain areas, we delineated this region as the maximum inundated extent

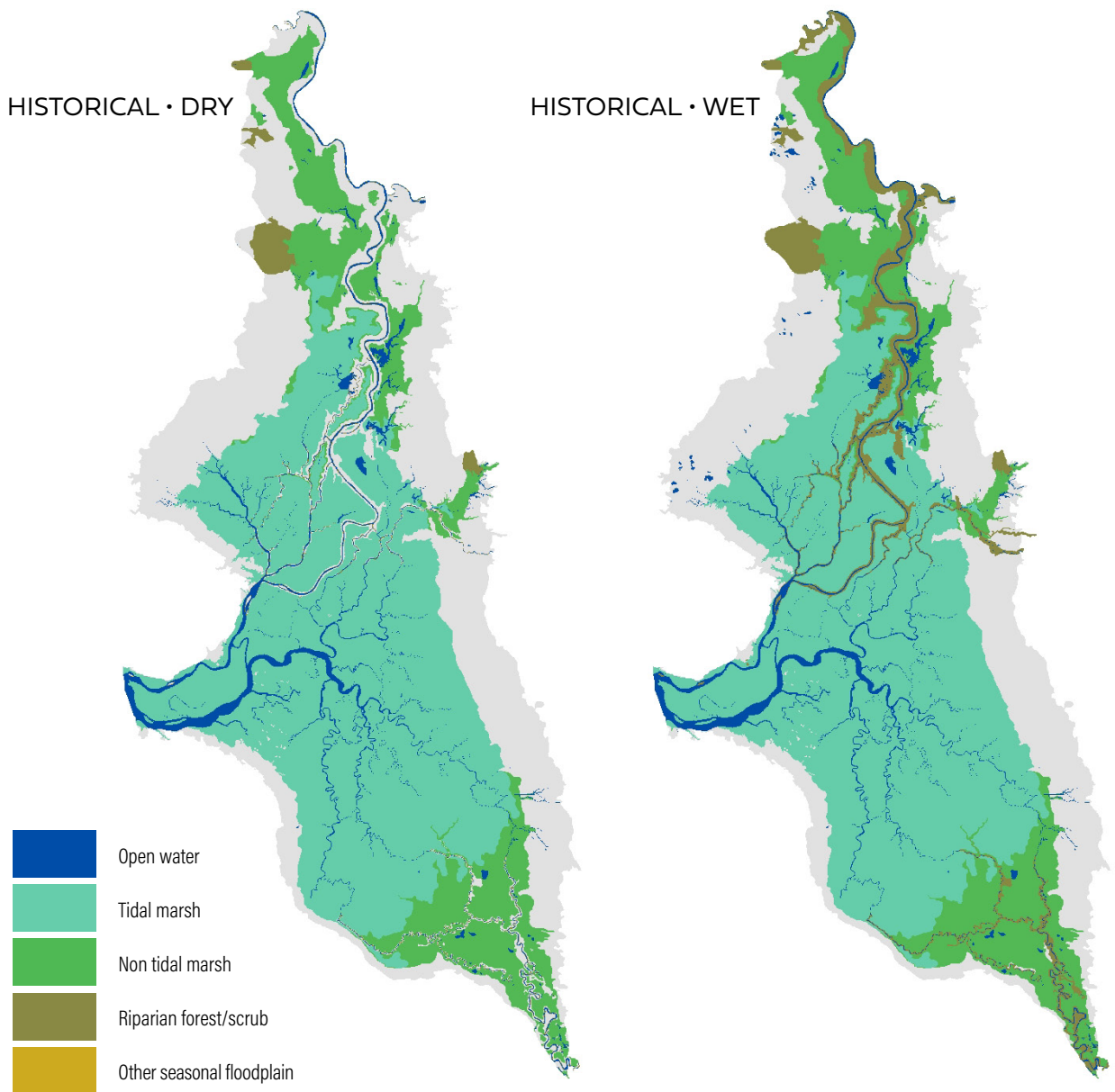
for wet or dry sets of years, based on all available satellite images for each water year type. We also counted only the portion of the riparian forest/scrub areas that is located within 25 m of a channel as hydrologically connected in dry years. Therefore, differences between wet and dry years in this analysis related only to expected differences in extent and duration of inundation for the modern flow regime. Actual differences between wet and dry years are expected to be much larger for both historical and modern eras. For a detailed description of our landscape change analysis methods and assumptions, see the online appendix: <https://www.sfei.org/projects/delta-landscapes-primary-production>.

Due to landscape change over the past 200 years, the extent of the hydrologically connected Delta, as defined here, has decreased by 77% in wet years (from 562,000 to 131,000 acres) and 85% in dry years (from 522,000 to 80,000 acres). The habitat types that comprise the hydrologically connected Delta have also shifted dramatically. Whereas the hydrologically connected Delta has lost 98% of its marsh area and 68-78% its riparian forest/scrub (depending on the water year type), the area of perennial open water has increased by ~80%, largely due to channel widening and the formation of novel flooded islands such as Liberty Island and Franks Tract.

Habitat type	Definition	Historical* (acres)	Modern* (acres)	Change (%)
<b>Open water</b>	Mostly permanently inundated areas devoid of emergent vegetation, including tidal and fluvial channels, ponds/lakes, and flooded islands. Can also include some seasonally or temporarily flooded depressions, largely devoid of emergent palustrine vegetation (e.g. large vernal pools).	36,000	62,500	+73%
<b>Tidal marsh</b>	Perennially wet areas with a high water table dominated by emergent vegetation and at least periodically wetted/inundated by tidal flows.	361,200	7,800	-98%
<b>Non-tidal marsh</b>	Temporarily to permanently flooded, permanently saturated, freshwater non-tidal wetlands dominated by emergent vegetation occupying upstream floodplain positions above tidal influence.	109,300	1,500	-99%
<b>Riparian forest/scrub</b>	Riparian vegetation dominated by woody trees, scrub, or shrubs generally occupying elevated, periodically flooded areas along channels.	55,000	12,100	-78%
<b>Other seasonal floodplain</b>	Other seasonally or temporarily flooded areas that are connected to the aquatic ecosystem via surface flows, including agricultural areas, managed wetlands, grasslands, and other areas dominated by short-statured herbaceous vegetation. Largely located within the Yolo Bypass and other floodplains along the Cosumnes and San Joaquin rivers.	0	46,900	--
<b>Total (all habitat types)</b>		<b>561,600</b>	<b>130,800</b>	<b>-77%</b>

\*Values shown for wet years only.

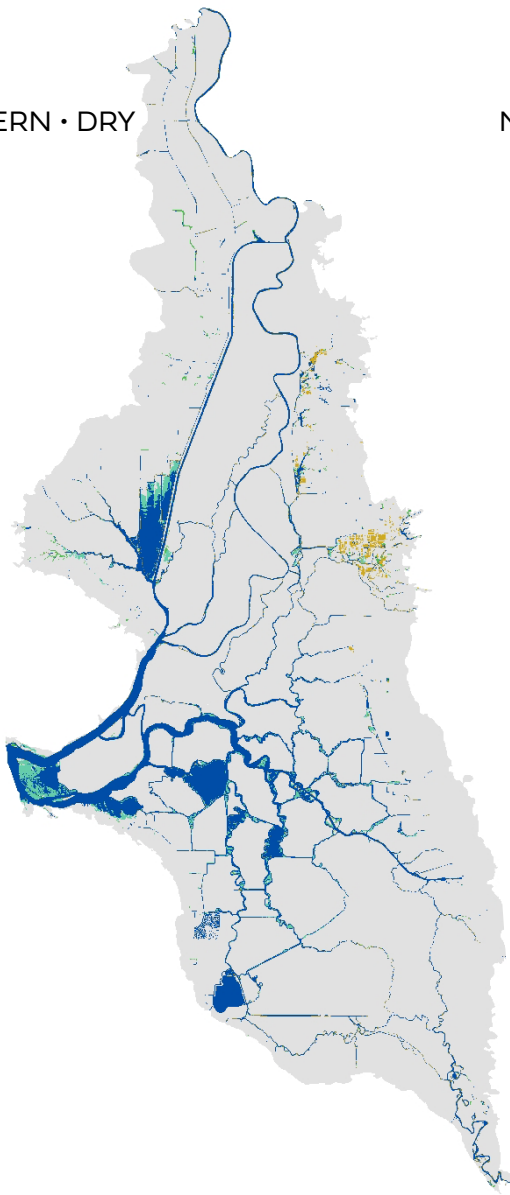
## 2. THE HYDROLOGICALLY CONNECTED DELTA



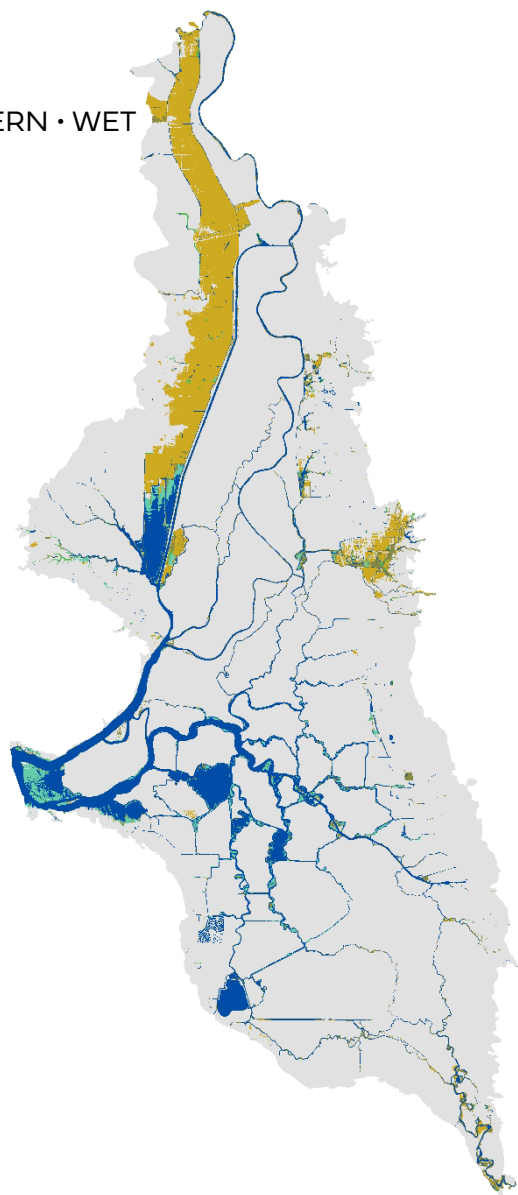
**KEY MESSAGE** • Landscape change has deeply altered the primary production engine of the Delta. By appropriating productivity for agriculture, humans have removed nearly all wetlands and most of the riparian vegetation that historically contributed to the base of the aquatic food web. These changes have created new types of seasonal floodplains and increased the area of open water, augmenting the importance of these habitat types for supporting aquatic food webs.



MODERN • DRY



MODERN • WET



Sandhill cranes at Stone Lakes National Wildlife Refuge. Photo by Justine Belson, courtesy of USFWS



We used best-available science to estimate changes in primary production due to landscape change in the Delta.




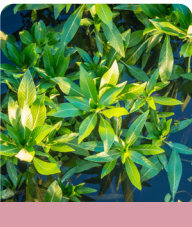



Five categories of primary producers within the hydrologically connected Delta contribute to the aquatic food web. These producers were identified by a panel of expert scientists and grouped according to major commonalities. These categories are meant to be comprehensive, covering all sources of primary production originating in the hydrologically connected Delta. Many of these groups contain a diverse array of producers, but reflect similar habitat associations.

**For each producer group, expert science advisors used relatively simple models and equations to derive estimates of production across the hydrologically connected Delta, measured in kilotonnes of carbon per year (kt C/yr).** Estimates are of net primary productivity (NPP), which measures the amount of carbon fixed through photosynthesis that is actually stored as biomass (the total amount of captured energy minus the portion used by the primary producers for their own metabolism/cellular respiration).

To focus on the direct effects of landscape change on production from each group, we made simplifying assumptions for other drivers of change. For example, for both historical and modern production estimates, we used the current flow regime (post-1980) to determine when and for how long each habitat type was inundated (i.e., we applied modern flows to the historical landscape). Similarly, by using modern production rates for both historical and modern estimates, we effectively assumed that other factors affecting productivity (e.g., temperature, salinity, nutrients, and water turbidity) were the same historically as they are now, and did not vary with water year. Finally, we assumed plants in areas classified as agriculture contribute zero production to the aquatic food web.

Delta-specific productivity measurements were available for marsh plants and phytoplankton in open water and non-tidal marsh. In other cases, a lack of data contributes uncertainty to our calculations. Where local data were unavailable, as for attached microalgae, aquatic plants, and woody riparian plants, we used NPP measurements from similar habitats in other geographical areas. Due to a lack of phytoplankton productivity measurements in tidal marsh, we used our open-water phytoplankton model for this habitat type. In the case of aquatic plants, we applied species abundance and spatial distributions from one year of remote sensing data to the historical and modern Delta. Due to large reported differences in productivity between aquatic plant species, this assumption is a likely source of error in our estimates. A detailed description of methods, assumptions, and uncertainty sources can be found in the online appendix: <https://www.sfei.org/projects/delta-landscapes-primary-production>.

	Producer Group & Expert Scientist	Definition of Producer Group and Occurrence in Habitat Types	Approach to Estimating Primary Production
	<b>Phytoplankton</b> James Cloern (USGS)	Occurring in all habitat types except riparian forest/scrub, phytoplankton are microalgae suspended in the water column.	We used a generalized additive model to estimate productivity as a function of water depth and season. Modeled productivity rates were scaled to annual Delta-wide production according to habitat area, depth class, duration of inundation, and light limitation.
	<b>Attached microalgae</b> James Pinckney (University of South Carolina)	Occurring in all habitat types, attached microalgae are benthic algae growing in or on sediments and epiphytic algae on vegetation.	We used separate calculations for three types of attached microalgae: (1) benthic microalgae, (2) epiphytes on emergent vegetation, and (3) epiphytes on aquatic plants. For each type, median literature-based values of areal productivity were scaled to annual Delta-wide production according to habitat area, duration of inundation, and light limitation.
	<b>Marsh plants</b> Judith Drexler (USGS)	Occurring in tidal marsh and non-tidal marsh habitat types, marsh plants are emergent freshwater macrophytes growing in tidal or non-tidal marshes (e.g., tules).	We estimated annual aboveground productivity from literature values of peak standing biomass. These productivity rates were scaled to annual Delta-wide production according to marsh habitat area and the fraction of organic carbon in standing biomass.
	<b>Aquatic plants</b> Katharyn Boyer and Melissa Patten (San Francisco State University)	Occurring in the open water habitat type, aquatic plants include aquatic macrophytes that are rooted or float on the water surface, as well as associated attached macroalgae.	We used remote sensing data and plant species lists from historical and modern periods to estimate the percent cover of dominant aquatic plant species. For each dominant species, literature-based values of areal productivity were scaled to annual Delta-wide production according to open water habitat area and percent cover by depth class.
	<b>Woody riparian plants</b> Robert Naiman (University of Washington)	Occurring in the riparian forest/scrub habitat type, woody riparian plants include trees, shrubs, and their woody and herbaceous understory. Our analysis is limited to material that could potentially enter the aquatic ecosystem (e.g., trees and their litter that fall into adjacent waterways or plant material captured by meandering channels).	We identified three processes by which riparian production enters the aquatic ecosystem: (1) litterfall, including leaf litter and small woody debris; (2) channel meandering, which contributes woody and herbaceous standing vegetation, and (3) tree mortality, which contributes large woody debris. For litter inputs, annual litterfall rates from the Central Valley were applied to the Delta's riparian forest/scrub areas (their full extent in wet years and the subset within 25 m of open water in dry years). For channel meandering, literature-based values of ecosystem carbon storage were used with the length of meandering channels and lateral channel migration rates to estimate carbon inputs to the aquatic ecosystem. Annual Delta-wide inputs from tree mortality were estimated from standing aboveground carbon stocks and mortality rates, scaled to the width of the contributing band along the length of the bank.

Phytoplankton photo by Philippe Garcelon CC by 2.0; attached microalgae photo by National Science Foundation

**KEY MESSAGE** • Our production estimates for each producer group combine simple modeling frameworks with parameters from the peer-reviewed literature.



Landscape change, largely the loss of marshes, has reduced by more than 90% the primary production that is potentially available to aquatic consumers.



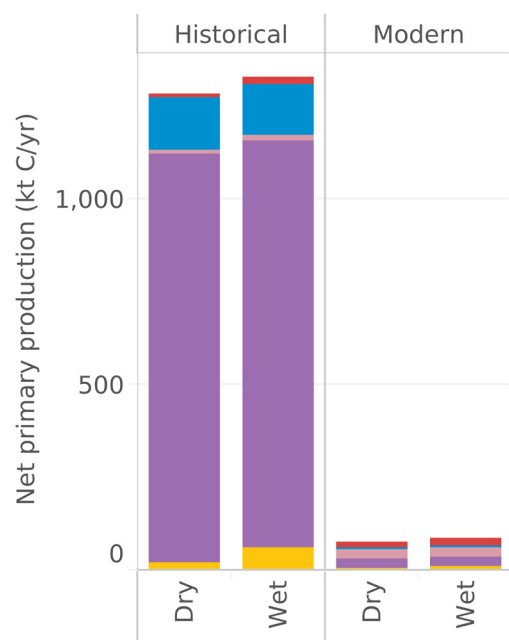
The loss of marshes and riparian forest/scrub has led to a dramatic reduction in primary production in the hydrologically connected Delta. In the historical Delta, the hydrologically connected region supported an estimated 1300 kt C/yr of primary production. Modern primary production in the hydrologically connected Delta is more than an order of magnitude lower, only 84 kt C/yr in wet years and 74 kt C/yr in dry years. This change is an estimated 94% loss of primary production.

**In the historical Delta, marshes contributed over 95% of the primary production in the hydrologically connected area.** These historical marshes produced an estimated 97% of the Delta's attached microalgae and over half of the phytoplankton (52-74% depending on water year type). **In stark contrast to these historical values, around half of all primary production in the modern hydrologically connected Delta comes from open water areas (~56% in dry years and ~49% in wet years),** which includes roughly a quarter of the attached microalgae and nearly all the phytoplankton.

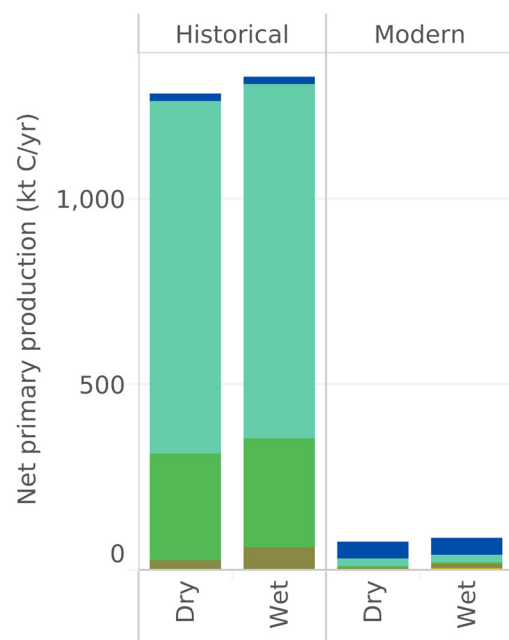
Across the five producer categories, all but aquatic plants have declined in annual production. Due to the loss of tidal and non-tidal marsh, production from marsh plants and attached microalgae decreased by over 95% between the historical and modern eras. In contrast, increases in open water led to a doubling in production from aquatic plants, with aquatic plants now supplying nearly 40% of the estimated primary production in the hydrologically connected Delta. Much of this aquatic vegetation is nonnative and/or invasive, supporting nonnative fishes in novel flooded island habitats. In spite of increased open water area, total phytoplankton production has decreased in the modern Delta due to reduced phytoplankton production in marshes.

Despite the precipitous decline in marsh area, marsh production remains significant in the modern hydrologically connected Delta. Although only 2% of their historical area remains, tidal and non-tidal marshes contribute ~30% of total annual primary production to the Delta's aquatic food web, reflecting the high productivity of marshes on a per-area basis (approximately 4 times as high as other habitat types). Marsh production is available both as immediately consumable and nutritious algae and as vascular plant tissue that enters the

## Net primary production (NPP) in the hydrologically connected Delta



Producer Group	Historical (kt C/yr)		Modern (kt C/yr)	
	Dry	Wet	Dry	Wet
Phytoplankton	12	20	11	16
Attached microalgae	140	140	4.8	4.8
Aquatic plants	13	14	30	30
Marsh plants	1,100	1,100	22	22
Woody riparian plants	21	59	6.4	12
<b>TOTAL</b>	<b>1,300</b>	<b>1,300</b>	<b>74</b>	<b>84</b>



Habitat Type	Historical (kt C/yr)		Modern (kt C/yr)	
	Dry	Wet	Dry	Wet
Open water	20	21	41	41
Tidal marsh	950	950	21	21
Non tidal marsh	290	290	4.0	4.1
Riparian forest/scrub	25	62	7.4	13
Other seasonal floodplain	0.0	0.0	0.0	5.0
<b>TOTAL</b>	<b>1,300</b>	<b>1,300</b>	<b>74</b>	<b>84</b>



## 4. PAST AND PRESENT PRIMARY PRODUCTION

detritivore food web, allowing it to be consumed and fuel the food web over a longer timeline. With such high areal rates of biomass production, diverse producer groups, and varied food-web pathways, marshes thus represent high-leverage habitats that, when restored, may offer multiple benefits for the Delta's aquatic food web.

Using our modeling approach, we found that water availability affected productivity in two modern Delta habitats: other seasonal floodplains, and riparian forest/scrub. When inundated, other seasonal floodplain areas contribute primary production to the aquatic system in the form of phytoplankton and attached microalgae. In this habitat type, the extent, depth, and duration of inundation exert strong controls on phytoplankton production, which varies by ~30% between wet and dry years, as defined in this analysis. By prioritizing flooding in this habitat type, water managers in the Delta may increase aquatic food web support from





these habitat types. This finding is consistent with empirical data and successes associated with managing the Yolo Bypass to benefit fish (Sommer et al. 2001).

Primary production from riparian forest/scrub is also sensitive to water year. Compared with dry years, estimated wet-year production is around 70% higher in this habitat type, contributing an additional 5 kt C/yr to the hydrologically connected Delta. In our calculations, this difference is due to increased contributions from litterfall. Specifically, a greater portion of the litter in riparian forest/scrub areas is assumed to reach the aquatic ecosystem in wet years, due to enhanced lateral transport of material from riparian to open water areas. The magnitude of this difference between wet and dry years is comparable to that of the 'other seasonal floodplain' habitat type. As support for aquatic food webs, however, the effect of this difference may not be as great, given that woody plant material must undergo significant decomposition to become valuable to aquatic consumers.



**KEY MESSAGE** • Restoring marshes that are hydrologically connected to aquatic ecosystems in the Delta is an efficient way to increase year-round food resources for aquatic consumers. During the growing season, marshes support grazing invertebrates and the production of attached microalgae and phytoplankton, important resources for Delta fish. During other times of year, decaying marsh vegetation fuels the detrital food web, which in turn supports a range of higher consumers.

Phytoplankton production in 'other seasonal floodplain' areas depends on inundation. This habitat type represents an opportunity for water management activities to influence primary production in the Delta.

## 5. PRIMARY PRODUCTION PORTFOLIO

For many decision makers in the Delta, primary production is valued as support for fish and other aquatic consumers. Seen this way, not all sources of primary production have equal value for the Delta's aquatic ecosystem.

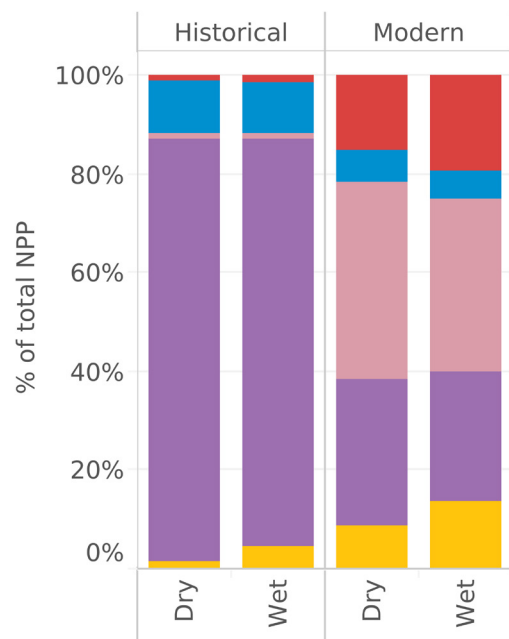


Primary production enters aquatic ecosystems at the base of a multi-step food web. Production by plants and algae is relayed to fish primarily via their invertebrate prey, which concentrate and deliver nutrients to higher-level consumers. The value of primary production in this complex aquatic food web depends on its nutritional composition, the timing of production, and the location of food resources (i.e., accessibility).

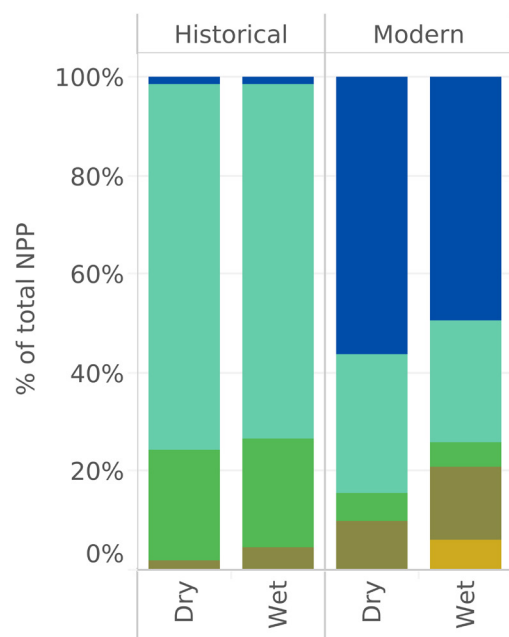
The portfolio of primary production in the modern hydrologically connected Delta bears little resemblance to its historical counterpart. This work shows that **in the historical Delta, wetland-based primary production was overwhelmingly (~95%) the largest source of organic matter entering aquatic food webs. This contrasts with the modern Delta, where around half the primary production in the hydrologically connected region is generated in open water.** The relative production of vascular plants to algae is about 60:40, similar now to what it was in the historical Delta. However, the location and type of algae and plant production has shifted from mainly marsh-based to mainly open-water-based. This shift in habitat types has brought a change in relative production from the five producer groups. Marsh plants and attached microalgae were the major sources of primary production in the historical hydrologically connected Delta, whereas the modern-day Delta is dominated by aquatic plants and their associated macroalgae. Notably, the proportion of NPP from open-water phytoplankton has increased by an order of magnitude since the historical era, now accounting for an estimated 15-20% of total primary production.

As food for aquatic consumers, the various producer groups offer different nutritional profiles. We measure primary production in units of carbon, but fish and other consumers require a suite of other nutrients in appropriate proportions, notably the macronutrients nitrogen and phosphorus. When these nutrients are not abundant enough in the consumer's diet, they can limit biomass, channeling excess carbon toward respiration ( $\text{CO}_2$ ) instead of growth. Compared with vascular plants, algae tend to be nutritionally dense, with higher nitrogen content per unit

## Relative contributions to total primary production in the hydrologically connected Delta



Producer Group	Historical (%)		Modern (%)	
	Dry	Wet	Dry	Wet
Phytoplankton	0.92	1.5	15	19
Attached microalgae	11	11	6.5	5.7
Aquatic plants	1.0	1.1	41	36
Marsh plants	8.5	8.5	30	26
Woody riparian plants	1.6	4.5	8.6	14



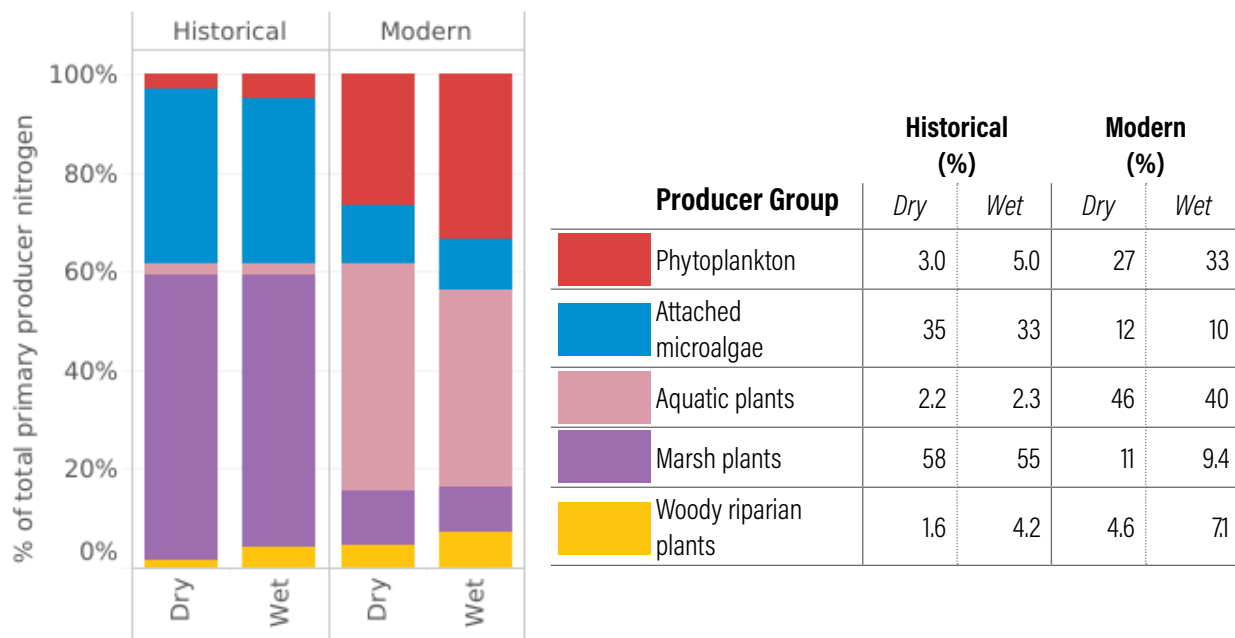
Habitat Type	Historical (%)		Modern (%)	
	Dry	Wet	Dry	Wet
Open water	1.5	1.6	55	49
Tidal marsh	73	73	28	25
Non tidal marsh	22	22	5.4	4.9
Riparian forest/scrub	1.9	4.8	10	15
Other seasonal floodplain	0.0	0.0	0.0	6.0



of biomass carbon. Using units of nitrogen instead of carbon, the algal producer groups (phytoplankton and attached microalgae) are particularly important food resources in the historical and modern Delta. While these groups historically comprised only ~12% of total primary production as measured in units of carbon, they accounted for ~38% of the available nitrogen in primary producer biomass. (These estimates are derived from the NPP calculations using the approximate ratio of carbon to nitrogen in each producer group). Compared with vascular plants, the high nitrogen concentrations of algal producers more closely match the nutritional needs of higher-level consumers. During the times of year when they are abundant, phytoplankton and attached microalgae thus offer a high value food source for aquatic consumers.

While we can make simple comparisons of nutritional quality among primary producer groups, many additional factors mediate their ultimate value to fish. These factors include complex food web dynamics (e.g., transfer of primary production from invertebrates to fish), environmental conditions (e.g., temperature, oxygen availability, and turbidity), and connectivity between habitats, which mediates consumer access to food resources and the transfer of those resources between ecosystems and through food webs. Integrating across these factors, the overall distribution of producer groups and habitat types in the historical Delta provides a model for historical food web support. In the

### *Relative contributions to total primary producer nitrogen in the hydrologically connected Delta*



highly modified Delta of today, native consumers may be poorly adapted to spatial and temporal patterns of production; i.e., they may lack the behaviors or anatomy required to access production, and the timing of primary producer biomass growth may not match their life cycle demands. For example, native fishes must now utilize different habitats to access their prey, with potentially greater risk of predation from nonnative bass-family fish in aquatic plant beds.

In the historical Delta, primary production from tidal and non-tidal marshes made up a far greater proportion of total primary production than it does today. Marshes offer food resources and habitat for invertebrates and detritivores that make up a large part of many fish diets. Although marsh vegetation is a relatively low-quality food source compared to algae, this habitat type offers indirect benefits that have been lost in the modern Delta. Marsh vegetation provides spawning surfaces, protection from predators, and water clarity improvement via sediment trapping, which can improve fish foraging success and energetic gains. As a food source, it provides year-round inputs to the aquatic food web, as fresh biomass in the growing season, as slow-decomposing litter fueling the detrital food web continuously through the year, and as a surface for nutritious microalgae to attach. This contrasts with phytoplankton, which exhibit strong seasonality in standing biomass stocks.

**KEY MESSAGE** • Not only has the magnitude of production changed in the Delta, but so have the dominant sources of organic matter that fuel the aquatic food web. Restoring a portfolio of habitat types and primary producers in the Delta that better reflects the environment in which fish and other native aquatic wildlife once thrived may help native populations recover.



Tules line a Delta slough. Photo by Sarah Pearce, SFEI

Even with dramatic losses in their historical extent, tidal marsh and non-tidal marsh remain an important food source for aquatic consumers.



Quantifying the value for fish of primary production presents a challenging problem. Food webs are dynamic in time and space, and consumer demands for primary production vary seasonally and inter-annually, depending on consumer life cycles, the composition of the consumer community, and other factors. The degree to which a system is food-limited is not the only consideration, as other factors, such as turbidity, temperature, and hypoxia, may limit the growth of consumer species. Additionally, the quality and availability of primary production varies through time as well, especially for plant material, whose biochemical contents differ among stages of growth and decomposition. For these reasons, quantifying the food value of a given unit of production is a nontrivial problem.

As a simple, first-order approach to assess food value, we performed a rough analysis of how much primary production becomes living tissue in primary consumers. These primary consumers, herbivores that feed on microalgae and plants, occupy an important place in the aquatic food web as nutritious prey for fish and other higher consumers. Using values from the literature on the fate of production and growth efficiencies, we translated our estimates of primary production to herbivore biomass. We first used data synthesized from 154 marine-based studies (medians and interquartile ranges from Duarte and Cebrian, 1996) to estimate the amount of production from each producer group that is consumed by herbivores in the Delta. For this portion of production, we applied literature-based growth efficiencies (medians and ranges compiled from Brett et al., 2012; Ferguson, 1973; Jacobsen and Sand-Jensen, 1994; and Straile, 1997) to convert production from each primary producer group to potential herbivore growth. We caution that values used in this calculation were not specific to the Delta.

**In the historical hydrologically connected Delta, we found that attached microalgae and marsh plants were the two most important food sources for aquatic herbivores, potentially supporting an estimated 13 kt C/yr (attached microalgae) and 35 kt C/yr (marsh plants) of consumer growth, equivalent to the carbon in 48,000 elephants. These numbers are dramatically lower in the modern-day Delta, with these two groups together supporting only an estimated 1.2 kt C/yr of herbivore production.**



Due to increased open-water habitat between the historical and modern eras, we estimate that phytoplankton supports nearly as much herbivore growth today as it did historically, and production from aquatic plants has doubled in importance. Nonetheless, phytoplankton and aquatic plants combined support only 2.3 kt C of annual herbivore growth. **Thus, the loss of historical marsh leaves an estimated gap of nearly 50 kt C/yr in herbivore biomass support.**

This simple analysis underscores the high value of marsh in the historical Delta food web, even given the large uncertainty range reported with these estimates. Important to note, this approach focuses exclusively on herbivory, whereas a large fraction of production typically moves through detrital pathways. Additionally, we caution that this analysis rests on limited data from other ecosystems and species. Accordingly, our herbivore support estimates do not capture the effects of producer and consumer biology and of varying environmental conditions. To refine these numbers and link them to higher level consumers, more Delta-specific data are needed in a more complex modeling framework.

Estimated support for herbivore biomass growth in the historical and modern Delta. Values were calculated from literature-based values for the fraction of total production consumed by herbivores (the herbivory fraction; Duarte and Cebrian, 1996) and the growth efficiency of herbivores consuming each primary producer group (Brett et al., 2012; Ferguson, 1973; Jacobsen and Sand-Jensen, 1994; Straille, 1997).

	Producer group	Herbivory fraction	Herbivore growth efficiency	Historical herbivore growth support* (kt C/yr)	Modern herbivore growth support* (kt C/yr)
	<b>Phytoplankton</b>				
	median	0.46	0.22	2.1	1.6
	(range)	(0.20-0.83)	(0.20-0.28)	(0.80-4.7)	(0.63-3.7)
	<b>Attached microalgae</b>				
	median	0.43	0.22	13	0.46
	(range)	(0.32-0.89)	(0.20-0.28)	(8.9-34)	(0.31-1.2)
	<b>Aquatic plants</b>				
	median	0.14	0.16	0.32	0.67
	(range)	(0.065-0.45)	(0.075-0.21)	(0.069-1.4)	(0.14-2.8)
	<b>Marsh plants</b>				
	median	0.20	0.16	35	0.70
	(range)	(0.053-0.79)	(0.075-0.21)	(4.4-180)	(0.087-3.6)
	<b>Woody riparian plants</b>				
	median	0.13	0.16	1.2	0.24
	(range)	(0.056-0.16)	(0.075-0.21)	(0.24-2.0)	(0.048-0.39)

\*Values shown for wet years only

## 6. TRACING PRIMARY PRODUCTION TO CONSUMERS

Stable isotope analysis offers an alternative, powerful approach to evaluating producer-consumer relationships. This method partitions consumer diets into relative proportions of their primary production sources. Within the Delta, stable isotopes have been measured from invertebrates and fish collected in Lindsey Slough, Liberty Island, Brown's Island, and Suisun Marsh (Howe et al., in prep; Young et al., in review). These measurements reveal that fish rely heavily on emergent marsh and aquatic plants, with less support from algal sources, particularly open-water phytoplankton. Additionally, Young et al report that the sources of primary production in fish diets shift according to habitat type (i.e. open water, dendritic tidal marsh channel, or turbid backwater slough), suggesting that access to food, not simply feeding preference, drives food web support. These findings contrast with our analysis of herbivore support, indicating that although phytoplankton offer a high-quality source of energy and nutrients, vascular plant material plays a greater role in food web support for a variety of consumer species.

**Even with dramatic losses in their historical extent and hydrologic connectivity, tidal marsh and non-tidal marsh remain an important food source for fish and their invertebrate prey.**

Although powerful for tracing food sources and identifying patterns of consumption, this stable isotope method does not quantify the amount of primary production that was originally consumed, both directly and by prey, at lower levels in the food web. Nor do stable isotope analyses indicate whether the system is currently food-limited. Because carbon is respired at each trophic step, this type of analysis would require detailed information on the food web structure and associated growth efficiencies.



*Daphnia magna*. Photo by Harald Olsen/NTNU CC by2.0

Several computational modeling frameworks have been designed to evaluate carbon or energy flow in aquatic systems, capturing food web dynamics and environmental influences such as the effects of turbidity and hypoxia on fish growth efficiencies due to metabolic and foraging costs. Appropriately parameterized, such ecosystem or energetics models could be used to quantify the food web connections and the flows of biomass or energy among producers and consumers in the Delta. While this type of computational model can be powerful for studying producer-consumer relationships, no off-the-shelf model can be easily tailored to translate this project's findings into units of fish biomass growth. This level of detailed model analysis requires extensive and site-specific input data that capture temporally-variable ecological dynamics. The quantitative information this study provides is a first and necessary step for developing and improving such models.

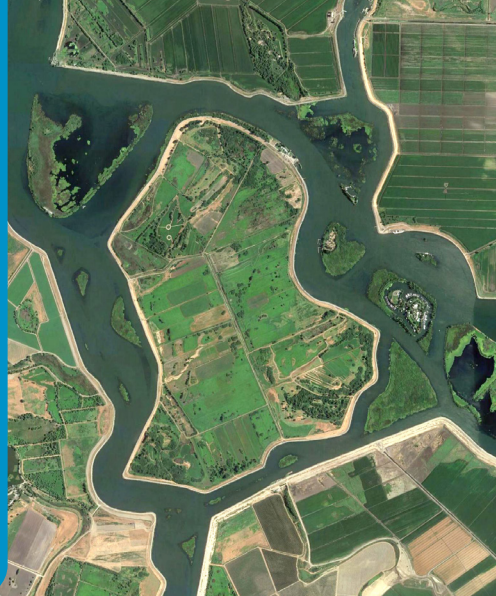
**KEY MESSAGE** • Stable isotope data from fish and aquatic invertebrates indicate that marsh-based detritus is important for consumers in the Delta, more so than would be predicted from simple growth efficiency calculations.



Delta smelt. Photo by Peter Johnsen, courtesy USFWS.



This work included a special project to investigate how the exchange of water from channels to marshes affects phytoplankton production and export to the aquatic food web.



Our approach to estimate primary production in the Delta effectively treats different habitat types as isolated from one another, with no flow-mediated exchange of material (e.g., transfer of organisms, detritus, nutrients, or sediment between open water channels and the vegetated marsh surface). We know, however, that these transport processes—the movement of matter between and within habitat types—can affect primary production and its value to consumers (Cloern, 2007). To further explore these effects of flow on primary production, we coupled an ecological model of phytoplankton production (Cloern, 2007) with a two-dimensional hydrodynamic model of a canonical tidal marsh. This “Channel-Marsh Production Model”, developed by Resource Management Associates, allows us to investigate how the configuration and connectivity of marsh and open water affect phytoplankton production. Although this model is still under development, preliminary findings offer insight into questions relevant to managers and point to a range of possible future research directions.

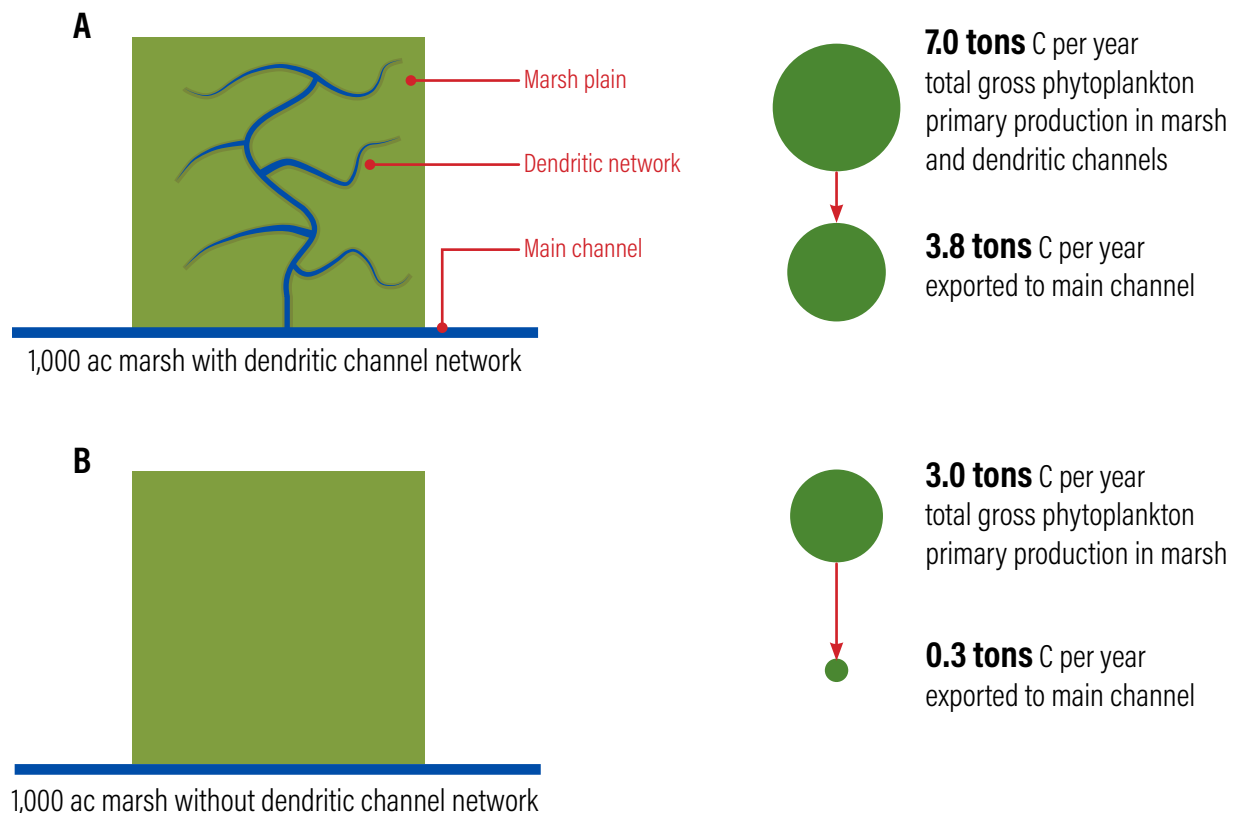
The Channel-Marsh Production Model is run over multiple tidal cycles and calculates the quantity and transfer of water, nutrients, phytoplankton, and zooplankton within and between model cells. The model accounts for key abiotic differences between the channels and marshes, such as water depth, suspended sediment, light availability, and temperature dynamics, all of which can vary over time. This framework enables testing the effects of different marsh and channel configurations on total phytoplankton production, where phytoplankton are generated (i.e., on the marsh vs. in channels), and how much production is exported out of the marsh system. Because the underlying production model includes consumption of phytoplankton by zooplankton, the model also allows us to begin exploring the routing of primary production to higher aquatic consumers.

Preliminary model results highlight the importance of internal dendritic channel networks for phytoplankton production in tidal marshes. **In our study, modeled phytoplankton production in a large (~1,000 acre) marsh with a dendritic channel network was twice as high as in the same marsh without a dendritic channel network, ultimately resulting in ~2.5x more zooplankton production. Additionally, as modeled, the proportion of marsh phytoplankton production exported to the**

**main channel was greater from the marsh with internal dendritic channels (54%) than without (9%). All told, the presence of a dendritic channel network in the model led to an order-of-magnitude increase in carbon export from marsh to the main channel. Phytoplankton production in marshes was sensitive to the modeled elevation of both the marsh plain and the small natural levees bordering the tidal channels, which together affect inundation frequency and residence time of water in the marsh system.**

These modeling results support empirical findings from the Delta that residence time is an important control on phytoplankton production in tidal channels (Stumpner et al., 2020). Because not all water moves into and out of the dendritic channel network on each tide, some portions of the channel network retain water over multiple tidal cycles. This longer residence time of water in marsh channels allows phytoplankton time to grow, reproduce, and fuel higher consumers such as zooplankton. On a different timescale, dendritic channel networks facilitate the periodic exchange of water from the main channel into the marsh system. This exchange exports phytoplankton produced on the marsh surface or in the marsh channels to the main channel, while fueling phytoplankton growth via the periodic influx of nutrients.

#### **Modeled large marshes with internal dendritic channel networks generate and export more phytoplankton biomass**





## 7. CHANNEL-MARSH PRODUCTION MODEL

For managers considering how to design tidal marsh restoration projects, these findings highlight the importance of restoring large marshes. Because dendritic channel networks that are longer than the average tidal excursion length are needed to generate water residence-time gradients (Morgan-King and Schoellhamer, 2013) and because the length of dendritic channels increases disproportionately with marsh size (Hood, 2007), **relatively large tracts of marsh are likely needed to support dendritic channel networks that enhance phytoplankton production.** The average amount of marsh drained by each dendritic channel network in the historical Delta was ~1,200 acres (SFEI-ASC, 2014). Today, the average size of Delta marsh patches is around 10 acres, and only three marsh patches are larger than 250 acres (SFEI-ASC, 2014). The model results presented here suggest that small marshes without channel networks, which are commonly observed in the modern Delta, would be expected to have relatively low total and per-acre rates of phytoplankton production compared to larger marshes with well-developed networks.







**KEY MESSAGE** • Relatively large tracts of marsh are likely needed to support dendritic channel networks that enhance phytoplankton production.



## Would achieving regional habitat restoration targets dramatically increase primary production?



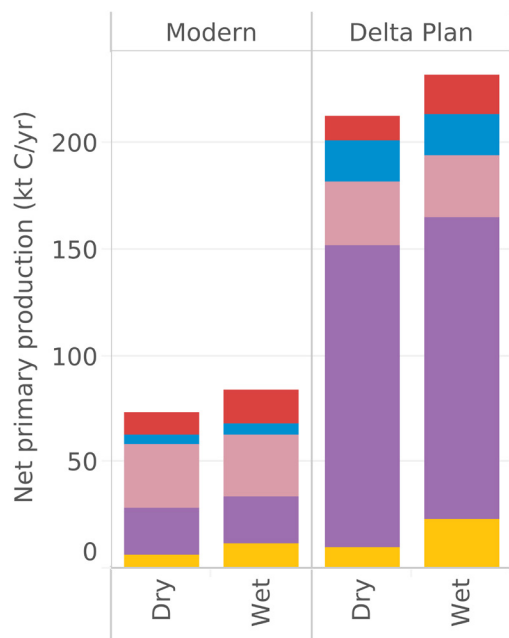
The approach developed here can estimate primary production gains from achieving restoration targets. The draft amendment to Chapter 4 of the Delta Plan ("Protect, Restore, and Enhance the Delta Ecosystem"), sets areal restoration targets for a suite of Delta natural community types. These targets are described in Preliminary Draft Performance Measure 4.16 (DSC 2019). Translated to the habitat types defined in this project, these targets would result in an approximate 2.6-fold increase in total tidal marsh area (+32,500 acres), a 4.8-fold increase in non-tidal marsh (+19,000 acres), and a 2.2-fold increase in riparian forest/scrub (+16,300 acres).

We used areal productivity rates developed in this project to estimate changes in primary production associated with these Delta Plan targets. In doing so, we altered only the extents of each habitat type; all other model assumptions and parameters were held constant. We assumed that increases in the extent of hydrologically connected areas would come entirely from areas that are currently hydrologically disconnected. To evaluate this scenario with our spatially-explicit model, we made additional assumptions about the spatial distributions of the restored habitat extents. The distribution of new non-tidal marsh between the Yolo region (52%), the Cosumnes/Mokelumne region (13%), and the San Joaquin region (35%) was based on regional targets described in the Delta Plan documentation. For riparian forest/scrub, the percentage of added area within 25 m of a channel was based on historical and modern data.

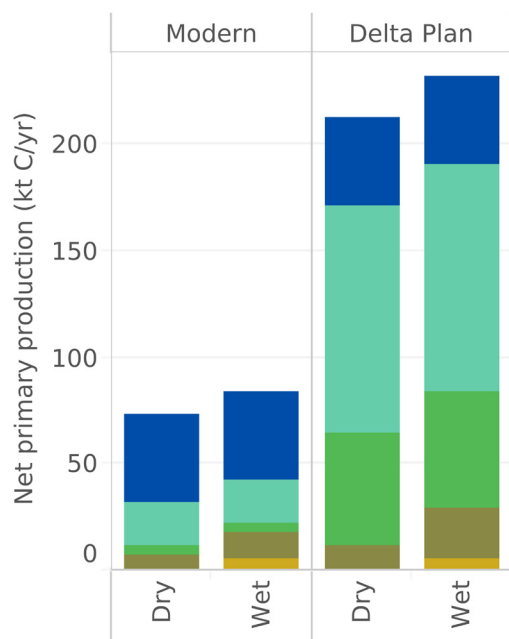
**Our model predicts that Delta Plan restoration targets would nearly triple the primary production in the modern hydrologically connected Delta, from 74 to 213 kt C/yr in dry years, and from 84 to 232 kt C/yr in wet years. These gains would recover approximately 12% of the annual primary production lost since the historical era, increasing contemporary primary production from 6% to 17% of its historical magnitude.**

These restoration targets aim to increase wetland habitat types (tidal marsh, non-tidal marsh, and riparian forest/scrub in our habitat classification). Accordingly, this restoration would shift the composition of primary production back from primarily open-water-based to wetland-based sources. In the modern hydrologically connected Delta, aquatic plants are far and away the dominant producers, accounting for ~35-40% of total primary production, depending on water year type. This analysis suggests that meeting **Delta Plan targets would cause a nearly 7-fold increase in marsh vascular plant production, a 4-fold increase in attached**

## Estimated effect of landscape-scale restoration on net primary production in the hydrologically connected Delta



Producer Group	Modern (kt C/yr)		Delta Plan (kt C/yr)	
	Dry	Wet	Dry	Wet
Phytoplankton	11	16	12	19
Attached microalgae	4.8	4.8	20	19
Aquatic plants	30	30	30	30
Marsh plants	22	22	140	140
Woody riparian plants	6.4	12	10	23
TOTAL	74	84	210	230



Habitat Type	Modern (kt C/yr)		Delta Plan (kt C/yr)	
	Dry	Wet	Dry	Wet
Open water	41	41	41	41
Tidal marsh	21	21	110	110
Non tidal marsh	4.0	4.1	54	55
Riparian forest/scrub	7.4	13	11	24
Other seasonal floodplain	0.0	5.0	0.0	5.0
TOTAL	74	84	210	230

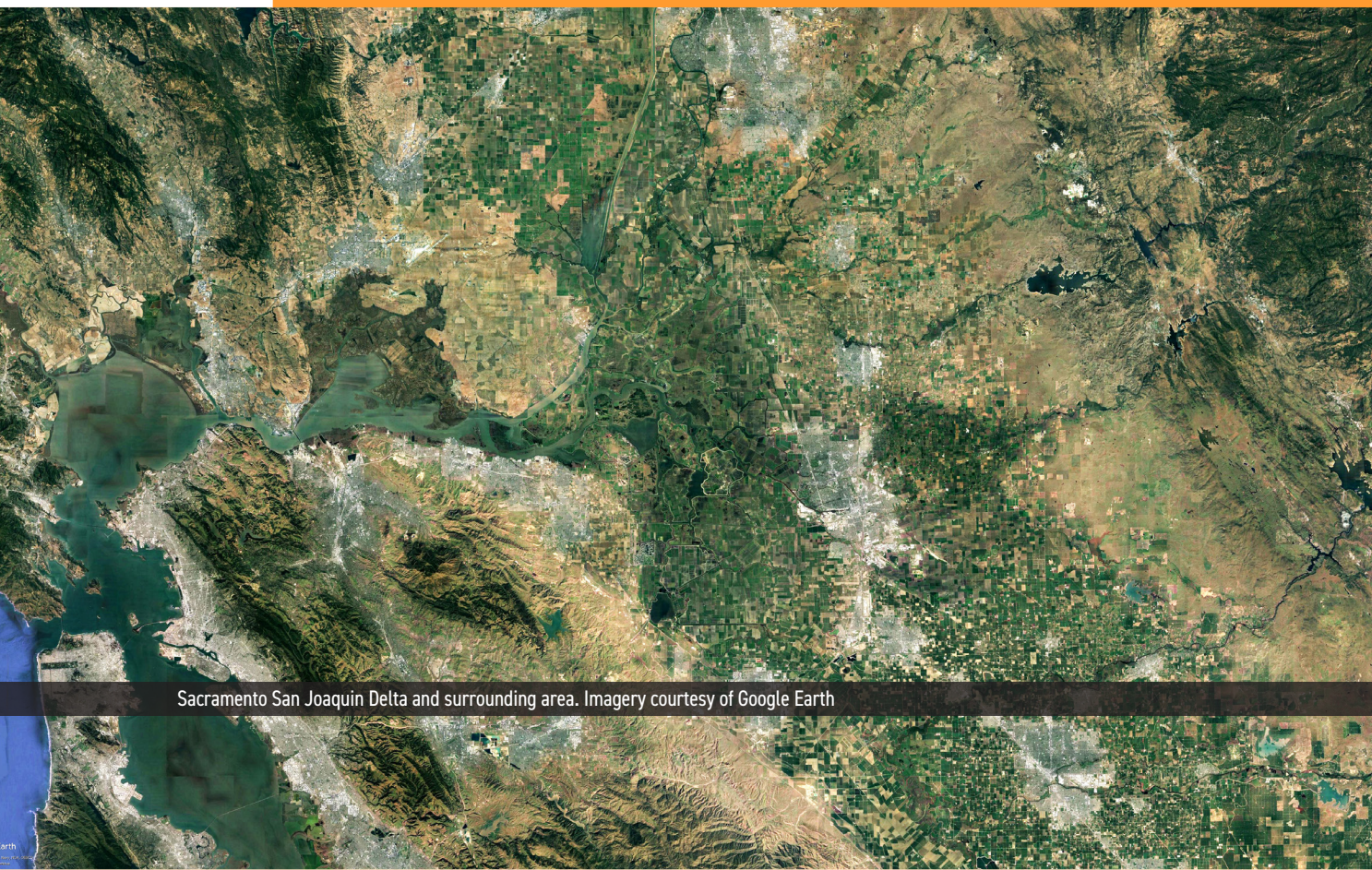


## 8. REGIONAL RESTORATION TARGETS

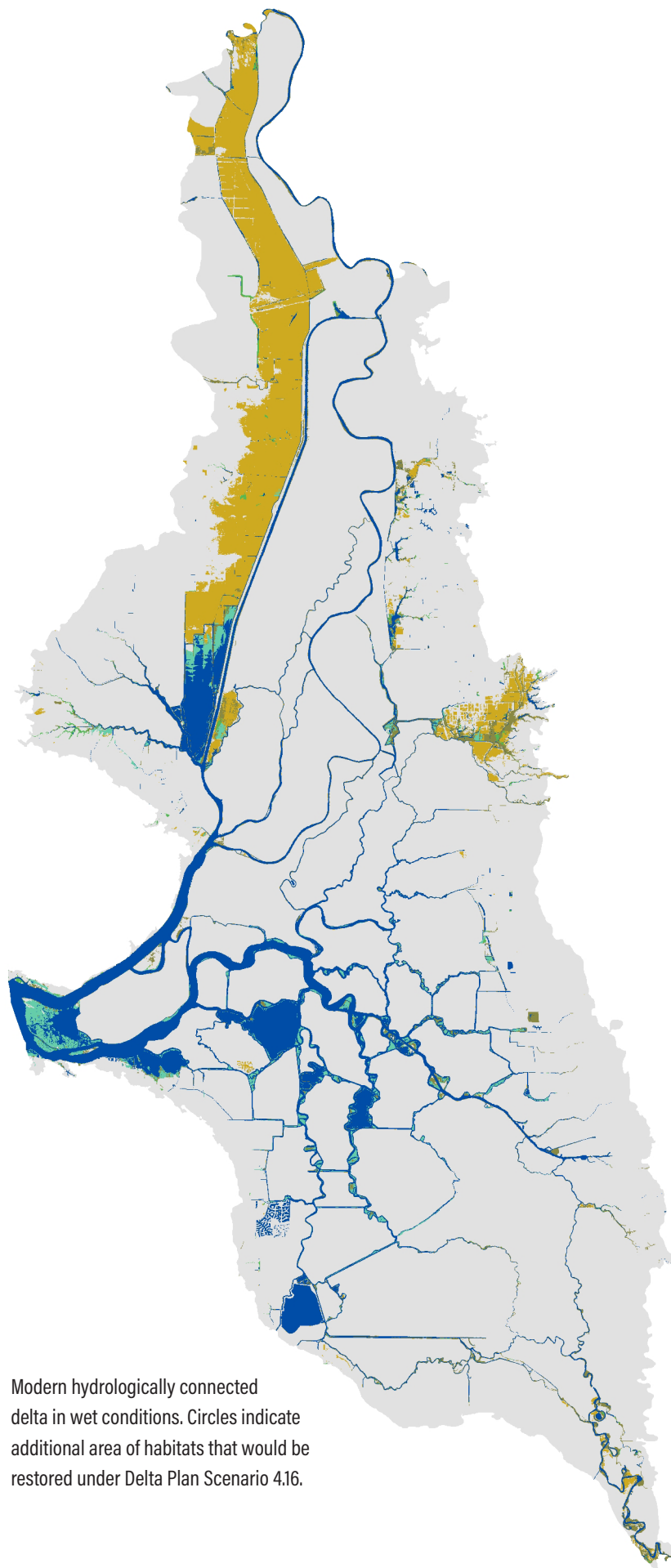
**microalgae, and a near doubling of carbon inputs from woody riparian plants,** with no concurrent increases in open water production.

The ambitious targets used in this analysis have the potential to increase food resources for aquatic consumers in the Delta while shifting the portfolio of production to more closely resemble its historical composition. Nevertheless, primary production gains associated with this scenario restore only 12% of the primary production that has been lost since the historical era. To replenish the lost primary production and reestablish the carbon flow pathways would require even greater amounts of wetland restoration.

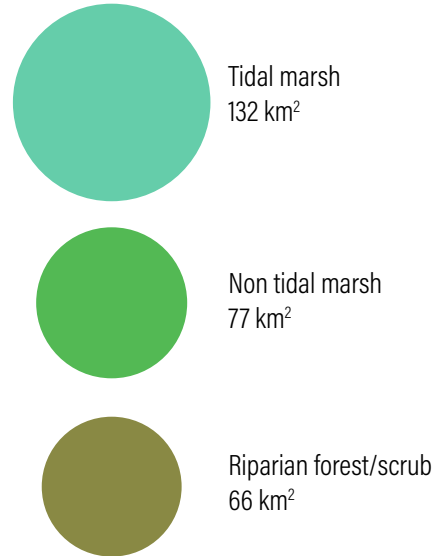
**KEY MESSAGE** • We estimate that Delta Plan targets for wetland restoration have the potential to nearly triple the primary production inputs to aquatic ecosystems. In particular, marsh restoration targets offer sizeable increases in production from both vascular plants and attached microalgae. These changes provide food for grazing invertebrates, the detrital food web, and higher level consumers such as fish, while shifting the balance of primary production back to more wetland-based sources.



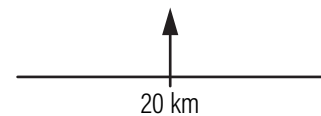
Sacramento San Joaquin Delta and surrounding area. Imagery courtesy of Google Earth



### Area of habitats restored under Delta Plan Scenario



### Modern Delta Habitat Types





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