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1. Determining habitat parameters

1.1. Study extent

Our study extent is defined by the area mapped in the SFEI-ASC Sacramento-San Joaquin Delta Historical Ecology Investigation (Whipple et al., 2012), an area originally selected to include the full extent of the Delta’s historical tidal wetlands, adjacent nontidal freshwater wetlands, and upland transitional areas. The study area was generally defined as “the contiguous lands lying below 25 feet (7.6 m) in elevation.” This differs from the extent of the legal Delta and encompasses an area of about 800,000 acres, including parts of Sacramento, Yolo, Solano, Contra Costa, and San Joaquin counties. The boundary was defined using the National Elevation Dataset (NED) 10m-Resolution (⅓-Arc-Second) Digital Elevation Model (DEM). The report authors “used GIS tools to generalize the boundary and removed upland (fluvial) channels less than 650 feet (200 m) wide.” To avoid holes in the study area, the authors included small hillocks within the outer boundary and also included areas within the sinks of Putah and Cache creeks that were above the 25-foot (7.6 m) elevation contour.

1.2. Land cover (habitat type) data sources

GIS data mapping historical Delta habitat types were obtained from SFEI-ASC’s Sacramento-San Joaquin Delta Historical Ecology Investigation (Whipple et al., 2012). Data on modern habitat types were from Robinson et al. (2014). As described by those authors, the modern habitat type map was compiled from multiple detailed vegetation mapping efforts, including the CDFW Vegetation Classification and Mapping Program’s 2007 Sacramento-San Joaquin River Delta data (Hickson and Keeler-Wolf, 2007) and the 2012 Central Valley Riparian Mapping Project Group Level data (Geographical Information Center, California State University, Chico 2012). Together, these two sources covered greater than 99% of the study extent. The alliance and group-level vegetation classifications from the compiled modern datasets were crosswalked to the historical habitat types (or groups of historical habitat types) with the assistance of local experts familiar with the data sources (Robinson et al., 2014).

1.3. Determining the area of hydrologically connected habitat types

As noted in the primary methods text, we estimate “potential aquatic net primary productivity” (PANPP), defined as the annual production of organic carbon that is available to aquatic food webs in hydrologically connected habitats. We use the term hydrologic connectivity to refer to hydrologic connections between landscape elements that allow for surface-water mediated transfer of energy, matter, and organisms (Pringle, 2003). For our purposes, hydrologically connected areas are places where organic matter generated by NPP has a direct physical pathway to the aquatic ecosystem via tidal or riverine surface-water flows. Methods for determining the extent of hydrologically connected habitat types in each era (historical vs. modern) and water year type (dry vs. wet) are described below. A summary of the hydrologically connected extent of each habitat type by era and water year type is provided in Table 1. Our calculations do not include some habitat types (e.g., wet meadows and vernal pool complexes) in the historical system that would have been periodically inundated, but not by tidal or riverine flows.
Unless otherwise indicated, all spatial analyses were performed with ArcMap 10.7.

1.3.1. Historical tidal and nontidal marsh

The historical Delta lacked artificial levees, meaning the hydrologically connected extent of habitat types was dictated by topography and flows. Since hydroperiod was considered by Whipple et al. (2012) when classifying and mapping habitat types (e.g., the “tidal freshwater emergent wetland” habitat type implicitly only includes areas that are hydrologically connected via tidal surface water flows), the hydrologically connected extent of historical habitat types could generally be derived directly from the total extent of the habitat types themselves.

The historical area of hydrologically connected “tidal marsh” in both wet and dry years was derived from the extent of area classified by Whipple et al. (2012) as “tidal freshwater emergent wetland.” The historical area of hydrologically connected “nontidal marsh” in both wet and dry years was derived from the extent of areas classified by Whipple et al. as “nontidal freshwater emergent wetland.” The area of hydrologically connected non-tidal wetlands was subdivided into three each of three hydrologic sub-regions (Yolo, San Joaquin, and Cosumnes-Mokelumne), to account for differences in the depth, duration, and timing of inundation (see Section 1.4.2).

1.3.2. Historical open water

The historical area of hydrologically connected “open water” differed between wet and dry years, based on the fine-scale historical habitat type classifications. Hydrologically connected open water areas in dry years included all areas classified by Whipple et al. (2012) as “fluvial low order channel,” “fluvial mainstem channel,” “nontidal perennial pond/lake,” “tidal low order channel,” “tidal mainstem channel,” and “tidal perennial pond/lake.” Hydrologically connected open water areas in wet years included the same classes, plus areas classified as “nontidal intermittent pond/lake” and “tidal intermittent pond/lake.” We also included the area of tidal channels mapped by Whipple et al. only as lines (not as polygons) in both wet and dry years by selecting all channel lines classified as tidal, buffering them by 3.5 m on each side (7 m total, which is half the minimum mapping unit Whipple et al. used for mapping channels as polygons), and dissolving these channels with the open water polygons. The additional open water areas derived from the tidal channel line features were subtracted from the other habitat type areas where they overlapped to avoid double counting areas in multiple habitat type groups. Similarly, we also included the estimated area of “unmapped” historical tidal channels (Robinson et al., 2014) in the extent of hydrologically connected open water in both dry and wet years. Specifically, we used the average of Robinson et al.’s upper and lower estimates for the length of unmapped channels and assumed these channels had a width of 5 m. To avoid double-counting, the additional open water area was subtracted from the tidal marsh area (where the unmapped channels are thought to have been concentrated; Robinson et al., 2014).

1.3.3. Historical riparian forest/scrub

The historical area of hydrologically connected “riparian forest/scrub” also differed based on water year type as a function of distance to the nearest area mapped as open water. Hydrologically connected riparian forest/scrub areas in dry years included all areas classified by Whipple et al. (2012) as “willow thicket,” plus the portion of areas classified as “valley foothill riparian” or “willow riparian scrub/shrub” located within 25 m of an open water area. Hydrologically connected riparian forest/scrub areas in wet years included the full extent of the
same habitat types. The 25 m buffer was chosen to capture the primary zone from where riparian forest/scrub litterfall is input into adjacent water bodies (Collins et al., 2006), without above average flows/inundation (see Section 2.5). The full extent of “willow thicket” was included in both dry and wet years because this classification, unlike “willow riparian scrub/shrub” and “valley foothill riparian,” was used to map areas that are perennially wet (Whipple et al., 2012). Finally, we also added an estimate of additional “willow riparian scrub/shrub” that had not been mapped by Whipple et al. (2012) but was understood to have been present along low-order fluvially-dominated Delta streams (mapped as single-line features and thus did not meet the minimum mapping width criteria). These estimates were generated by buffering the low-order fluvial channels by 15 m on each side (the smallest width class employed by Whipple et al.) and adding the resulting area to the above totals wherever it intersected habitat type polygons not classified as one of the woody riparian types or open water.

1.3.4. Identifying modern hydrologically connected areas

Quantifying the modern extent of hydrologically connected areas in the Delta is complicated by the presence of more than 1000 km of levees and other water control infrastructure. Tens of thousands of hectares of land in the modern Delta are now located below sea level on subsided islands, disconnected from the surrounding perched channel network by levees. While these subsided lands are mostly covered by cultivated agriculture, there are also patches of woody riparian vegetation and freshwater emergent wetlands, yet these areas of habitat are no longer connected by tidal or riverine flows to the channel network or larger aquatic ecosystem. Therefore, to determine the extent of hydrologically connected habitat types we could not rely on vegetation or habitat type alone and had to first separate hydrologically connected from hydrologically disconnected areas. To determine the maximum possible extent of hydrologically connected areas, we used the California Levees Database (v3r2; CDWR 2013) to mask out areas located entirely behind levees that lack possible surface water connections to riverine and tidal waterways. We also masked out areas on the Delta periphery that drain into subsided leveed tracts and do not have surface water connections to the Delta’s channel network.

1.3.5. Modern tidal and nontidal marshes

To determine the modern extent of hydrologically connected tidal marsh in both wet and dry years we selected any areas outside of the leveed area (see Section 1.3.4) classified by Robinson et al. (2014) as “freshwater emergent wetland” or “willow-marsh complex” that were also determined by Robinson et al. to likely be tidal (those polygons contiguous with open water and falling within the historical extent of tidal marsh). The modern extent of hydrologically connected nontidal marsh in wet and dry years was determined by selecting any areas outside of the leveed area classified by Robinson et al. as “freshwater emergent wetland” or “willow-marsh complex” but not deemed likely to be tidal (polygons not contiguous with open water or not falling within the historical extent of tidal marsh). The area of hydrologically connected non-tidal wetlands was subdivided into three each of three hydrologic sub-regions (Yolo, San Joaquin, and Cosumnes-Mokelumne), to account for differences in the depth, duration, and timing of riverine inundation (see Section 1.4.2).
1.3.6. Modern open water

The modern extent of hydrologically connected open water in both wet and dry years was determined by selecting any areas outside of the leveed area classified by Robinson et al. (2014) as "open water."

1.3.7. Modern riparian forest/scrub

Methods for identifying modern hydrologically connected riparian forest/scrub in wet and dry years were similar to those used to calculate the historical extent, with the additional step of masking out hydrologically disconnected riparian vegetation polygons from the modern habitat type dataset (Robinson et al., 2014) located behind levees. Unlike the methods for the historical Delta, we only counted the portion of modern willow thicket polygons within 25 m of a channel as hydrologically connected in dry years (vs. the full extent of this habitat type in dry years in the historical Delta), given our understanding that most of the modern-day areas classified as willow thicket by Robinson et al. have a hydrology and landscape position more akin to the willow riparian scrub/shrub class. This decision only reduced the total extent of hydrologically connected riparian forest/shrub in dry years by 70 ha (~3% of the total) and does not affect total PANPP at the level of significance we report in the results.

1.3.8. Modern other seasonal floodplains

We also included a fifth hydrologically connected habitat type in the modern Delta, “other seasonal floodplain,” that covers all areas that are not captured by any of the above habitat types or located behind a levee, but are still subject to periodic inundation, as mapped by Pekel et al. (2016). These other seasonal floodplains do not have a direct analog in the historical Delta due to the underlying land cover type and hydroperiod (e.g., periodically flooded agricultural fields). For each water year (October 1st through September 30th), we used Google Earth Engine to query the Global Surface Water (GSW) dataset to generate annual maximum surface water extents, specifically using the monthly surface water image collection to select all cells classified as water in at least one observation. Maximum annual surface water extents were then clipped to mask out inundated areas located behind levees (e.g., flooded agricultural fields located within subsided and hydrologically-disconnected Delta islands) and then clipped again to isolate hydrologically connected inundated areas classified by Robinson et al. (2014) as agriculture, managed wetlands, seasonal wetlands, or a terrestrial habitat type (all habitat types not already captured in the other hydrologically connected habitat type groups). For each of three hydrologic sub-regions (Yolo, San Joaquin, and Cosumnes-Mokelumne), all water years classified as dry and wet (see Section 1.4.2), respectively, were combined to generate the maximum hydrologically connected extent of other seasonal floodplains in each water year type and sub-region. Though combining maximum extents across years likely overestimated the extent of inundation in any single dry or wet year, we opted for a generous estimate of the maximum extent of hydrologic inundation in each water year type to align with the approach we used to define the hydrologically connected extent of seasonally inundated habitat types in the historical era (for which we selected the maximum extent of nontidal marsh). Combining years also compensates for the tendency for large flood events in the Delta to occur in the winter when cloud cover is typically higher, thus preventing these events from being fully captured in the remotely sensed surface water extents. Note that inundation in each sub-region and water year type was only counted if the flow record analysis also indicated at least one day of flow above floodplain-inundation thresholds in that sub-region and water year (see Section 1.4.2).
Without zero days of inundation these areas cannot contribute to total PANPP in our calculations, (in most cases PANPP is generally calculated as the product of production rates, hydrologically connected area, and inundation, so a zero value for any of those terms results in no PANPP). In these cases, the mismatch between the remotely sensed data to determine inundated extent and flow threshold analysis to determine the number of days of inundation likely results from local areas of managed inundation, such as rice fields and irrigated agriculture, which, despite being located in an area that can be hydrologically connected under high flows, are generally impounded and hydrologically disconnected other periods.

1.4. Determining the depth and duration of inundation in hydrologically connected habitat types

1.4.1. Depth and duration of inundation in tidal marsh

The historical area of tidal marsh was partitioned into two areas based on data from Whipple et al. (2012) that were each assigned different inundation depth and frequency parameters: (1) the area thought to have been at least wetted daily by tidal inundation and (2) the area only thought to have been inundated during spring tides. We assumed an average depth in the area at least wetted on a daily basis during non-spring tide events of 3 cm. We assumed that the average depth during the inundated period was higher during spring tide overbank flood events (46 cm, based on historical accounts summarized by Whipple et al.), and used this value for spring tide events. Based on information that approximately 15% of high tide events in the upper San Francisco Estuary flood over tidal marsh channel banks (Enright et al., 2013), we assumed that day-time spring tide inundation events occurred on 4 days each month (twice each spring-neap cycle), meaning the portion of the tidal marsh area inundated on a daily basis was assigned an average depth when inundated during the day of 46 cm for 48 days a year and 3 cm for the remaining 317 days a year. Areas only inundated during spring tide events were assigned a depth when inundated of 46 cm for 48 days a year and 0 cm the remaining 317 days. It should be noted that our simplified approach discretizes cyclical tidal processes with substantial daily, fortnightly, and seasonal, and interannual variability in the timing, frequency, and depth of tidal marsh inundation (Enright et al., 2013).

Lacking data on spatial variability in tidal inundation frequency in the modern Delta, we assumed that all areas of tidal marsh in the modern Delta have tidal inundation characteristics akin to the portion of the historical Delta that was at least wetted during the day by tides daily, with deeper day-time inundation during spring tides (an average depth when inundated of 46 cm for 48 days a year and 3 cm for the remaining 317 days a year).

While we assumed that the depth and duration of inundation in tidal marshes was the same in both wet and dry years, there is some uncertainty about the influence of fluvial inundation on the hydrology of this habitat type during wet years in the historical Delta (riverine flows likely increased the depth and duration of inundation in tidal marshes for a portion of the year). We tested the sensitivity of our results to this by assuming deeper and more-sustained inundation on tidal marshes during the winter in the historical scenario (allowing 1 m of water to remain on tidal marshes from December through May) and found that it increased total Delta PANPP in that scenario by <1%, and so used the simplified set of assumptions (no water year type differences in the depth and duration of inundation in historical tidal marshes).
As noted in Section 2.1, we assumed that tidal marshes are wetted or inundated for half of each daily photoperiod. This was a rough estimate based on data collected by Enright et al. (2013) from the nearest remnant tidal marsh-channel system in the downstream estuary, where observed water levels in tidal marsh channels were above the elevation of the marsh plain during spring tide events in June for approximately 4.3 hours per day. Maximum day length in the Delta during the summer is approximately 14.75 hours, which yields a period with channel water levels above the marsh plain for approximately one third of the photoperiod. Accounting for some additional drainage time yielded our final rough estimate for the fraction of the photoperiod during which tidal marshes are inundated. We tested the sensitivity of our results to this assumption by varying the fraction between 0 and 1 and found that, though it affected total PANPP from phytoplankton by up to 55% in some scenarios (historical dry years being the most sensitive scenario to this parameter), it changed total PANPP by <1% across all scenarios and did not affect any of our other key findings.

1.4.2. Depth and duration of inundation in nontidal marsh and other seasonal floodplains

While inundation characteristics in tidal marshes were assumed to be similar in wet years and dry years, we sought to account for known interannual differences in the extent and duration of inundation in habitat types affected by riverine flooding (nontidal marsh and other seasonal floodplains). Given the focus of this effort on the effects of altered land cover on productivity, we used contemporary flow data to determine the timing and duration of inundation for both the historical and modern scenarios.

Hydrologic analysis to define wet and dry years

To determine which water years represent wet and dry years, we used daily flow records that represent the current flow regime (1980-2018; CDWR 2019). We considered the inflows of the three primary river systems (or “hydrologic sub-regions”) with large areas of flood basin and floodplain areas: Sacramento River, San Joaquin River, and Cosumnes River. We calculated the total annual inflow volume for each system (“sub-region”) and, to represent wet and dry years, determined the water years associated with the upper (0.8-1.0) and lower (0-0.2) quintiles, respectively (8 years each for the 38-yr period).

Duration of inundation in wet vs. dry years

To determine the duration of inundation expected by month for wet and dry years in nontidal marshes and other seasonal floodplains in each of the three river systems, we used a flow threshold approach (monthly values were needed to calculate PANPP from phytoplankton, which has strong seasonal variability in production rates; see Section 2.1). Specifically, for each year and each sub-region, we first identified days where flow exceeded the identified flow threshold. We then summarized the number of days associated with each year and month and took the median monthly number of days for each of the previously defined water year types (e.g., median number of days in December of wet years). These median values were used as the estimated number of days of inundation per year in nontidal marshes and other seasonal floodplains. For the Yolo Basin/Bypass flow threshold, we used the Yolo Bypass inundation flows of 4,000 cfs (YOLO inflow from DAYFLOW; Takata et al., 2017; Sommer et al., 2001). For the San Joaquin River, we used a flow threshold of 18,000 cfs, which represents the flow at which Paradise Cut is known to inundate (Andrews et al., 2016). For the Cosumnes River, we used a threshold of 800 cfs, based on previous studies (Florsheim and Mount, 2002).
the inundation threshold approach assumes that, once the floodplain or flood basin inundation threshold has been reached for a daily flow, the whole area of potential inundation (hydrologically connected extent) is assumed to be inundated. Therefore, we do not account for the substantial variation in the extent of inundation depending on flow magnitude. Similarly, we do not account for areas with prolonged inundation in the modern Delta due to human management of wetlands or agricultural areas. While the areas of managed wetlands and agriculture are included (i.e., satellite imagery shows large areas inundated even in dry years), the duration of their inundation is determined by the flow regime alone. We also do not address flood attenuation that prolongs inundation within floodplains (even after flows in the mainstem channel have dropped below floodplain-inundation thresholds).

**Depth of inundation in wet vs. dry years**

To estimate inundated areas associated with representative inundation depths, we binned the nontidal marsh and other seasonal floodplain historical and modern inundated area for wet and dry years into different depth classes. This was done by applying a depth distribution (in 1 m depth increments up to 10 m) of percent area inundated based on previous hydrodynamic modeling performed for the Yolo Bypass (Table 1.4.1, courtesy UC Davis Center for Watershed Sciences, funded by Yolo County).

<table>
<thead>
<tr>
<th>Depth class</th>
<th>% of total area</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-1 m</td>
<td>30%</td>
</tr>
<tr>
<td>1-2 m</td>
<td>24%</td>
</tr>
<tr>
<td>2-3 m</td>
<td>31%</td>
</tr>
<tr>
<td>3-4 m</td>
<td>11%</td>
</tr>
<tr>
<td>4-5 m</td>
<td>1%</td>
</tr>
<tr>
<td>5-6 m</td>
<td>1%</td>
</tr>
<tr>
<td>6-7 m</td>
<td>&lt;1%</td>
</tr>
<tr>
<td>7-8 m</td>
<td>1%</td>
</tr>
<tr>
<td>8-9 m</td>
<td>&lt;1%</td>
</tr>
<tr>
<td>9-10 m</td>
<td>&lt;1%</td>
</tr>
<tr>
<td>&gt;10 m</td>
<td>&lt;1%</td>
</tr>
</tbody>
</table>

*Table 1.4.1. Depth distributions applied to areas inundated by riverine flows (areas classified as nontidal marsh or other seasonal floodplain) based on previous hydrodynamic modeling performed for the Yolo Bypass (courtesy UC Davis Center for Watershed Sciences, funded by Yolo County).*
This modeling was conducted for a moderately large (~100,000 cfs) Yolo Bypass flooding event and the depth distribution was based on the peak flow day. This depth distribution was compared against and found to be similar to distributions at similar flows from modeling of a larger flood event (~300,000 cfs) performed by Resource Management Associates (RMA, 2013). The depth distribution was used for all seasonally inundated areas (both nontidal marsh and other seasonal floodplains), with the assumption that it was a reasonable representation of depth distributions for inundated floodplains. While depths are based on single points in time of modeled flooding, depth can be highly variable in space and time over the duration of a flood event, and thus the application of a constant depth class proportion is only a rough approximation of areas inundated at particular depths. We assumed that non-tidal marsh (but not other seasonal floodplains) were at least wetted during periods that they were not inundated (enough to support the growth of attached microalgae year-round).

1.4.3. Depth and duration of inundation in open water

Areas mapped in each scenario as open water were assumed to be perennially inundated (the vast majority of these areas are subtidal rivers, channels, lakes, and flooded islands).

The depth of historical areas mapped as open water was generally determined from a topographic-bathymetric digital elevation model (DEM) of the historical Delta (Robinson et al., 2014) based on the map of historical habitat types developed by Whipple et al. (2012) and early bathymetric surveys, binned into 1 m increments up to 10 m (water depths were referenced to mean lower low water, MLLW). Areas without data from the historical Delta DEM were assumed to have the same distribution of depths as areas with data, except for the area associated with unmapped tidal channels (see Section 1.3.2), which we assumed was entirely within the 0-1 m and 1-2 m depth bins (40% and 60% of the total area, respectively), based on simple assumptions about the geometry of these small channels.

The depth of modern areas mapped as open water was generally derived from the U.S. Geological Survey (USGS) and the California Department of Water Resources (DWR) combined topographic-bathymetric DEM of the Delta (Fregoso et al., 2017). Absolute elevations referenced to the North American Vertical Datum (NAVD88) were converted to MLLW elevations using maps indicating the elevation of local MLLW (Siegel and Gillenwater, 2019). Areas mapped as open water without depth data from the DEM were assumed to have the same distribution of depths as areas with data.

1.4.4. Depth and duration of inundation in riparian forest/scrub

Depth and duration of inundation in areas mapped as riparian forest/scrub were not explicitly estimated. The amount of litterfall entering the aquatic food web from riparian forest/scrub was simply a function of the maximum annual extent of hydrologically connected riparian forest/scrub area (See Section 1.3.3). When calculating PANPP from attached microalgae we assumed that only portions of areas mapped as “valley foothill riparian” and “willow riparian scrub/shrub” within 5 m of a channel and the full hydrologically connected extent of “willow thickets” were sufficiently moist to support attached microalgae. The 5 m buffer was based on research from the Pacific Northwest indicating that relative humidity in riparian vegetation rapidly decreases with distance from stream edges between 0 and 10 m and is similar to upland conditions beyond that distance (Danehy and Kirpes, 2000).
1.5. Habitat parameters references


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2. Calculating production for each primary-producer group

2.1. Phytoplankton

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Phytoplankton are defined as suspended microalgae. Phytoplankton occur in all habitat types except riparian forest/scrub.

2.1.1. Methods

We estimated annual phytoplankton primary production during wet and dry scenarios in four freshwater habitat types of the historical and modern Delta: (1) open-water habitats; (2) tidal marshes inundated by the semidiurnal tides; (3) nontidal marshes that were historically inundated during the wet winter-spring months; and (4) other seasonal floodplains that are periodically flooded in the modern Delta.

Open water

Over the period February 1993 to July 2000, we measured daily phytoplankton primary productivity PP (mg C m⁻² d⁻¹) across a range of open-water habitat types in the Delta including tidal lakes (flooded islands), shallow sloughs, and deep tidal rivers (see Jassby, Cloern, and Cole, 2002; Sobczak et al., 2002). Measurements were made all months of the year, and at habitat depths ranging from 0.5 to 20 m. PP was derived from 30-min assays to measure ¹⁴C assimilation by phytoplankton collected in surface waters and exposed to 17 different irradiance levels. Each assay yielded a site- and date-specific photosynthesis-irradiance function that was
integrated numerically over time and water depth to compute depth-integrated daily PP. Detailed methods are provided by Jassby, Cloern, and Cole (2002).

The data set includes 210 measurements of PP having an overall mean of 152 and range of 7 to 1551 mg C m$^{-2}$ d$^{-1}$. From these data, we built a Generalized Additive Model of (log-transformed) PP as a function of habitat depth d (m) and season (month number m), using R package rms (Harrell, 2017). The relationships between log(PP) and depth and month were both significant and nonlinear, as shown in partial residual plots (Fig. 2.1). This model explained 52% of the measured PP variance across years, months and habitat depths. Model residuals reflect the influence of other factors that regulate phytoplankton productivity such as turbidity, grazing, flows and residence time.

![Figure 2.1.1. Partial residual plots showing the functional relationships between log-transformed daily phytoplankton primary productivity PP and habitat depth d (m) and season m (month number). Gray bands represent 95% confidence intervals of model-estimated log(PP) over the range of habitat depths and months of PP measurements.](image)

We used this model to estimate annual phytoplankton primary production in open water habitats of the historical and modern Delta. Since PP varies with habitat depth (Fig. 2.1.1), we binned the areal extent of open-water habitats by their depth, using 1-m depth increments (Table 1.4.1). Then, for each depth bin (d), its area (a), month number (m), and number of days per month (t), we used the model to estimate phytoplankton carbon production ($C_m$, mg C month$^{-1}$) as:

$$C_m = a \times \text{PP}(d,m) \times t$$

We summed monthly values of $C_m$ for all months and depth bins to yield annual production in open water habitat for each landscape (historical, modern) and hydrologic (dry, wet) scenario.
**Tidal wetlands**

Our estimates of phytoplankton production in the open water habitat type are grounded in measurements of daily phytoplankton primary productivity in the modern Delta. However, there is no comparable record of phytoplankton productivity measurements in the shallow waters that oscillate tidally across vegetated wetlands of the Delta or, as far as we are aware, any other tidal freshwater marsh. Therefore, we applied the open water PP model above to estimate annual phytoplankton production in tidal wetlands, assuming they are inundated half of each photoperiod, and the depth (d) and areal extent (a) of inundation vary between spring and neap tides (see Section 1.4.1). For these perennally vegetated habitats, we accounted for light attenuation by emergent vascular plants using the factor $f$, the fraction of light above plant canopies that reaches the water surface. Monthly production $C_m$ in tidal wetlands was estimated as:

$$C_m = a \times PP(d,m) \times t \times f$$

The light factor $f$ has not been systematically measured in Delta tidal marshes, but it has in freshwater marshes of the central US with similar plant communities (Williams et al., 2017). We used the mean value of $f = 0.68$ from light profiles measured in 25 tule ($Schoenoplectus acutus$) stands of those freshwater marshes (Table 4, Williams et al., 2017).

**Nontidal marsh and other seasonal floodplains**

The historical Delta included 44,000 hectares of flood plain and other low-elevation habitats covered by nontidal marsh that were inundated by river inflow during winter-spring of wet years. These habitats are now leveed and disconnected from rivers. However, river flow is diverted into flood plains during wet years to provide spawning habitat for native fishes and promote phytoplankton productivity and the food webs it supports (Sommer et al., 2001). We used phytoplankton productivity measurements made by Lehman et al. (2008) in the Yolo Bypass floodplain when it was intentionally flooded in 2003. From these measurements (Fig. 2, Lehman et al., 2008), we computed mean daily $PP_m$ for each month; these ranged from 50 to 540 mg C m$^{-2}$ d$^{-1}$. Then, for each month of the wet season (December-June) we estimated total monthly production as:

$$C_m = a \times PP_m \times t \times f$$

where the areal extent (a) and number of days of inundation (t) varied by month and between landscape and hydrologic scenarios. For the light factor we used a value of $f = 1$ when calculating $C_m$ in other seasonal floodplains (productivity rates from Lehman et al. (2008) were largely sampled from an area without emergent vegetation that we classify as other seasonal floodplains, so adjusting rates for lower light levels was not required) and a value of $f = 0.68$ when calculating $C_m$ in nontidal marshes, as described above for tidal marshes). Annual phytoplankton production in each habitat type was computed for each scenario as the sum of monthly $C_m$ values.

**2.1.2. Results and Conclusions**

The approach used here indicates that annual phytoplankton production in the Delta is of order 10-40 kt C. Across that range, the lowest production occurs in the modern Delta during dry years, and the highest occurred in the historical Delta during wet years (Table 2.1.1). Several key
patterns emerge from these results. First, landscape transformation of the Delta has reduced phytoplankton primary production, both in dry years (from 18 to 11 kt C y\(^{-1}\)) and in wet years (from 39 to 15 kt C y\(^{-1}\)). Second, tidal wetlands were important habitats for phytoplankton production in the historical Delta, especially during dry years when they contributed about 60% of total estimated production (Table 2.1.1). Third, seasonal wetlands were even more important habitats for phytoplankton production in the historical Delta during wet years (23 kt C y\(^{-1}\)), when 44,000 hectares of flood plains were inundated by high river inflow during winter-spring. This led to a pronounced seasonal pattern of phytoplankton production that was highest from December to April, and about a two-fold difference in primary production between dry (18 kt C y\(^{-1}\)) and wet years (39 kt C y\(^{-1}\)). The loss of seasonal wetlands eliminated this pulse of winter-spring production that was large in wet years. That lost spring production in wet years is partly offset in the modern Delta by production of 4 kt C y\(^{-1}\) in managed wetlands, mostly in the Yolo Bypass. Fourth, open-water habitats contributed a relatively small fraction (15–30%) of phytoplankton production in the historical Delta, but they are now the largest source, contributing 98% in dry years (Table 2.1.1).

Our primary conclusion is that landscape transformation of the Delta has reduced phytoplankton primary production, altered the seasonal pattern of production from peaks in the wet season to peaks in the dry season, shifted the main source of phytoplankton production from wetlands to open-water habitats and, as a result, reduced the variability of phytoplankton production between wet and dry years.

Table 2.1.1. Estimates of annual phytoplankton primary production (kt C y\(^{-1}\)) in four aquatic habitat types of the historical and modern Delta for dry- and wet-year scenarios.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Tidal Wetlands</th>
<th>Seasonal Wetlands</th>
<th>Managed Wetlands</th>
<th>Open Water</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Historical Dry</td>
<td>10</td>
<td>2</td>
<td>0</td>
<td>5</td>
<td>18</td>
</tr>
<tr>
<td>Historical Wet</td>
<td>10</td>
<td>23</td>
<td>0</td>
<td>6</td>
<td>39</td>
</tr>
<tr>
<td>Modern Dry</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>11</td>
<td>11</td>
</tr>
<tr>
<td>Modern Wet</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>11</td>
<td>15</td>
</tr>
</tbody>
</table>
2.1.3. Uncertainties

The multiple steps used to estimate phytoplankton production lead to multiple sources of uncertainty in those estimates. A large, and unmeasurable, uncertainty would come from an assumption that productivity measurements in the modern Delta apply to the historical Delta. However, all controls on phytoplankton biomass and productivity in the modern Delta, such as seasonal flows and residence time, nutrient concentrations, turbidity (light limitation) and consumption by non-native clams (Jassby et al., 2002), would have differed substantially in the historical Delta. Therefore, our comparison of primary production between the historical and modern Delta (Table 3, Table 4) is best interpreted as an estimate of how phytoplankton production would differ between historical and modern landscapes set in the modern environment of flows, nutrients, turbidity and grazers. This interpretation is consistent with our goal of isolating and understanding the effects of landscape change on the important ecosystem function of primary production.

Open-water habitats

Each entry for phytoplankton PANPP in Tables 3 and 4 has large uncertainty from potential errors in assumptions we have made and from measurement and model errors. One source of uncertainty is error in the model of daily PP (Fig. 2.1). We used the Mean Absolute Error (MAE) to assess that uncertainty (Willmott and Matsuura, 2005), computed as the mean of the absolute value of differences between modeled and measured PP. This index of model error was 62 mg C m$^{-2}$ d$^{-1}$ compared to the mean measured PP of 152 mg C m$^{-2}$ d$^{-1}$. This implies that the values reported for open waters in Tables 3 and 4 were computed from PP estimates having a model uncertainty of about 40%.

Tidal wetlands

For tidal wetlands, an additional uncertainty comes from potential errors in assumptions we made about the depths of tidal inundation (assumed 3 cm on neap tides, 46 cm on spring tides; Section 1.4.1) and area of inundation during the photoperiod. However, a much larger issue is the absence of data to validate our estimates of phytoplankton production in tidal marshes from a model based on measurements in open-water habitats. Although many measurements of phytoplankton productivity have been made in channels and sloughs that drain tidal marshes (e.g., Moll, 1977), we are not aware of annual phytoplankton production measurements in tidally oscillating waters over a marsh surface. However, Robinson et al. (1997) conducted a rigorous five-year study to measure phytoplankton productivity, using a method similar to ours, in a freshwater prairie marsh having emergent vegetation ($f$ ranged from 0 to 1). At their sampling site of shallowest inundation (7-28 cm), annual-mean PP was 169 mg C m$^{-2}$ d$^{-1}$ and ranged from 76 to 280 mg C m$^{-2}$ d$^{-1}$ (Table 3, Robinson et al., 1997). If this mean is a characteristic value of PP in tidal marshes, and assuming tidal inundation over half the photoperiod, then annual phytoplankton production in tidal marshes of the historical Delta landscape would be about 36 kt C. Therefore, our estimate of phytoplankton production loss in tidal marshes is highly uncertain and, on this basis, could be underestimated by a factor of 3-4. This ecologically significant uncertainty will persist until direct measurements of phytoplankton primary productivity are made in tidal marshes.
Nontidal seasonal wetlands and other seasonal floodplains

These are habitat types for which we have some direct measurements of phytoplankton productivity and its variability. Lehman et al. (2008) measured PP in the Yolo Bypass twice during months February through May, and the difference between those monthly measurements ranged from 10% to 61% of their mean. These values are indices of one source of uncertainty – daily variability of PP not captured in twice-monthly sampling. These measurements were made at one location, so there is additional uncertainty about the magnitude of spatial variability of production across this large flood plain. Further uncertainty comes from potential errors in assumptions we made in assigning areal extent and monthly duration of inundation both in the historical Delta and modern Delta where inflows are managed.

2.1.5. References


2.2. Attached microalgae

James Pinckney, University of South Carolina

Attached microalgae are benthic algae growing in or on sediments or epiphytic algae on vegetation surfaces. Attached microalgae occur in all habitat types.

2.2.1. Methods

We estimated annual attached microalgae primary production during wet and dry scenarios in five freshwater habitat types of the historical and modern Delta: tidal marsh, nontidal marsh, riparian forest/scrub, other seasonal floodplains, and open water.

Direct measurements of epiphyte and benthic microalgal net primary production (NPP) were not available for the study area. Peer-reviewed scientific publications (44 different studies, listed below) were examined to obtain estimates for analogous habitat types and vegetation. Where necessary, literature rates were converted to annual estimates of NPP in units of g C m\(^{-2}\) y\(^{-1}\) based on areal coverage for the particular habitat type and host species. Each reference was classified into one of 3 categories: 1. Epiphytes on emergent vegetation, 2. Epiphytes on aquatic plants (SAV/FAV), 3. Benthic microalgae on non-shaded sediments. Rates for benthic microalgae on shaded sediments (beneath the plant canopy) were estimated based on a light attenuation by emergent vascular plants using the factor \(f\), the fraction of light above plant canopies that reaches the sediment surface. The light factor \(f\) has not been systematically measured in Delta tidal marshes, but it has in freshwater marshes of the central US with similar plant communities (Williams et al., 2017). We used the mean value of \(f = 0.68\) from light profiles measured in 25 tule (\(Schoenoplectus\) \(acutus\)) stands of those freshwater marshes (Table 4, Williams et al., 2017). Thus, the literature NPP rates for benthic microalgae on non-shaded sediments was multiplied by 0.68 to estimate NPP of benthic, shaded sediments. Similarly, NPP estimates for sediments submerged by 0 – 1 m of water were obtained using \(f = 0.05\). For sediments submerged by 1 – 2 m of water, we used \(f = 0.01\). For epiphytic algae we assumed no light attenuation (\(f = 1\)).

The mean, median, standard deviation, and interquartile ranges were calculated for each of the 5 NPP rate categories. The median value was selected for use in calculating NPP for the GIS habitat categories provided by SFEI. The upper and lower interquartile ranges were used to illustrate the uncertainty in the estimates.

Respective rates of NPP were multiplied by the habitat area for wet/dry and historical/modern scenarios to obtain habitat-type potential NPP for attached microalgae in units of kt C y\(^{-1}\).

\[
NPP (\text{kt C y}^{-1}) = t^* f^* R^* H^* (1.0 \times 10^{-5})
\]

\(t\) = fraction of the year for the wetted habitat (\(x/365\))

\(f\) = light attenuation factor

1.0 for no attenuation

0.05 for 95% attenuation by waters 0 – 1 m depth
0.68 for 68% attenuation by plant canopy at sediment surface
0.01 for 99% attenuation by waters of 1 – 2 m depth

\[ R = \text{median rate of NPP from literature (g C m}^{-2}\text{y}^{-1}) \]

\[ H = \text{habitat area (m}^2\text{)} \]

The statistics for the estimated rates of attached microalgal net primary production (NPP) as derived from literature values are shown in Table 2.2.1. These rates were used in the equations above to estimate potential annual NPP for five habitat types and the 4 scenarios based on habitat areas and inundation periods described in Section 1.

2.2.2. Results and Conclusions

The statistics for the estimated rates of non-phytoplankton microalgal net primary production (NPP) as derived from literature values are shown in Table 2.2.1. These rates were used in the equations above to estimate annual NPP for five habitat types and the 4 scenarios based on habitat areas and inundation periods supplied by SFEI (Table 2.2.2).

Table 2.2.1. Summary statistics for literature-derived rates of non-phytoplankton microalgal net primary production in units of g C m\(^{-2}\) y\(^{-1}\). The number of references, median values for the references, first (Q1) and third quartiles (Q3), mean, and ± 1 standard deviation (SD) are indicated in the respective columns.

<table>
<thead>
<tr>
<th>Group</th>
<th>References</th>
<th>Median</th>
<th>Q1</th>
<th>Q3</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Epiphytes on emergent vegetation</td>
<td>13</td>
<td>43.5</td>
<td>14.3</td>
<td>71.0</td>
<td>59.5</td>
<td>66.7</td>
</tr>
<tr>
<td>Epiphytes on FAV/SAV</td>
<td>16</td>
<td>23.8</td>
<td>9.2</td>
<td>29.2</td>
<td>30.4</td>
<td>50.5</td>
</tr>
<tr>
<td>BMA on non-shaded sediment</td>
<td>8</td>
<td>40.0</td>
<td>32.6</td>
<td>162.3</td>
<td>121.9</td>
<td>165.7</td>
</tr>
</tbody>
</table>
Table 2.2.2. Estimates of annual non-phytoplankton net primary production for 5 habitat types under 4 inundation scenarios.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Tidal Wetlands</th>
<th>Non-Tidal Wetlands</th>
<th>Seasonal Wetlands</th>
<th>Woody Riparian</th>
<th>Open Water</th>
<th>Total (kT C y⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Historical Dry</td>
<td>66.51</td>
<td>20.15</td>
<td>0.00</td>
<td>3.14</td>
<td>0.10</td>
<td>89.90</td>
</tr>
<tr>
<td>Historical Wet</td>
<td>66.51</td>
<td>16.00</td>
<td>0.00</td>
<td>10.11</td>
<td>0.10</td>
<td>92.72</td>
</tr>
<tr>
<td>Modern Dry</td>
<td>1.44</td>
<td>0.28</td>
<td>0.00</td>
<td>1.01</td>
<td>0.07</td>
<td>2.80</td>
</tr>
<tr>
<td>Modern Wet</td>
<td>1.44</td>
<td>0.24</td>
<td>1.16</td>
<td>2.23</td>
<td>0.07</td>
<td>5.14</td>
</tr>
</tbody>
</table>

The primary conclusion from exercise is that non-phytoplankton NPP under the modern scenario is 3.1 to 5.5% of estimated rates for the historical condition. Thus, the contribution of this group of primary producers has been reduced by > 95% in modern years relative to undisturbed historical habitats. The relative contribution of different habitat types to total non-phytoplankton microalgae NPP has also shifted between historical and modern scenarios. The most notable change has occurred in the tidal wetlands, where the majority of the NPP has been reduced due to habitat loss. Epiphytic microalgae on tule stems present a very nutritious and accessible food source for a variety of aquatic and insect fauna. Loss of this major food subsidy likely has had major impacts on the structure and function of this ecosystem.

2.2.3. Uncertainties

The absence of direct measurements NPP for non-phytoplankton microalgae in the different habitat types has resulted in the use of literature-derived rates for “similar” habitats in a variety of geographical areas. Therefore, the NPP rates used have a high degree of inherent uncertainty. Quartiles (see Table 2.2.1) were used to provide upper and lower limits for the range in uncertainty for the habitat specific NPP estimates. Another source of potentially significant uncertainty is the fixed value used for light attenuation in the different habitat types. Direct measurements in the studied habitats would be very useful in minimizing this source of uncertainty.

2.2.4. References

References for epiphytes on emergent vegetation


References for epiphytes on aquatic vegetation


References for benthic microalgae on non-shaded sediments


2.3. Marsh plants

Judith Drexler, United States Geological Survey

Marsh plants are defined in this analysis as emergent freshwater macrophytes growing in tidal or nontidal marshes.

2.3.1. Methods

Tidal freshwater marshes dominated by Schoenoplectus (bulrush) spp. are the main wetland type in the Delta. Several methods are available to estimate annual net primary productivity (NPP) of marsh vascular plants including (1) measuring peak aboveground biomass (Giroux and Bedard, 1988; Stefanik and Mitsch, 2014; Byrd et al., 2017; 2018), (2) using remote-sensing approaches (Byrd et al., 2018; Ye et al., 2019), and (3) determining the net ecosystem carbon balance of a wetland (Knox et al., 2015; Schäfer et al., 2019; Gnanamoorthy et al., 2020). Currently, only peak aboveground biomass measurements are available for tidal freshwater marshes in the Delta, so we used this approach to estimate NPP of the marsh plant producer group.

Several assumptions were required for estimating NPP of marsh plants because of the need to simplify PANPP calculations and the lack of any data from the historical period in the Delta. We assumed that marsh plant communities in the Delta are composed entirely of emergent vascular plants and that tidal, nontidal, slightly brackish, and freshwater emergent marsh communities have approximately the same productivity. We also assumed that NPP doesn't differ between wet and dry years and hasn't changed between the historic and modern periods.
In our approach, the NPP of the marsh producer group was estimated using area estimates together with peak aboveground standing crop measurements. Area estimates for tidal emergent marsh and nontidal emergent marsh for the historical and modern periods in the Delta were determined following the methods provided in Sections 1.3.1 and 1.3.5. We used plot measurements of peak aboveground biomass (live vascular plant standing crop) that were collected during 2005 and 2008 in Delta tidal marshes (Byrd et al., 2017; 2018; 2020). The data consist of 186 aboveground biomass measurements collected in 0.25 m² plots in marshes at Browns Island, Sherman Lake, and Sand Mound Slough in the western and central Delta. At each site, plots were established along a grid to generate an even sampling distribution across the entire site. All biomass plot measurements were checked for extreme outliers, which were removed from the dataset. Biomass measurements were only used if they were collected during the period of peak standing crop in July and August. The peak aboveground dry biomass measurements were converted to marsh carbon production rates by multiplying by 0.441, the mean plant organic carbon content for marsh vegetation across six regions of the United States \((n = 1384, 95\% \text{ C.I.} = 43.99\%–44.37\%; \text{Byrd et al.}, 2018)\). NPP of marsh plants in the Delta region was determined by multiplying carbon production rates of marshes by the area of the Delta covered by marsh during the historic and modern periods. The median NPP of marsh plants was 5.76 Mg C/ha/yr. This value was used to estimate PANPP reported in the main text (Table 3)).

### 2.3.2. Results and conclusions

![Net Marsh Vascular Plant Productivity Per Hectare](chart.png)

*Figure 2.3.1. Estimates for yearly net aboveground vascular plant productivity per hectare in the Delta.*

In this analysis, the net aboveground marsh vascular plant productivity per area is assumed to be the same in the historic period as in the modern period and during wet and dry years (Fig. 2.3.1, median productivity = 5.76 Mg C/ha/yr). Therefore, the change that this analysis shows is
the tremendous impact of emergent marsh loss on primary productivity following the large-scale conversion of the Delta to agriculture in the late 1880s and early 1900s (Fig. 2.3.2).

Figure 2.3.2. Total Delta-wide aboveground net vascular plant productivity of marshes shown with linear (a) and (b) log scales, demonstrating the scale of marsh productivity loss after large-scale conversion to agriculture.
The total loss of these tidal freshwater “blue carbon” systems subsequent to conversion to agriculture has only recently been quantified (Drexler et al. 2019) and the impact of such loss has only now been put into the context of the entire primary productivity of the Delta region. Although submerged aquatic vegetation (SAV) productivity has replaced a good portion of primary productivity in the Delta (+30%), this increase cannot simply be viewed as a positive gain for Delta ecosystems. Invasive SAV makes up the bulk of SAV in the Delta and these species have been shown to be ecosystem engineers. Egeria densa and other invasive SAV alter habitat and ecosystem properties including water flow rates, temperature regimes, and oxygen and nutrient levels (Getsinger and Dillon, 1984; Simenstad, 1999; Toft et al., 2003; Malik, 2007). Invasive species of SAV also trap sediment within and beneath vegetation patches (Petticrew and Kalff, 1992; Wilcock et al., 1999). The widespread infestation of SAV in the Delta may be serving to block sediment from depositing on adjacent marshes, reducing the resilience of marshes under sea-level rise. Recent research by Drexler et al. (in review) has also shown that invasive SAV is a new carbon sink and may be changing carbon cycling in Delta marshes as well as other infested freshwater ecosystems around the world.

2.3.3. Uncertainty

A statistical range was used to provide upper and lower bounds for the uncertainty in the NPP estimates for Delta marsh plants. NPP estimates cover a wide range from a minimum value of 0.52 Mg C/ha/yr to a maximum of 28.13 Mg C/ha/yr (Fig. 2.3.1). Because of this, there was a broad range of estimates for total marsh productivity across the Delta region (Fig. 2.3.2). Future work would benefit from having NPP estimates for Delta tidal marshes from remote-sensing approaches and eddy covariance flux measurements against which to compare these results.

2.3.4. References


2.4. Aquatic plants

*Katharyn Boyer and Melissa Patten, San Francisco State University*

Aquatic plants, also known as submersed and floating aquatic vegetation, includes aquatic macrophytes that are rooted or float on the water surface, as well as associated attached macroalgae. Aquatic plants are found in open water areas.

**2.4.1. Methods**

To estimate primary production of submersed and floating aquatic vegetation (SAV and FAV) in the modern Delta, we used remote sensing data from 2015 to determine the primary FAV species present (S. Khanna, unpubl. data; Ustin et al., 2015). This data set also identified SAV but did not distinguish by species, thus the composition was assumed to reflect that documented by Santos et al. (2011). For the historic Delta, we consulted a review by SFEI (2012) and references therein, and consulted with a botanical expert, Peter Baye. However, ultimately, we assumed that the most abundant species native to the region today were abundant in the historical Delta even if not reported in historic records.

Selecting the numerically dominant native and introduced species present today, we conducted a literature review to determine aerial rates of productivity for each. We included 30 peer-reviewed studies from around the world, which often each reported productivity rates measured under a range of field or mesocosm conditions and sometimes reported rates for multiple species of interest to this project. (See reference list below, organized by species.) In all, 116 productivity rates were included across nine species. We sought values reported in units of g C m$^{-2}$ d$^{-1}$ but also included values reported in g dry weight m$^{-2}$ d$^{-1}$ converted to units of C with literature-derived conversion ratios (Table 2.4.1; ~ 0.38 for both submersed [Westlake, 1965; Brooker and Edwards, 1973; Spencer et al., 1997; Miller and Provenza, 2007; Sebillian Wittyngham et al., 2019] and floating species [Spencer et al., 1997; Humne et al., 2002]).
Daily C productivity values were multiplied by 365 days, then adjusted down to 2/3 of the year to be conservative; all the species are considerably less productive in the winter months (K. Boyer unpubl. data; Boyer and Sutula, 2015; S. Khanna pers. comm.). This produced annual production in g C m$^{-2}$ y$^{-1}$ and the median and interquartile ranges of the values for each species were calculated. The median values were used to calculate Delta-wide net primary production on an annual basis (see below). The upper and lower interquartile ranges were used to explore uncertainty in the values.

Table 2.4.1: Conversion rates of dry weight to carbon. Values used to convert productivity rates reported in units of dry weight to units of carbon. When multiple rates were found, these were averaged for the species. When no rates were found, the average for submersed or floating species was used.

<table>
<thead>
<tr>
<th>Species</th>
<th>Rate used</th>
<th>Contributing rates</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ceratophyllum demersum</td>
<td>0.372</td>
<td></td>
<td>Miller and Provenza 2007</td>
</tr>
<tr>
<td>Egeria densa</td>
<td>0.3747</td>
<td></td>
<td>Spencer et al. 1997</td>
</tr>
<tr>
<td>Elodea canadensis</td>
<td>0.3789</td>
<td>mean of all submersed species</td>
<td></td>
</tr>
<tr>
<td>Eichhornia crassipes</td>
<td>0.3867</td>
<td></td>
<td>Spencer et al. 1997</td>
</tr>
<tr>
<td>Hydrocotyle umbellata</td>
<td>0.38</td>
<td></td>
<td>Hume et al 2002</td>
</tr>
<tr>
<td>Ludwigia peploides</td>
<td>0.3834</td>
<td>mean of E. crassipes and H. umbellata</td>
<td></td>
</tr>
<tr>
<td>Myriophyllum spicatum</td>
<td>0.39375</td>
<td>mean of rates below:</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.3975</td>
<td>Spencer et al. 1997</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.39</td>
<td>Brooker and Edwards 1973</td>
</tr>
<tr>
<td>Potamogeton crispus</td>
<td>0.3789</td>
<td>mean of all submersed species</td>
<td></td>
</tr>
<tr>
<td>Stuckenia pectinata</td>
<td>0.3753</td>
<td>mean of rates below:</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.39</td>
<td>Westlake 1965</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.34</td>
<td>Miller and Provenza 2007</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.36</td>
<td>Sebillian Wittyngham et al. 2019</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.3965</td>
<td>Spencer et al. 1997</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.39</td>
<td>Brooker and Edwards 1973</td>
</tr>
</tbody>
</table>
For the modern Delta, we used remote sensing data to estimate the acreage occupied by FAV and SAV; FAV made up 15% and SAV 85% of the total acreage of the two groups in 2015 (S. Khanna, unpubl. data; Ustin et al., 2015). The primary FAV species, *Eichhornia crassipes*, *Ludwigia peploides*, and *Hydrocotyle umbellata* made up 47, 46, and 3% of the total FAV detected (the other 4% a combination of other species including water fern, *Azolla* spp. and duckweed, *Lemna* spp.). Most of the coverage (89%) was over water less than 3 m deep (as parsed by a bathymetry layer in the GIS data), with the remainder in water 3-9 m deep, likely in areas of relatively low flow velocities. Similarly, for SAV, 85% of area detected was in water less than 3 m deep; however, in this case, we elected to exclude the other 15% due to 1) personal observations and expectations that light limitation would preclude much growth in water deeper than 3 m, as well as concerns over at least partial misclassification of these areas using bathymetry data with a 10 x 10 m pixel size (S. Khanna, pers. comm.). As SAV in the remote sensing data was not distinguished by species, we assumed relative abundances according to a rake sampling method used to sample the vegetation in fall 2007 (Santos et al., 2011): *Egeria densa*, 60%; *Ceratophyllum demersum*, 19%; *Potamogeton crispus*, 9%; *Myriophyllum spicatum*, 6%; *Stuckenia pectinata*, 4%; and *Elodea canadensis*, 3%. Using the areas (in hectares) of FAV or SAV coverage across depths (to 9 m or 3 m, respectively), the median aerial productivity rate for each species, and the proportion of the total represented by that species, we calculated the total production for the modern Delta in kt C y⁻¹.

For the historic Delta, to be conservative, the historic acreage potentially occupied was adjusted down according to today's occupied proportion. We assumed modern relative abundances of native species were the same in the historical Delta. FAV was assumed to comprise 15% of the FAV + SAV coverage like in the modern Delta, but to have been composed entirely of the only common native FAV species at present, *Hydrocotyle umbellata*. Similarly, SAV coverage in the historical Delta was assumed to include only the more common natives of the modern Delta: *S. pectinata*, *C. demersum*, and *E. canadensis*, with a relative composition of 16, 71, and 13% of the coverage, respectively, based on modern Delta estimates (Santos et al., 2011). To estimate historic production in kt C y⁻¹, hectares of potentially available habitat in the historic Delta were corrected for the proportion of each depth occupied by FAV or SAV in the modern Delta; these values were multiplied by the median productivity rate for each species, adjusted for the proportion of the total represented by that species.

### 2.4.2. Results and conclusions

SAV and FAV net primary production (NPP) as derived from literature values varied by two orders of magnitude across species (Table 2.4.2). The introduced SAV species *Potamogeton crispus* had the lowest median NPP value (23 g C m⁻² y⁻¹), and the native SAV *Elodea canadensis* and introduced SAV *Myriophyllum spicatum* also had relatively low median values (131 and 97 g C m⁻² y⁻¹, respectively). The introduced FAV species *Ludwigia peploides* had the highest median NPP of all species (3914 g C m⁻² y⁻¹), followed by the introduced FAV *Eichhornia crassipes* and the native FAV *Hydrocotyle umbellata* (2087 and 1118 g C m⁻² y⁻¹, respectively). The native SAV species *Ceratophyllum demersum* and *Stuckenia pectinata* had intermediate median NPP values (335 and 330 g C m⁻² y⁻¹, respectively), similar in median production to that of the invader *Egeria densa* (326 g C m⁻² y⁻¹). Variation in the estimates was quite high for a number of the species (Table 2.4.2).
Table 2.4.2. Summary statistics for literature-derived estimates of SAV and FAV net primary production for species commonly found in the modern Delta, in units of kg C hectare\(^{-1}\) year\(^{-1}\). Included are the number of studies, the total number of values found for the species, the mean, standard deviation (stdev), median, first (Q1) and third (Q3) quartiles and the interquartile range (IQR). N = native, I = introduced. *Ludwigia in the modern Delta is a combination of L. peploides, L. hexapetala, and L. grandiflora, but only L. peploides productivity rates were found in the literature.

<table>
<thead>
<tr>
<th>Species</th>
<th>n studies</th>
<th>n total values</th>
<th>mean</th>
<th>stdev</th>
<th>median</th>
<th>Q1</th>
<th>Q3</th>
<th>IQR</th>
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</thead>
<tbody>
<tr>
<td>$Stuckenia\ pectinata$ [N]</td>
<td>7</td>
<td>20</td>
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<td>4,660</td>
<td>3,298</td>
<td>1,499</td>
<td>6,676</td>
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<tr>
<td>$Hydrocotyle\ umbellata$ [N]</td>
<td>2</td>
<td>11</td>
<td>10,136</td>
<td>4,306</td>
<td>11,177</td>
<td>7,298</td>
<td>12,517</td>
<td>5,219</td>
</tr>
<tr>
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<td>3</td>
<td>2,901</td>
<td>2,506</td>
<td>3,345</td>
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<td>4,250</td>
<td>2,476</td>
</tr>
<tr>
<td>$Elodea\ canadensis$ [N]</td>
<td>5</td>
<td>8</td>
<td>1,982</td>
<td>1,830</td>
<td>1,307</td>
<td>605</td>
<td>3,464</td>
<td>2,859</td>
</tr>
<tr>
<td>$Myriophyllum\ spicatum$ [I]</td>
<td>2</td>
<td>8</td>
<td>1,146</td>
<td>1,364</td>
<td>972</td>
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<td>$Eichhornia\ crassipes$ [I]</td>
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<td>27</td>
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<td>5,828</td>
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<tr>
<td>$Egeria\ densa$ [I]</td>
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<td>22</td>
<td>4,549</td>
<td>3,549</td>
<td>3,261</td>
<td>2,432</td>
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<tr>
<td>$Potamogeton\ crispus$ [I]</td>
<td>2</td>
<td>6</td>
<td>322</td>
<td>214</td>
<td>230</td>
<td>184</td>
<td>414</td>
<td>230</td>
</tr>
<tr>
<td>$Ludwigia\ peploides$ * [I]</td>
<td>1</td>
<td>11</td>
<td>34,738</td>
<td>11,224</td>
<td>39,144</td>
<td>27,028</td>
<td>43,804</td>
<td>16,776</td>
</tr>
</tbody>
</table>

Table 2.4.3 provides annual production for the Delta in kt C y\(^{-1}\) for wet and dry scenarios of available acreage in the historic and modern Delta. We conclude that Delta-wide submersed and floating vegetation production has increased by 114% between the historic and modern periods (119 or 108% in dry versus wet periods, respectively).

Table 2.4.3. Estimates of annual SAV and FAV (submersed and floating aquatic vegetation) production (kt C y\(^{-1}\)) in wet and dry periods in the historic and modern Delta. Blank cells indicate introduced species that would not have been present in the historic Delta. Species abbreviations are: $Stuckenia\ pectinata$ (STPE), $Hydrocotyle\ umbellata$ (HYUM), $Ceratophyllum\ demersum$ (CEDE), $Elodea\ canadensis$ (ELCA), $Myriophyllum\ spicatum$ (MYSP), $Eichhornia\ crassipes$ (EICR), $Egeria\ densa$ (EDGE), $Potamogeton\ crispus$ (POCR), and $Ludwigia\ peploides$ (LUPE). Note that Ludwigia in the modern Delta is a combination of L. peploides, L. hexapetala, and L. grandiflora, but only L. peploides productivity rates were found in the literature.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Species</th>
<th>STPE</th>
<th>HYUM</th>
<th>CEDE</th>
<th>ELCA</th>
<th>MYSP</th>
<th>EICR</th>
<th>EGDE</th>
<th>POCR</th>
<th>LUPE</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Historical Dry</td>
<td></td>
<td>1.19</td>
<td>6.57</td>
<td>5.34</td>
<td>0.38</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13.49</td>
</tr>
<tr>
<td>Historical Wet</td>
<td></td>
<td>1.25</td>
<td>6.90</td>
<td>5.64</td>
<td>0.40</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>14.21</td>
</tr>
<tr>
<td>Modern Dry</td>
<td></td>
<td>0.51</td>
<td>0.20</td>
<td>2.45</td>
<td>0.15</td>
<td>0.23</td>
<td>6.68</td>
<td>7.55</td>
<td>0.08</td>
<td>11.71</td>
<td>29.55</td>
</tr>
<tr>
<td>Modern Wet</td>
<td></td>
<td>0.51</td>
<td>0.20</td>
<td>2.45</td>
<td>0.15</td>
<td>0.23</td>
<td>6.68</td>
<td>7.55</td>
<td>0.08</td>
<td>11.71</td>
<td>29.55</td>
</tr>
</tbody>
</table>
2.4.3. Uncertainties

Due to the very large difference in aerial productivity rates among the species, we felt it was critical to include the most abundant species in our estimates and in the correct proportions. However, assumptions about which species were abundant in the historic Delta contribute uncertainty to our estimates of production for that time period. Similarly, our estimates for the modern Delta are based on abundance of species from remote sensing in one particular year (2015, the most recent available data set); however, interannual variation in coverage and relative abundance is high (Ustin et al., 2015). Further, nearly all the direct measurements of NPP we used to estimate Delta-wide production were from other regions of the world (with the exception of one value for *Egeria densa* and all eleven of the values for *Ludwigia peploides*) and may not represent Delta conditions, historical or modern. High variation in these measurements contributes uncertainty to our calculations.

2.4.4. References

Behr, H.H., 1884. Synopsis of the genera of vascular plants in the vicinity of San Francisco, with an attempt to arrange them according to evolutionary principles. Payot, Upham & Co., San Francisco, CA.


San Francisco Estuary Institute (SFEI)., 2012. Sacramento-San Joaquin Delta historical ecology investigation: exploring pattern and process. SFEI Aquatic Science Center publication #672.


References for production estimates by species [location of study; number of values]

*Ceratophyllum demersum*


**Egeria densa**


Sloane, E., Boyer, K., Unpublished data. From manuscript in preparation tentatively entitled “Interactions of light and salinity on the growth of native and non-native submerged aquatic vegetation in the upper San Francisco Estuary” [mesocosms, Tiburon, CA, USA; 1]


**Eichhornia crassipes**


Elodea canadensis


Hydrocotyle umbellata


Ludwigia peploides


Myriophyllum spicatum


Potamogeton crispus


Stuckenia pectinata


2.5. Woody riparian plants

Robert Naiman, University of Washington

This producer category includes woody riparian plants (trees, shrubs, and scrub) and their herbaceous understory that could potentially enter the aquatic ecosystem (e.g., from litterfall into adjacent waterways or plant material captured by meandering channels). Woody riparian plants occur only in the riparian forest/scrub habitat type.

2.5.1. Methods

Natural riparian/floodplain forests have been described as patch mosaics of vegetative communities that vary in species composition and age (Décamps, 1996; Naiman et al., 2005a; Latterell et al., 2006), with the inherent structural heterogeneity (Van Pelt et al., 2006) shaping community characteristics and input rates of plant litter. This can have an important influence on nutrient cycling, successional pathways, and plant community organization. One ecological trait associated with riparian floodplains is the substantial production of plant litter as leaves, needles and woody debris. The fine-scale spatial and temporal variability in input rate and in litter type, and the connectivity among these patches by water, are defining features of riparian environments (Naiman et al., 2005b).

The amount of plant litter produced annually from riparian vegetation is influenced by forest type, successional stage, stream size, site productivity, and latitude. Many of these factors are interrelated, of course. There have been several attempts to identify factors influencing litterfall patterns across broad spatial and ecological scales (e.g., Xiong and Nilsson, 1997). Litter may be especially important in riparian corridors because of a higher production and a faster...
decomposition than occurs in uplands, with direct effects on nutrient retention and cycling in the aquatic environment.

In general, litter production appears to be related to the total net production of aboveground biomass with litter averaging 47% of the annual NPP in riparian forests (Brinson, 1990), which is slightly higher than upland forests. Leaf litter production accounts for 72% and 80% of the total litter production in deciduous and coniferous riparian forests, respectively.

There are three major pathways by which litter may enter rivers and deltas. The first is through the fall of leaves, needles and other relatively small organic particles directly into the water (litterfall). The second is via physical meandering by channels to undercut banks to deliver entire plants and associated soils into aquatic channels (meandering). The third is through natural plant mortality whereby large pieces of the plants fall into the water after death (tree mortality). We address each pathway in the following narrative for historical and modern environmental conditions in the Delta.

**Litterfall**

Adequate historical and modern data are generally not available for tree densities and diameters in the Delta's riparian zones. Therefore, we estimated litterfall in each scenario by multiplying the hydrologically connected area of each woody riparian habitat type by average associated annual litterfall biomass rates from the Central Valley of California (Matzek et al., 2016). Specifically, for older overstory riparian trees (areas mapped as “valley foothill riparian”), we used the average rate of 5.21 Mg/ha/yr reported by Matzek et al. (2016) for remnant forests. Though data for the Delta and Central Valley are limited, we note that this litterfall biomass rate is comparable to those found by O'Keefe and Naiman (2006) for mature terrace forest in the Pacific Northwest (6-7.6 Mg/ha/yr). For younger understory trees/shrubs (areas mapped as “willow riparian scrub/shrub” or “willow thicket”) we used the average rate of 1.65 Mg ha\(^{-1}\) yr\(^{-1}\) that Matzek et al. (2016) report for young restoration sites. To convert biomass rates to carbon rates, we assumed carbon constituted 50% of the total dry biomass. This conversion yielded litterfall rates of 260.5 g C m\(^{-2}\) yr\(^{-1}\) for areas classified as valley foothill riparian and 82.5 g C m\(^{-2}\) yr\(^{-1}\) for areas classified as willow scrub/shrub or willow thicket.

The available data on litterfall rates were not sufficient to calculate median, 1st quartile, and 3rd quartile production rates to estimate a range of production estimates, as done for other producer groups.

It was assumed that only areas classified as valley foothill riparian and willow riparian/scrub shrub near open water (within 25 m) contribute litter to the aquatic food web in dry years, whereas litterfall from the full extent of these riparian habitat types contributes to the aquatic food web in wet years (when large flood events have the potential to inundate a greater portion of the riparian corridor and transport litterfall from a wider area into the aquatic ecosystem). The buffer width of 25 m is the average maximum width over which litterfall into adjacent water bodies is observed to occur (or recommended to be maintained to provide that function), as reported by Collins et al. (2006).

**Channel meandering**

River meandering captures woody plants (as well as associated riparian soil) and transports this organic material into the aquatic ecosystem. To estimate the total amount of organic carbon
transferred into rivers via channel meandering, we used river lengths and annual lateral migration rates to estimate the area of riparian forest/scrub captured by river migration each year, and then extrapolated the amount of carbon captured within this area from empirical data on carbon stocks in California riparian plant communities.

Data on historical river lengths in the Delta were derived from Whipple et al. (2012) and binned based on their relative meander rate (“meandering,” “low meandering,” and “not meandering”) and adjacent woody riparian habitat type (valley foothill riparian, willow riparian scrub/shrub, or willow thicket; see Section 1.3.3). Meander rate categories for historical channels were assigned based on information regarding their geomorphology compiled by Whipple et al. (2012): the Sacramento River and its distributaries were assigned to the “meander” category upstream of the Feather River confluence and “not meandering” downstream of that point; the Feather River was categorized as “meandering”; the American River was categorized as “low meandering”; the Mokelumne River were categorized as “meandering” upstream of the head of tide and “low meandering” downstream to the Cosumnes River confluence, where the river corridor enters tidal emergent wetlands (areas downstream of that confluence were categorized as “not meandering”); the San Joaquin River was categorized as “meandering” from its most upstream location in our study extent downstream to where it first splits into major distributaries. The distributaries were classified as “low meandering” downstream to the points where they first enter tidal emergent wetlands. Most river reaches in the modern Delta are constrained by artificial levees and are not able to meander; we assigned these reaches to the “not meandering” category. Reaches in the modern Delta with some ability to meander that we categorized as “low meandering” were portions of the San Joaquin upstream of Mossdale, portions of the Cosumnes River, the Mokelumne River upstream of New Hope Road, and short reaches of the Sacramento River upstream of the Feather River confluence.

Actual meander rates were derived from Larsen (2006), who quantified lateral migration rates on the Sacramento River seven times between 1956 and 1975 (i.e., after the construction of Shasta Dam). The study site was located on a meandering section of the Sacramento River between river miles 196 and 199 at the confluence with Pine Creek. Larsen et al. (2006) measured an average channel migration rate of 7.7 m/yr (range 2.0 to 13.3 m/yr), which we applied to all reaches categorized as “meandering.” For reaches categorized as “low meandering” we used a rate equal to one-third of the average (2.6 m/yr), which is on the low end of the observed range.

Data on carbon stocks potentially mobilized through river meandering were from Matzek et al. (2018), who assembled a database of carbon stocks in 654 forest inventory plots of known age (3–108 years) from replanted and naturally recruiting California riparian forests. Since channel migration can capture a mix of stand ages, we opted to take the average of the reported values for the amount of stored carbon 30 and 100 years after establishment. When computing these averages, we only included carbon from three of the five pools quantified by Matzek et al. (2018) (“canopy carbon”, “downed dead wood,” and “understory”). We excluded the “forest floor” pool because it is primarily derived from fine woody debris and leaf litter, which we quantified separately as part of the litterfall calculations, and excluded the “soil” carbon pool to be consistent with the PANPP calculations for marsh plants, which do not include belowground carbon. For areas captured by meandering classified by Whipple et al. (2012) as “valley foothill riparian” we used the values reported by Matzek et al. for the “upland riparian class”; for areas classified as “willow riparian scrub/shrub” or “willow thicket” we used values reported for the “willow scrub” class. After controlling for age class, forest type, and carbon pools, as described
above, the final carbon densities used to determine riparian forest/scrub carbon captured via meandering were 9,306 g C m\(^{-2}\) for areas classified as “valley foothill riparian” and 4,996 g C m\(^{-2}\) for areas classified as “willow riparian scrub/shrub” or “willow thicket.”

**Mortality**

In areas without active river migration, we account for PANPP associated with inputs of large woody debris associated with tree mortality. Nearly 50 years of research focused on large wood (LW) in rivers provide a basis for the current understanding how wood enters rivers; how wood decays, breaks, and is transported downstream; and how at least temporarily stable wood influences channel geometry, fluxes of water, sediment, and organic matter, and the abundance and diversity of aquatic and riparian organisms (Maser and Sedell, 1994; Bilby and Bisson, 1998; Wohl, 2016). Nevertheless, with respect to wood recruitment, there is a general dearth of information on the relative importance of mass tree mortality as well as transport of buried or surficial downed wood from floodplains into channels.

Forest dynamics relevant to inputs of riparian LW include a variety of community characteristics, including the spatial density of trees, tree age and size, and species composition, and the mortality of individual trees and of multiple trees (Fig. 2.5.1). Spatial density and tree age influence rates of LW recruitment. Tree size influences LW piece size, which in turn influences LW load and piece mobility within the river corridor. Tree species indirectly influences LW loads through mortality rates and tree size and shape and wood density, each of which partly governs eventual LW mobility in the river. Tree species also directly influences loads through rates of decay within the river corridor. Individual and mass mortality of trees govern the volume of LW available for recruitment to the river corridor and partly determine the rate at which LW is introduced. Mass tree mortality can be caused by fire, insects, and ice and/or wind storms (Naiman et al. 2002, Wohl 2016).

![Flow chart illustrating the interactions among forest stand characteristics, tree mortality, and LW load in river corridors](from Wohl 2016)

**Figure 2.5.1. Flow chart illustrating the interactions among forest stand characteristics, tree mortality, and LW load in river corridors (from Wohl 2016).**
The forest ecology literature can be used to characterize individual tree mortality for many regions of the world. Rates of individual tree mortality vary with stand age, tree species, climate, topography, and other factors, but average or background rates can be used to reasonably estimate long-term (up to several decades) potential LW recruitment rates through individual mortality when mortality rates are combined with information on volume of standing trees and tree size (Wohl, 2016).

While tree mortality is an important demographic process and primary driver of forest dynamics, there are surprisingly few plot-based studies that explicitly quantify mortality and compare the relative contribution of endogenous and exogenous disturbances at regional scales. In general, there is little empirical data that quantifies mortality as a demographic rate and compares among disturbance agents and biophysical settings at a regional scale (Reilly and Spies, 2016). Even though it is widely recognized that riparian LW recruitment comes from processes close to the river, such as tree mortality, a reliable prediction of potential wood fluxes still remains to be developed (Ruiz-Villanueva et al., 2016).

An important variable in the LW recruitment process is the directionality of tree fall. Directionality can strongly influence predictions of large wood recruitment to streams, yet accuracy of this model parameter has rarely been assessed with field data. The central overall tendency for directional tree fall toward the stream most likely is related to the growth forms of riparian trees. Specifically, Sobota et al. (2006) believe that (1) undercutting of root mass by channel erosion processes, (2) light exposure to the natural canopy opening over a stream, and (3) soil movements on hillslopes all influence tree fall direction relative to the stream channel by shifting a tree's center of gravity toward the stream. While their results indicate that some degree of preferential tree fall toward the stream is an appropriate first approximation in recruitment modeling, performing periodic field surveys to validate this model parameter is critical to assess accuracy of model predictions.

Another significant consideration is that the geomorphic process domain concept predicts consistent associations between stream channel geomorphology and LW input mechanisms. For instance, in British Columbia, LW originated at ground distances up to 65 m from a variety of geomorphic surfaces, but 90% of the LWD originated within 18 m of the channel at 90% of the sites (Johnston et al., 2011).

The successional sequencing and mature ages of the riparian tree community are equally important. In northwest riparian zones along large, unconfined rivers, conifers generally invade after the initial cohort of hardwood trees begin senescence: 20–30 years for willow and 40–60 years for alder. Through accumulation of sediments from floods and channel downcutting, surfaces become perched above the reach of annual floods after 40–80 years and are then slowly colonized by late successional tree species (e.g., maple, hemlock). A mature fluvial terrace community is attained at about 100 - 130 yrs (Van Pelt et al., 2006), which may approximate the mature age for the Delta's riparian forests.

Based on the literature examined, and on conversations with experienced riparian researchers, we made the following assumptions to provide an order-of-magnitude estimate of large wood entering the Delta's rivers from age-related (successional) mortality.
We used measured lengths of non-meandering channel reaches (see “Channel meandering” section above) derived from Whipple et al. (2012) and Robinson et al. (2014), binned by adjacent woody riparian habitat type (“Valley foothill riparian,” “Willow riparian scrub/shrub,” or “Willow thicket”). The channel lengths were doubled to reflect riparian inputs from both banks of the channel. Carbon inputs from meandering channel lengths have been calculated separately since they reflect a different input process from age-related senescence (the meander-related carbon calculations include downed dead wood along meandering reaches).

While modern riparian vegetative communities are structurally less diverse and complex, and contain a somewhat different mix of species, the data are not sufficient to accurately explore effects on carbon inputs. Therefore, it is assumed for the calculations that historic and modern riparian communities are similar.

Potential carbon inputs from tree mortality arise from a 3 m band width for the willow habitat types and 15 m width for valley foothill riparian forests. Band width is a reflection of the mature height of the respective riparian communities.

Mortality rates are set at 1% annually. The mature age of the willow shrub community is 30 years and 100 years for valley foothill riparian forests.

30% of plants experiencing age-related senescence fall toward the channel.

Data on the standing stocks of carbon in the respective communities (Matzek et al., 2018), are an accurate reflection of historic and modern conditions. The standing stocks used in the following calculations are 4,319 g C m⁻² for willow shrub and 8,413 g C m⁻² for valley foothill riparian forest habitat types. To derive these rates from Matzek et al.’s database we used the same methods as described above under “Meandering,” but included only the “canopy” carbon pool. The general form of the calculation, for each riparian habitat type is:

Annual wood input from tree mortality (g C yr⁻¹) = (Standing stock of aboveground carbon for willow shrub or for valley foothill, 4,319 g C m⁻² or 8,413 g C m⁻²)(Mortality rate, 0.01/yr)(Proportion of trees falling in direction of channel, 0.30)(Bank length, m)(Band width for willow shrub or for valley foothill, 3 m or 15 m)

Estimated annual riparian carbon inputs (kt C yr⁻¹) to the Delta from these analyses for each individual riparian habitat are reported in table 2.5.4. These were summed to yield the total estimated PANPP from the woody riparian plant producer group.

2.5.2. Results and conclusions

Litterfall

The largest litterfall contributions to the Delta are generally from valley foothill habitat in both wet and dry historical and modern periods (Table 2.5.1). Inputs from the foothill habitat comprise 75-84% to 42-71% for wet and dry periods, respectively, with the only exception being contributions from willow habitats during historically dry conditions.

There are substantial reductions in riparian litterfall from historical to modern periods. During wet periods, for all habitat categories, reductions ranged from 41-96% with a total reduction of
79%. During dry environmental conditions reductions ranged from 27-98% with an overall reduction of 57%. Total amounts of litterfall generally decline substantially during dry conditions, especially for the valley foothill habitat.

Table 2.5.1. Annual riparian litterfall estimates (Mg C/yr) for historical and modern wet and dry years, by habitat type.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Historic, Wet</th>
<th>Modern, Wet</th>
<th>Percent Reduction</th>
<th>Historic, Dry</th>
<th>Modern, Dry</th>
<th>Percent Reduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Valley Foothill Riparian</td>
<td>77,910</td>
<td>14,535</td>
<td>81%</td>
<td>8,335</td>
<td>6,095</td>
<td>27%</td>
</tr>
<tr>
<td>Willow Riparian Shrub</td>
<td>7,805</td>
<td>4,622</td>
<td>41%</td>
<td>4,340</td>
<td>2,375</td>
<td>45%</td>
</tr>
<tr>
<td>Willow Thicket</td>
<td>7,134</td>
<td>264</td>
<td>96%</td>
<td>7,134</td>
<td>124</td>
<td>98%</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>92,849</strong></td>
<td><strong>19,421</strong></td>
<td><strong>79%</strong></td>
<td><strong>19,809</strong></td>
<td><strong>8,594</strong></td>
<td><strong>57%</strong></td>
</tr>
</tbody>
</table>

We conclude that the absolute amounts of riparian litterfall have declined substantially from historical to modern periods. There are numerous causes for these reductions, all of which are attributed to the expansion of cultural land uses which include the cutting of riparian forests, diking channels, draining marshes, and other activities associated with the expansion of agriculture and with improving navigation (ref needed). While the estimated amounts of carbon added to the Delta are less than inputs from phytoplankton (and perhaps other sources), reductions in riparian-based carbon represent an important loss to overall productivity. For instance, it is well known that many aquatic organisms relied on the predictable seasonality and generally high quality of riparian inputs to fulfill important life history functions.

**Channel meandering**

Most channel meandering is associated valley foothill riparian habitat, accounting for nearly all (~95%) the inputs of vegetation and soils during historical and modern periods (Table 2.5.2). The extent of annual meandering has sharply declined in the modern period, concomitant with the artificial stabilization of river banks, resulting in a 71% reduction in carbon associated with vegetation and soils.
Table 2.5.2: Estimated annual riparian wood (and soil) inputs from channel meandering (Mg C/yr).

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Historical</th>
<th>Modern</th>
<th>Percent Reduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Valley Foothill</td>
<td>12,599</td>
<td>3,615</td>
<td>71%</td>
</tr>
<tr>
<td>Willow Shrub</td>
<td>610</td>
<td>222</td>
<td>64</td>
</tr>
<tr>
<td>Willow Thicket</td>
<td>0</td>
<td>0</td>
<td>N/A</td>
</tr>
<tr>
<td>Total</td>
<td>13,209</td>
<td>3,837</td>
<td>71%</td>
</tr>
</tbody>
</table>

We conclude that organic matter inputs from channel meandering, in absolute amounts, are currently a minor contribution to the Delta. Nevertheless, the nature of the organic matter – mostly as tree boles and other decay resistant woody material – has other positive long term consequences through the physical diversity they provide. It has been well established that dead wood in channels is vitally important for ecological productivity, and that the removal of dead wood in the late 19th and early 20th centuries fundamentally altered productivity (see Maser and Sedell 1994, Naiman et al. 2002).

Mortality

While total bank length declined only 8% between historical and modern periods, there are substantial changes associated with specific rivers (Table 2.5.3). Notably, there is 34% more bank length supporting valley foothill vegetation in the modern period but 48% less willow shrub. Most valley foothill riparian vegetation occurs on the Sacramento River (94% historically vs. 57% in the modern period; Table 2.5.3). This difference in bank lengths over time is reflected in the estimated amounts of carbon entering the Delta through vegetative mortality. Willow shrub contribute only minor amounts of carbon through mortality, as compared to valley foothill vegetation. In the historical period it contributed only 11% of the total mortality inputs and only 6% in the modern period. Overall, organic matter inputs have increased 27% since the historical period, largely through increased valley foothill inputs from the San Joaquin River.

We conclude, compared to other carbon sources in the Delta, inputs from age-related senescence in riparian communities appear to be a relatively minor contribution on an annual basis. It is, however, somewhat comparable to wood inputs captured from river meandering in the historical but not the modern period. Nonetheless, it is important to recognize the ecologically vital structural role(s) of the slowly decomposing wood in the aquatic system to help maintain overall ecosystem system productivity, which persists for decades.

Total riparian contributions to the Delta

There have been substantial changes in riparian inputs to the Delta since historical periods. Overall, inputs have declined from 51 to 73% depending on whether wet or dry conditions prevailed with much of the change attributed to litterfall. During historical wet conditions litterfall contributed 83% of the total as compared to 52% of the total under dry conditions. In the
modern period, litterfall contributed 65% in wet conditions and 46% in dry conditions. Not surprisingly, channel meandering appears to be an important input mechanism during the historical period but not during the modern period. Vegetative mortality was a relatively minor contribution in the historical period but became a potentially significant input (22-34% of the total) during modern wet and dry conditions, respectively.

Table 2.5.3. Historical and modern bank lengths (km) by habitat type and river. Annual wood input from riparian tree mortality (Mg C/yr) are estimated for historical and modern periods.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>River</th>
<th>Historical Bank Length (km)</th>
<th>Modern Bank Length (km)</th>
<th>Historical Amounts (Mg C/yr)</th>
<th>Modern Amounts (Mg C/yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Valley Foothill</td>
<td>Sacramento</td>
<td>813</td>
<td>660</td>
<td>4,354</td>
<td>3,534</td>
</tr>
<tr>
<td></td>
<td>San Joaquin</td>
<td>1</td>
<td>336</td>
<td>5</td>
<td>1,799</td>
</tr>
<tr>
<td></td>
<td>Mokelumne</td>
<td>48</td>
<td>161</td>
<td>257</td>
<td>862</td>
</tr>
<tr>
<td></td>
<td>Subtotal</td>
<td>862</td>
<td>1,157</td>
<td>4,616</td>
<td>6,195</td>
</tr>
<tr>
<td>Willow Shrub</td>
<td>Sacramento</td>
<td>580</td>
<td>686</td>
<td>224</td>
<td>265</td>
</tr>
<tr>
<td></td>
<td>San Joaquin</td>
<td>718</td>
<td>216</td>
<td>277</td>
<td>83</td>
</tr>
<tr>
<td></td>
<td>Mokelumne</td>
<td>184</td>
<td>101</td>
<td>71</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>Subtotal</td>
<td>1,482</td>
<td>1,003</td>
<td>572</td>
<td>387</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td><strong>2,344</strong></td>
<td><strong>2,160</strong></td>
<td><strong>5,188</strong></td>
<td><strong>6,582</strong></td>
</tr>
</tbody>
</table>

We conclude that while riparian litterfall is consistently a significant input under both wet and dry conditions, additional quantification of litterfall is needed and, as well, quantifying inputs via vegetative mortality are warranted. We also note that restoration efforts to increase channel meandering could improve riparian contributions to the Delta.

Table 2.5.4. Estimated total annual riparian carbon inputs (kt C yr$^{-1}$) to the Delta during historical and modern periods, in both wet and dry water year types, from litterfall, channel meandering, and tree mortality.
### Woody riparian vegetation references


Irons, A.M., Stella, J.C., Battles, J.J., Bevilacqua, E., 2017. Tree colonization timing and forest dynamics along the Sacramento River, California.


Maser, C., Sedell, J.R., 1994. From the forest to the sea: the ecology of wood in streams, rivers, estuaries, and oceans. St. Lucie Press, Delray Beach, FL.


3. Estimating future primary production gains with landscape-scale restoration

3.1. Methods

The methods developed to estimate the magnitude of NPP within the Delta available to the aquatic food web historically (ca. 1800 CE) and today can also be used to estimate changes in total production from future land use change. This section describes the methods used to estimate future production under one possible future land use scenario: the landscape that would exist if Delta Plan habitat restoration targets are met.
The draft amendment to Chapter 4 of the Delta Plan ("Protect, Restore, and Enhance the Delta Ecosystem"), which is currently under consideration by the Delta Stewardship Council, sets specific areal restoration targets for a suite of Delta natural community types (equivalent to what we refer to in this article as "habitat types"). These targets were derived from individual conservation and restoration targets identified in Delta conservation and recovery plans that together cover 35 species of special-status plants and 86 fish and wildlife species of conservation concern. They are described in detail in Preliminary Draft Performance Measure 4.16 (DSC, 2019). Relevant targets for this effort include net increases in the area of the following habitat types: tidal freshwater emergent wetland (+32,500 acres), seasonal wetland / wet meadow / nontidal freshwater emergent wetland (+19,000 acres), and willow riparian scrub/shrub / valley foothill riparian / willow thicket (+16,300 acres). These net changes would result in an approximate 2.6x increase in the total area of tidal freshwater emergent wetlands, a 4.8x increase in the nontidal wetland habitat types, and a 2.2x increase in the woody riparian habitat types.

When estimating potential future changes in productivity we only altered the areas of the different individual habitat types; all other model assumptions and parameters (including hydroperiod) were held constant. The area of hydrologically connected habitat types that are included in the production model but do not have Delta Plan restoration targets (e.g., open water) were also held constant. In other words, we made the simplifying assumption that increases in the area of hydrologically connected areas will come entirely at the expense of areas that are currently hydrologically disconnected. Other simplifying assumptions made to translate the restoration targets into formats accepted by the production model were as follows.

For the new area of seasonal wetland / wet meadow / nontidal freshwater emergent wetland (+19,000 acres):

- All new areas in this habitat type group are restored as nontidal freshwater emergent wetlands.
- The regional distribution of new nontidal freshwater emergent wetlands (needed to assign a hydroperiod) is as follows: 52% of new areas are located in the Yolo region, 13% in the Cosumnes/Mokelumne region, and 35% in the San Joaquin region. These proportions were assigned based on documentation in the Delta Plan, which derived the total nontidal wetland restoration target from regional targets in the 2016 CVFPP Conservation Strategy, with 65% of the total coming from the Sacramento Conservation Planning Area (CPA) and 35% from the San Joaquin CPA. We made the additional simplifying assumption that 80% of the Sacramento CPA portion will be achieved within the Yolo region and 20% within the Cosumnes/Mokelumne region, based on the approximate relative areas of these regions as defined for this project.

For the new area of willow riparian scrub/shrub / valley foothill riparian / willow thicket (+16,300 acres):

- 50% of the woody riparian restoration target is valley foothill riparian forest and 50% is willow riparian scrub-shrub (willow riparian scrub/shrub and willow thicket are treated equivalently in the production model).
26% of the new valley foothill riparian and 53% of the new willow riparian scrub is within 25 m of a channel (the average of the historical and modern percentages).

3.2. Results

Table 3.2.1. Estimated production by producer group in the historical Delta (early 1800s), the modern Delta (early 2000s), and with future restoration from the draft amendment to chapter 4 of the Delta Plan

<table>
<thead>
<tr>
<th>Total production by producer groups</th>
<th>Historical Wet</th>
<th>Historical Dry</th>
<th>Modern Wet</th>
<th>Modern Dry</th>
<th>Future Wet</th>
<th>Future Dry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phytoplankton</td>
<td>20.5</td>
<td>12.0</td>
<td>16.1</td>
<td>11.0</td>
<td>18.6</td>
<td>12.0</td>
</tr>
<tr>
<td>Non-phytoplankton microalgae</td>
<td>136.4</td>
<td>139.3</td>
<td>4.8</td>
<td>4.8</td>
<td>19.0</td>
<td>19.5</td>
</tr>
<tr>
<td>Submerged and floating aquatic</td>
<td>14.2</td>
<td>13.5</td>
<td>29.5</td>
<td>29.5</td>
<td>29.5</td>
<td>29.5</td>
</tr>
<tr>
<td>Marsh vascular plants</td>
<td>292.2</td>
<td>292.2</td>
<td>5.8</td>
<td>5.8</td>
<td>37.8</td>
<td>37.8</td>
</tr>
<tr>
<td>Woody riparian</td>
<td>58.7</td>
<td>21.3</td>
<td>11.6</td>
<td>6.4</td>
<td>22.9</td>
<td>10.1</td>
</tr>
<tr>
<td>Total</td>
<td>522</td>
<td>478</td>
<td>68</td>
<td>58</td>
<td>128</td>
<td>109</td>
</tr>
</tbody>
</table>

Total magnitude

- Delta Plan restoration targets would nearly double NPP within the Delta potentially available to the aquatic food web in both dry and wet years, relative to modern conditions. Specifically, modeled production would increase from 58-68 ktC/yr to 109-128 ktC/yr (an increase of 88-89%).
- These gains would recover approximately 13% of the annual production lost since the historical period, increasing contemporary production from ~13% of its historical magnitude to ~24% of its historical magnitude.

Composition

- The Delta Plan restoration targets, if realized, would be expected to result in a shift in the dominant producer group from SAV/FAV (accounting for ~47% of all production today but only 25% under the Delta Plan scenario) to marsh vascular plants (9% today, but ~32% under the Delta Plan)
- The Delta Plan would not notably shift the relative proportion of production from vascular plants and algae.

3.3. Future primary production references

4. Estimating support for primary consumer growth

4.1. Methods

To assess the value of primary production as support for aquatic consumers, we translated production rates for each producer group to an annual rate of herbivore biomass growth. Translating from primary production to herbivore biomass growth depends on two generalized processes. First, not all carbon produced in the Delta is eaten by primary consumers. Alternative fates for this primary producer carbon are decomposition to CO$_2$, export from the region, or burial in sediments. The partitioning of primary production among these possible fates is likely to depend on a variety of factors, including producer identity, location within habitat type, season, and other physical environmental variables. Second, the rate with which ingested carbon is converted to herbivore biomass carbon varies among primary producers and consumers, dependent on the nutritional composition and nutritional needs of the primary producer and consumers, as well as consumer metabolic rates. This ability to support growth is summarized by the gross growth efficiency (GGE), which is defined as the fraction of carbon consumed that is converted to consumer biomass carbon.

Accounting for these two generalized processes, primary production can be converted to herbivore biomass growth according to:

$$H = PP_i \times f_i \times GGE_i$$

where for producer group i, $H$ is the rate of herbivore biomass growth in kt C/yr, $PP$ is the annual rate of primary production in kt C/yr, $f$ is herbivory fraction, defined as the fraction of primary production consumed by herbivores, and $GGE$ is the gross growth efficiency of herbivores consuming primary producer biomass.

Values for $f$ and and GGE were based on the published literature. Duarte and Cebrian (1996) compiled “published reports on herbivory, autotrophic respiration, decomposition, carbon storage, and export rates as fractions of net primary production (NPP) in ecosystems dominated by different types of autotrophs (i.e. oceanic and coastal phytoplankton, microphytobenthos, coral reef algae, macroalgae, seagrasses, marsh plants, and mangroves).” From this report, we extracted values for the rate of export, decomposition (to CO$_2$), herbivory, and storage of producers. We note that this report is a synthesis of marine-based studies, so values may not be an ideal representation of freshwater systems like the Delta. We extracted the median and range (upper and lower quartile) for each producer group, using seagrasses as a proxy for aquatic plants, benthic microalgae (microphytobenthos) as a proxy for attached microalgae, mangroves as a proxy for woody riparian plants, salt marsh plants as a proxy freshwater marsh plants, and coastal phytoplankton as a proxy for estuarine phytoplankton. We assumed that much of the biomass exported from the Delta is consumed in the estuary downstream, and still has regional value. Accordingly, we used the exported fraction to compute the percent of production retained locally, and from those adjusted values computed median values of the percent of NPP that is decomposed into CO$_2$, consumed by herbivores, and stored in sediments.
The fraction consumed by herbivores (herbivory percentage / 100) is equivalent to our coefficient $f_i$, the herbivory fraction.

Table 4.1. Percentage of production channeled to herbivory, decomposition to CO2, and burial in sediments, based on Duarte and Cebrian (1996). Values are shown as medians and interquartile ranges. Note that median percentages don't add to 100%. The herbivory fraction $f$ is equal to the percentage channeled to herbivory / 100.

<table>
<thead>
<tr>
<th>Producer group</th>
<th>Herbivory</th>
<th>Decomposition</th>
<th>Burial</th>
</tr>
</thead>
<tbody>
<tr>
<td>phytoplankton</td>
<td>46 (20-83)</td>
<td>49 (33-73)</td>
<td>3.7 (0.54-4.0)</td>
</tr>
<tr>
<td>marsh plants</td>
<td>20 (5.3-79)</td>
<td>52 (43-100)</td>
<td>15 (9.6-31)</td>
</tr>
<tr>
<td>woody riparian plants</td>
<td>13 (5.6-16)</td>
<td>57 (44-77)</td>
<td>5.2 (4.4-32)</td>
</tr>
<tr>
<td>aquatic plants</td>
<td>14 (6.5-45)</td>
<td>63 (45-117)</td>
<td>6.0 (4.3-49)</td>
</tr>
<tr>
<td>attached microalgae</td>
<td>43 (32-89)</td>
<td>34 (16-45)</td>
<td>2.7 (0-4.1)</td>
</tr>
</tbody>
</table>

We identified separate GGE values for algal and vascular plant producers. GGE values for the two algal producer groups (phytoplankton and attached microalgae) were based on studies of phytoplankton consumption by copepods, rotifers, and cladocerans (Straile 1997), as well as daphnia (Brett et al 2012), yielding a median 0.22 (range = 0.20-0.28). The median GEE for primary consumers eating vascular plant material was 0.16 (range = 0.075-0.21), based on mysids feeding on detritus (Ferguson 1973) and trichoptera larvae consuming woody riparian vegetation and aquatic plants (Jacobsen and Sand-Jensen 1994).

4.2. Primary consumer support references


