# Landscape Transformation and Variation in Invasive Species Abundance Drive Change in Primary Production of Aquatic Vegetation in the Sacramento–San Joaquin Delta

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## ABSTRACT

Conversion of wetlands in the Sacramento–San Joaquin Delta beginning in the mid-1800s resulted in a pronounced shift from a wetland-dominated food web to one driven by open-water primary producers. Submersed and floating aquatic vegetation (SAV and FAV) now rank highest in potential net primary production (NPP) among producer groups, and provide a comparable amount of carbon to the detrital food web as marshes. However, important details of this contribution that relate to shifts in species composition and habitat extent were not understood. Here, we review how changes in aquatic vegetation influence NPP and trophic support from the historical to modern periods, within the modern period (the last 2 decades), and under future management and climate scenarios. We estimate that NPP of SAV and FAV during the historical period was approximately half that of today, before increases in open water and introduction of the highly productive water primrose. During the modern period (the last 20 years), high interannual variability in the extent and relative composition of aquatic vegetation species has driven significant variation in total NPP. This recent temporal variation is 6 to 13 times larger than projected changes in production from the potential future scenarios we modeled, including a reduction in FAV by 20% through control measures, substantial wetland restoration (and thus increased channel area that could support SAV and FAV), and increased salinity intrusion in the western Delta with climate warming, which favors native species with greater salinity tolerance. Large temporal swings in NPP of SAV and FAV cascade to influence the degree of carbon that flows to consumers through detrital pathways and herbivory. This volatility and interannual inconsistency in aquatic vegetation support of food webs make achieving wetland restoration goals for the Delta—which could lead to recovery of a portion of the NPP lost since historical times—even more imperative.

## KEY WORDS

FAV, SAV, food web, tidal freshwater wetland, primary production, detritus, San Francisco Estuary

## INTRODUCTION

Wetland landscapes have been transformed worldwide as human populations and their intensity of land use have increased. In the last century, over half of wetland ecosystems globally were converted to agricultural, industrial, or commercial uses, or filled in to build cities and towns and their associated infrastructure (Mitsch and Gosselink 2007; Davidson 2014). The Sacramento–San Joaquin River Delta (the Delta), which is the upstream, generally freshwater portion of the San Francisco Estuary, has undergone one of the most extensive conversions of wetlands to human uses reported globally (Cloern et al. 2021). This river-delta system formed from its two namesake rivers and their tributaries depositing sediment from the Sierra Nevada mountain range and foothills, creating 2,300 km$^2$ of tidal freshwater marshes with an extensive and highly distributed network of channels (Figure 1; also see Whipple et al. 2012; Robinson et al. 2014). Beginning in the early- to mid-1800s, levees were used to convert the majority of these wetlands to farmland or urban uses, and the remaining channels are now largely disconnected from the surrounding landscape. This transformation had significant consequences for the Delta ecosystem and the species it supports, including severe decreases in net primary production (NPP) and energy available to consumers through herbivory and detrital pathways. The percentage loss to food webs is estimated to be even greater than the loss of acreage of hydrologically connected wetlands—a 77% decrease in area drove a 94% loss of NPP (Cloern et al. 2021).

The Delta's transformation resulted in a 75% increase in open water through channel creation, channel widening, and—more recently—through levee failure events and the subsequent flooding of highly subsided islands (Figure 1; Robinson et al. 2014). A large increase in both shallow and deep open water provided additional habitat for submersed and floating vascular plants ("SAV" and "FAV"; together "aquatic vegetation"). The last 4 to 5 decades have also seen a proliferation of non-native aquatic vegetation species, probably in response to changes in abiotic conditions. For example, the submersed species *Egeria densa* (Brazilian waterweed), although introduced in the 1940s (Light et al. 2005), did not reach "nuisance levels" of coverage until the 1990s (Jassby and Cloern 2000). Today, it covers thousands of hectares of Delta waters, and is subject to control efforts (see Christman et al.; this issue; Conrad et al., this issue). *Egeria densa* may now benefit from a trend of decreased turbidity that results from depletion of the suspended sediment pool from the post-Gold Rush mining years (Schoellhamer 2011), and further decreases turbidity itself by trapping suspended sediments (Hestir et al. 2013, 2016; Drexler et al. 2020; Lacy et al. 2020). In addition, the introduced floating species *Eichhornia crassipes* (water hyacinth) covered hundreds of hectares by the early 1980s and is favored by a decreased frequency of winters with frost (Khanna et al. 2012, 2018). Policies and practices that reduce salinity intrusion from the lower estuary into the Delta encourage non-native species that have little salinity tolerance (e.g., *E. densa*) at the expense of native species that evolved with greater variability in salinity (e.g., *Stuckenia pectinata* [sago pondweed]; Borgnis and Boyer 2016). Invasive aquatic plants may alter the landscape for native fish species of concern through modification of open waters and enhancement of rearing habitat for non-native predatory fish (Conrad et al. 2016), but also contribute substantially to the diets of invertebrates that are then consumed by many fish species (Grimaldo et al. 2009; Young et al. 2021).

SAV and FAV now contribute more to ecosystem NPP than any other major producer group in the modern Delta, including marsh plants, woody riparian plants, phytoplankton, and attached microalgae. This represents a pronounced change from historical conditions, when aquatic plants contributed an order of magnitude less NPP than emergent marsh plants (Cloern et al. 2021). Further, SAV and FAV may now provide a comparable amount of carbon to the detrital food web as marsh plants (the relative contribution
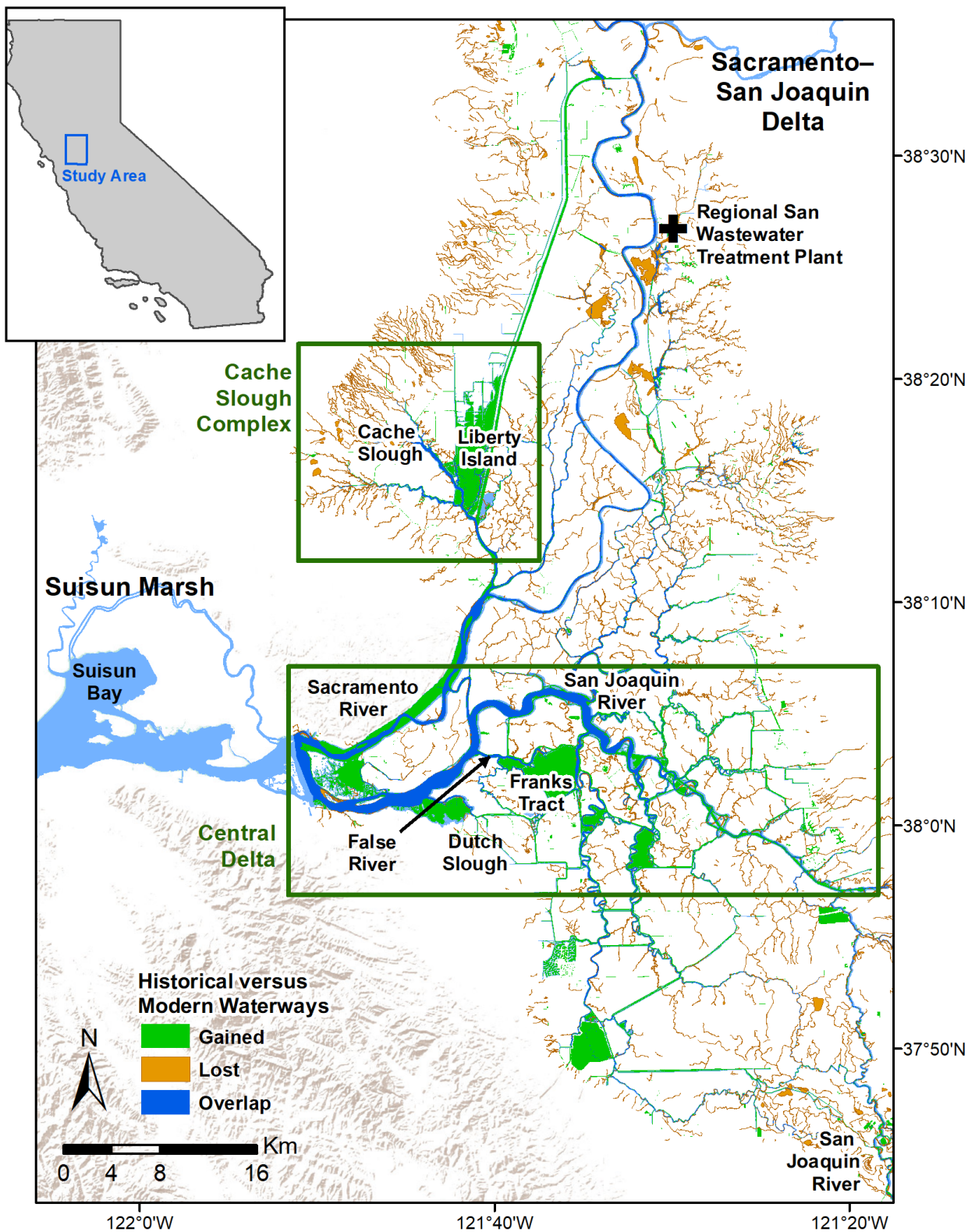
**Figure 1** The Sacramento–San Joaquin Delta, comparing historical and modern hydrography with water gained since mid-1800s (*green*), lost (*orange*), and overlap (*deep blue*) of aquatic area (*adapted from Robinson et al. 2014*). Place names mentioned in this article are indicated. The *top inset* shows the location in California. The *green boxes* indicate the regions from which acreages were sourced for Figures 3 and 4.

from aquatic vegetation is estimated to have been negligible historically; Cloern et al. 2021). Hence, in addition to the overall decrease in NPP by > 90% with wetland loss, there has been a substantial shift from a wetland-dominated food web to one driven by open-water producers, especially aquatic plants (Cloern et al. 2021).

The massive loss of Delta food web support since historical times may be partially recoverable through management activities that change the landscape configuration. The Delta Plan aims to restore wetland acreage and connectivity to support native species and achieving wetland restoration goals as envisioned (DSC 2019) could recover 12% of lost NPP by doubling carbon available to herbivores and tripling detritus production from current levels (Cloern et al. 2021). This wetland restoration will result in more channel and other open water area, which may encourage additional coverage of non-native aquatic vegetation, if control measures currently underway and in development are not successful (Conrad et al., this issue). Although an increase in acreage of aquatic vegetation may be deemed negative in some ways (summarized above), additional NPP and food web support would be gained in deeper waters alongside the emergent plants in the wetland restoration projects planned.

In addition to landscape configuration determining the acreages of primary producers, the relative abundance of component species could be important to total carbon production and related food web metrics. The Delta aquatic vegetation assemblage shifted through species introductions in the last half century or so, and new introductions continue (Christman et al., this issue). Because interannual variation in species' relative abundances can be high (Santos et al. 2012; Khanna et al. 2018) and production rates vary greatly among SAV and FAV species (Cloern et al. 2021), incorporating variation in community composition and relative abundance into calculations of NPP can aid our understanding of trophic transfer and inform management decisions.

Here, we delve into the contributions of aquatic vegetation species to primary production and trophic transfer in the historical, modern, and future Delta (Figure 2), examining a range of scenarios and their implications for the food web. We refine previous estimates of changes in production by accounting for variability in aquatic vegetation species' production rates and coverage, improving on previous analyses that may have over-simplified their contribution to total ecosystem production and food web support. We briefly review SAV and FAV extent, community composition, and NPP estimated for the historical and modern Delta from a recent analysis (Cloern et al. 2021). We then (1) describe alternative scenarios for the historical Delta, (2) consider how large shifts in aquatic vegetation coverage and species' relative abundances over the last 2 decades affected Delta-wide production, and (3) envision several future scenarios that include invasive vegetation control measures, wetland restoration, and increased salinity intrusion. Finally, we evaluate how these scenarios translate to food web support, and discuss science and management recommendations.

## HISTORICAL AND MODERN NPP OF AQUATIC VEGETATION: A RECENT ANALYSIS

The recent analysis by Cloern et al. (2021) quantified the extent of hydrologically connected area in the Delta using a spatially explicit reconstruction of land cover in the early 1800s (Whipple et al. 2012), and did the same for the modern Delta using detailed vegetation and land cover maps (Robinson et al. 2014). The authors used remote sensing data from one time point, 2015, to determine the primary FAV species present in today's Delta and their relative abundances (Ustin et al. 2016), and used SAV species composition from field sampling in 2007 by Santos et al. (2011). A literature review revealed that productivity rates of the most common species varied by three orders of magnitude, with median rates in the tens to a few hundred g C m$^{-2}$ for SAV and in the one to four thousand range for FAV (Cloern et al. 2021). Total production was calculated for the modern Delta using the area of FAV or SAV from remote sensing data (Ustin et
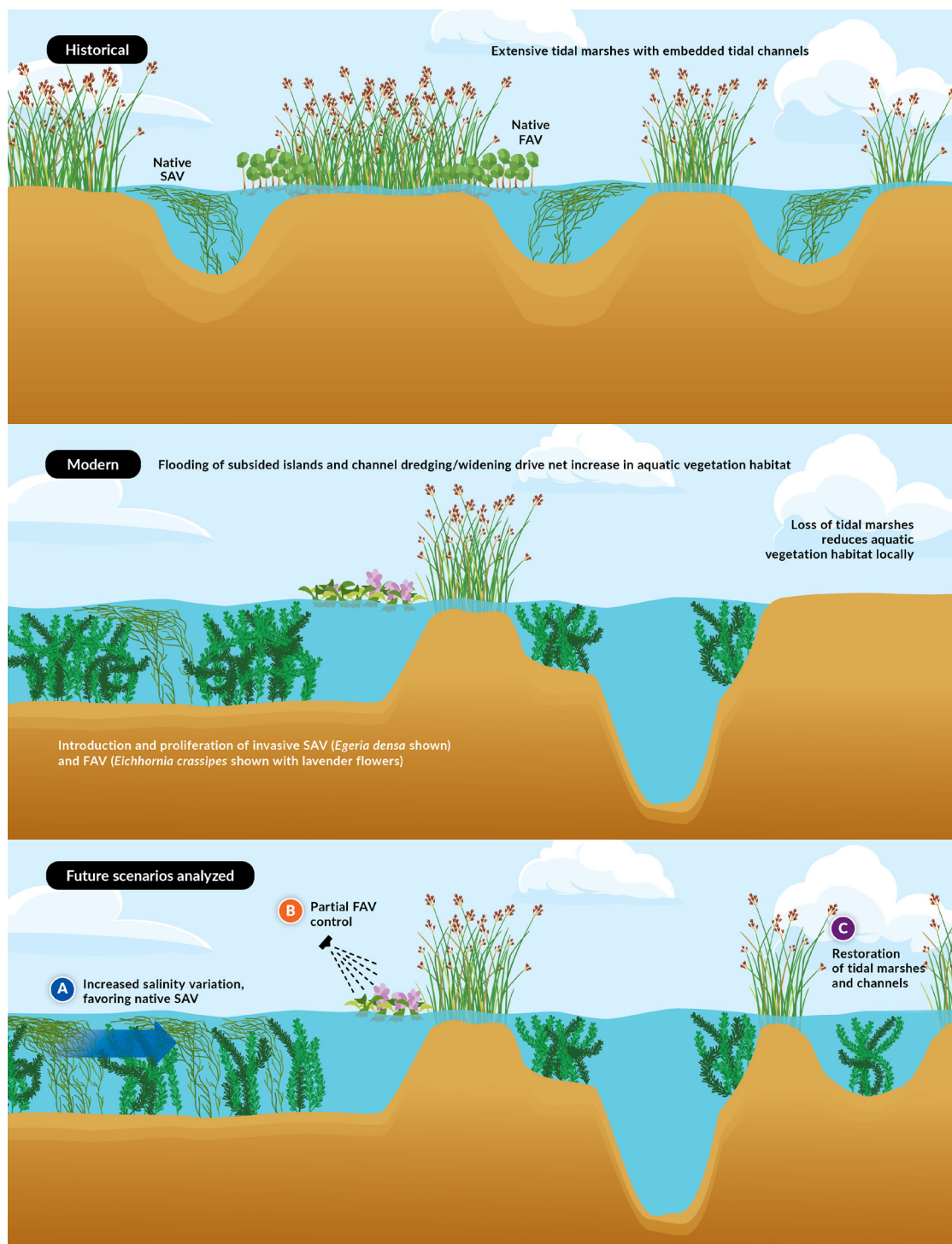
**Figure 2**    Historically, the Sacramento–San Joaquin Delta contained a vast expanse of tidal marshes (dominated by "tules", the bulrush *Schoenoplectus acutus*) with embedded tidal channels supporting native submersed (sago pondweed, *Stuckenia pectinata*, shown) and floating (pennywort, *Hydrocotyle umbellata*, shown) aquatic vegetation. In the modern period (since the mid-1800s), the area of open water increased through deepening and widening of channels and filling of marshes to create islands, which subsided and, in some cases, flooded; introduced aquatic vegetation proliferated. Here, we evaluate historical and modern conditions for their effects on net primary production (NPP) and food web support, in comparison to several potential future scenarios, including (**A**) increased salinity variation, (**B**) partial control of invasive FAV, and (**C**) restoration of tidal marshes and channels. Illustrated by Vincent Pascual with the California Office of State Publishing.

al. 2016), the median productivity rate for each species, and species-specific relative cover data derived from field sampling.

To estimate aquatic vegetation production in the mid-1800s, the historical acreage potentially occupied based on depth was adjusted down to reflect the proportion of area at the same depths that SAV and FAV occupied in 2015. The most abundant species native to the region in today's Delta were assumed present historically with the same relative abundances; this was a large assumption, but allowed a reconstruction of the aquatic vegetation community for production estimates (Cloern et al. 2021). This comparison determined that the Delta-wide submersed and floating vegetation production totaled approximately $14\,\mathrm{kt\,C\,y^{-1}}$ historically, compared to $30\,\mathrm{kt\,C\,y^{-1}}$ in the modern Delta (based on 2015 acreages), thus increasing 114% between the historical and modern periods (Cloern et al. 2021).

## CONSIDERING ALTERNATIVE SCENARIOS

To better understand how different assumptions regarding historical, modern, and future conditions affect estimates of Delta-wide aquatic plant production, here we test several alternative scenarios. In addition to a "baseline" historical condition (Cloern et al. 2021), we test the effects of two additional possibilities: the first assumes *Ludwigia peploides* (water primrose) joined the historical species assemblage early on, and the second assumes *Ceratophyllum demersum* (coontail) was absent (see reasoning in "The Historical Delta: Uncertain Species Composition"). Because we also explore the effects of these scenarios in combination, we test a total of four unique historical scenarios. For the future Delta, we test the effects of three potential future changes: (1) an increase in FAV control, (2) extensive tidal wetland restoration, and (3) salinity intrusion. As we test all possible combinations of these three changes, we analyze a total of eight future scenarios. Note that one of these eight future scenarios (the one where none of the three possible changes is implemented) is equivalent to the modern scenario.

Across all historical and future scenarios, we account for differences in estimates resulting from the choice of modern reference year used to determine the relative cover and species composition of aquatic vegetation, testing the effects of six different years (2004, 2005, 2007, 2015, 2019, 2020). These interannual differences in cover/composition are also analyzed and reported individually for contemporary conditions, resulting in six scenarios of modern production (although we refer to these different estimates as modern "scenarios," they reflect estimates of productivity derived from empirical measurements of recent conditions). The years chosen above are those for which estimates of aquatic vegetation cover are available from data collected in the study area (Khanna et al. 2022). The available years capture a wide range of water-year types, including critically dry (2015), dry (2004, 2007, 2020), and wet (2005, 2019) years (CDWR n.d.).

Across all scenarios, we account for uncertainty in the per-unit area productivity of each individual plant species (see Tables A1–A3 for the complete list of literature values used and summary statistics), yielding a range of estimates for each (see "Evaluating Alternative Scenarios: Methods"), but these differences are not treated as individual scenarios themselves. A list of all evaluated scenarios is found in the "Evaluating Alternative Scenarios: Results and Discussion" section, and each is described in more detail below.

### The Historical Delta: Uncertain Species Composition

The assumptions in the section "Historical and Modern NPP of Aquatic Vegetation: A Recent Analysis" about aquatic vegetation species expected to have been abundant in the historical Delta produced a reasonable estimate of Delta-wide production for that time-period (Cloern et al. 2021). However, assuming that *Hydrocotyle umbellata* (pennywort) was the primary FAV species circa 1800, leads to much lower production estimates than an alternate assumption that *L. peploides*—with a more than three times greater median productivity rate—was present at that time. *L. peploides* is believed to

be an early introduction; it appears in one early record from south San Francisco Estuary (near Newark; Behr 1884), is noted as a lost specimen or record from Cache Creek (west of Cache Slough, Figure 1; Jepson 1901), and appears to be present in a photograph from the Delta taken in 1905 (Whipple et al. 2012, p. 269). Given the relative frequency of herbarium specimens from the late 19th and early 20th centuries, if *L. peploides* was present at all circa 1800, it was probably much less common than *H. umbellata*. However, Greene (1894) reported *Ludwigia* spp. as abundant in Delta sloughs by 1888, and W. L. Jepson collected *L. peploides* herbarium specimens from Ryer Island in Suisun Bay in 1891 and from Cache Slough in 1893 (Jepson Herbarium, UC Berkeley). Below, we consider the possibility that *Ludwigia* spp. quickly established and thus contributed to the production of the historical aquatic vegetation community. Note that *Ludwigia* in the modern Delta is a combination of *L. peploides*, *L. hexapetala*, and *L. grandiflora*, but it is not clear when the latter two introduced species began to contribute meaningfully to the FAV assemblage in terms of abundance and production.

Another FAV species known to be present in fresh waters of the historical Delta (and generally absent today) is the yellow water lily, *Nuphar polysepala* (Whipple et al. 2012). It was recorded to have been found in lakes and sloughs near Stockton (Jepson 1901), and as part of the "epihydrous mosaics" vegetation community (Mason n.d.). Sediment coring and pollen analysis confirm its historical presence (West 1977), and a circa 1850 account noted its thick coverage of leaves on the surface of one lake (Whipple et al. 2012). Although it may have been abundant in some quiescent fresh waters of the historical Delta, its contribution to Delta-wide production was probably limited by available habitat, and we have not included it in our estimates.

With regard to SAV in the historical Delta, we assume that natives of the modern Delta were present, including *C. demersum*, *S. pectinata*, *Potamogeton nodosus* (American pondweed), *P. richardsonii* (Richardson's pondweed), *Najas guadalupensis* (southern naiad), and *Elodea*

*canadensis* (Canadian waterweed) (Santos et al. 2011; Ustin et al. 2021). Pondweeds (*Potamogeton* and *Stuckenia* species) may have been abundant in the historical Delta considering that seeds from the family Potamogetonaceae were found throughout a peat core in the vicinity (Goman and Wells 2000). Note that although some previous studies recorded the presence of *Stuckenia filiformis* (broad-leaf sago pondweed) in Suisun Bay and the Delta, recent genetic analyses determined that widely collected specimens resembling its growth form were all *S. pectinata* (Patten and Boyer 2023).

Although *C. demersum* is the most common native SAV species in the modern Delta (Santos et al. 2011; Christman et al., this issue), it does not appear in the historical records. Thus, below (see "Historical Estimates" section) we consider an additional scenario that excludes *C. demersum*. This alternative scenario of *C. demersum* as absent or rare in the historical Delta fits with the hypothesis that its abundance in the modern Delta has followed the proliferation of *E. densa* (Santos et al. 2011), with which it co-occurs about 70% of the time (Khanna, unpublished data). However, it is known in other regions to grow in monoculture stands (Wells et al. 1997), thus supporting the baseline scenario of presence in the historical Delta long before the introduction of *E. densa*.

### The Modern Delta: Interannual Variation
Estimates of aquatic vegetation production for the modern Delta by Cloern et al. (2021) were based on abundance of species from remote sensing in one particular year, 2015, the most recent available data set at the time of the study. However, interannual variation in coverage and relative abundance has been high according to observations and time-series analyses (Khanna et al. 2012, 2018; Ustin et al. 2021), and this variation warrants a closer look in our production estimates.

From 2004 to 2008, SAV (dominated by *E. densa*; see below) occupied anywhere from 1,600 hectares to a maximum of 3,200 hectares in the Delta. Liberty Island and the Cache Slough
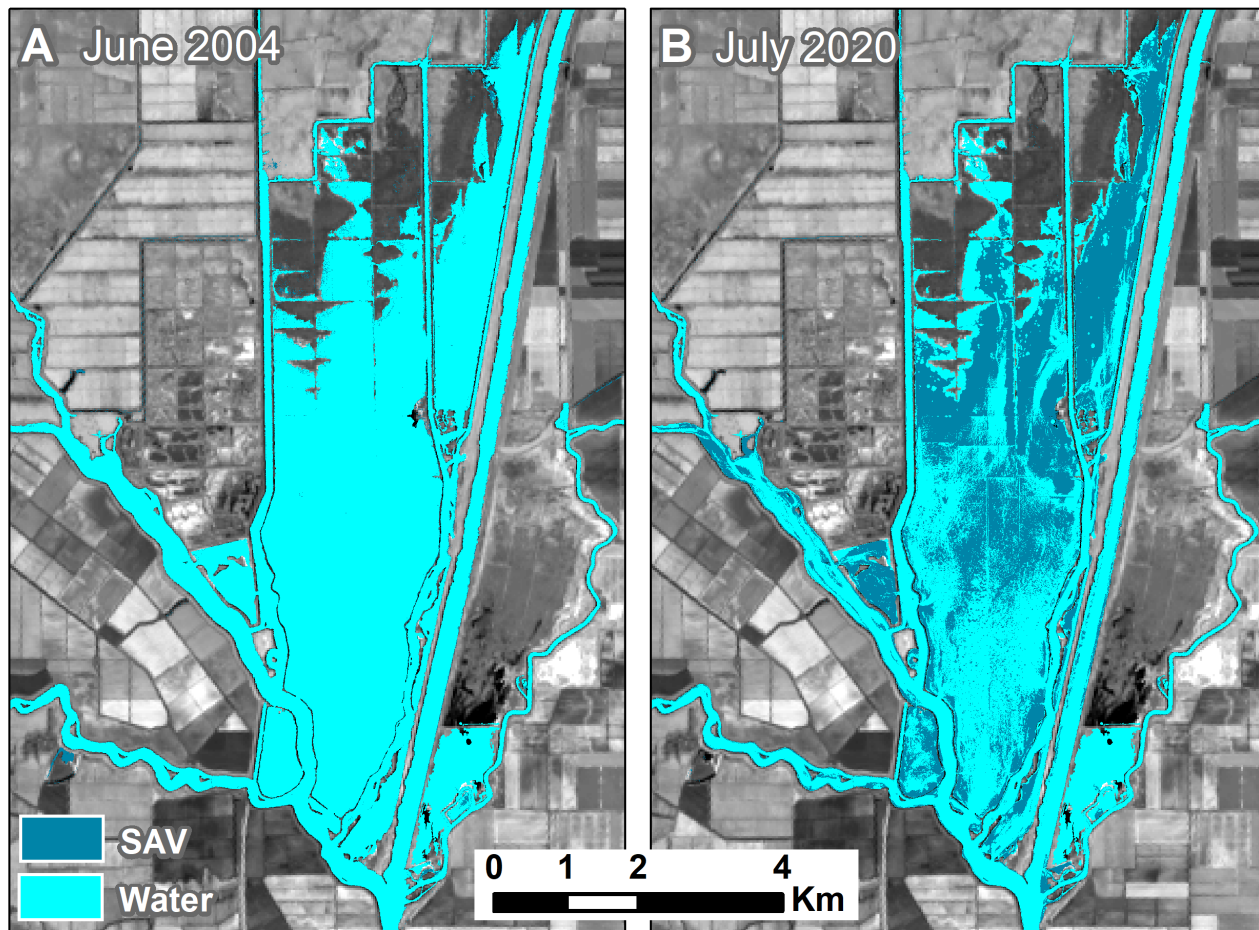
**Figure 3** Increased cover of submersed aquatic vegetation at Liberty Island between (**A**) 2004 and (**B**) 2020

complex (see Figure 1 for these and other named locations) were largely free of SAV. The central region of Franks Tract, which experienced strong tidal pumping and water flow, was free of SAV. However, after the recent drought ending in 2017, SAV went from coverage of 8% of Delta waterways in 2008 (1,075 hectares) to 34% in 2018 (4,290 hectares) (Ustin et al. 2021). The most drastic change has been at Liberty Island, where SAV cover has risen steadily over the past 15 years (Figure 3). Further, after installation of a temporary salinity barrier across False River in 2015 to exclude saline water and deflect tidal pumping, the central rib of Franks Tract was colonized by SAV and today has continuous SAV cover even after removal of the barrier (Kimmerer et al. 2019). The SAV community within Franks Tract, however, has changed from predominantly *E. densa* in 2006 to a more mixed

community in recent years, with the native pondweed *P. richardsonii* having the highest frequency of occurrence (Caudill et al. 2019; Ustin et al. 2021).

In terms of relative abundance, the introduced *E. densa* has dominated the SAV at 41% to 58% of cover, followed by native *C. demersum* (11% to 18%) and the introduced *Myriophyllum spicatum* (Eurasian watermilfoil; 10% to 14%) (Table 1). Other, less prevalent species have displayed no apparent pattern in relative abundance during the years sampled, although the introduced *Cabomba caroliniana* (Carolina fanwort) and native *N. guadalupensis* may be trending upward, along with native *P. richardsonii* increasing primarily due to the high abundance in Franks Tract described above (Table 1).

**Table 1** Estimates of the relative cover of individual SAV species from visual and rake data collected in the field across the Delta annually during summer (2007, 2020) and fall (2015, 2019) by the Center for Spatial Technologies and Remote Sensing at University of California, Davis (*Ustin et al. 2021*). Species are ordered from most to least abundant in 2020. Because not all years when the Delta-wide extent of SAV was measured via remote sensing have field estimates of SAV species composition, we used the closest year with field data to estimate the composition of remotely sensed SAV. Field measurements from 2007 were used to calculate the species composition of SAV mapped in 2004 and 2005.

| Species | Status | Percent SAV cover by year | | | |
| --- | --- | --- | --- | --- | --- |
| | | 2007 | 2015 | 2019 | 2020 |
| *Egeria densa* | Introduced | 57.8 | 43.6 | 51.6 | 41.4 |
| *Ceratophyllum demersum* | Native | 10.7 | 17.5 | 14.2 | 14.9 |
| *Myriophyllum spicatum* | Introduced | 13.5 | 11.3 | 12.3 | 10.1 |
| *Potamogeton richardsonii* | Native | 0.0 | 0.0 | 4.0 | 6.6 |
| *Potamogeton crispus* | Introduced | 8.7 | 12.8 | 3.3 | 5.8 |
| *Elodea canadensis* | Native | 0.0 | 1.3 | 3.1 | 5.6 |
| *Najas guadalupensis* | Native | 0.0 | 0.0 | 0.9 | 5.4 |
| *Stuckenia pectinata* | Native | 5.4 | 10.7 | 3.5 | 5.3 |
| *Cabomba caroliniana* | Introduced | 1.3 | 1.1 | 6.6 | 4.1 |
| *Potamogeton nodosus* | Native | 2.5 | 1.8 | 0.6 | 0.9 |

Floating vegetation coverage and species composition has also varied greatly over recent decades (Figure 4). In the early 2000s, *H. umbellata* was one of the three dominant floating species in the Delta. Since then, this native pennywort declined, the invasive water hyacinth *E. crassipes* maintained somewhat constant coverage (varying by climatic conditions and level of treatment effort; FLOAT–MAST 2020), and the invasive water primrose *Ludwigia* spp. increased. In 2005, Delta coverage of FAV included 120, 200, and 160 hectares of *H. umbellata*, *E. crassipes*, and *Ludwigia* spp., respectively (Khanna et al. 2012). By fall 2019, these coverages had shifted to roughly 0, 110, and 510 hectares, respectively, with *Ludwigia* spp. also encroaching into emergent marsh areas (Khanna et al. 2018; Christman et al., this issue). There has also been a recent increase in the area of *Azolla* spp. (mosquito fern) in the Delta (Khanna, personal observation).

In the "Modern Estimates" section of the results, we account for interannual variability in the total coverage and relative abundance of different aquatic vegetation species by estimating production in 6 years with available data: 2004, 2005, 2007, 2015, 2019, and 2020. These years capture the important recent changes in aquatic
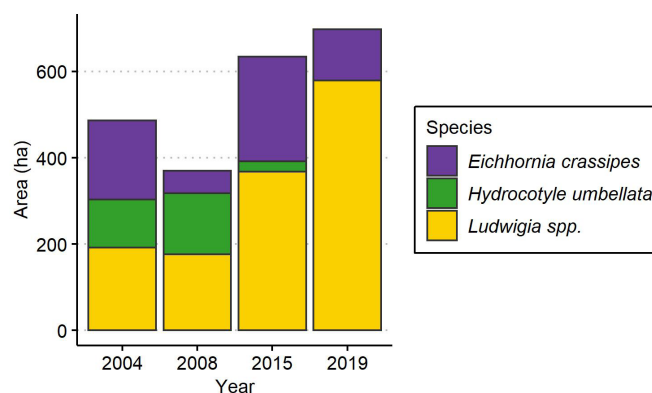


**Figure 4** Interannual differences in the total extent and relative cover of floating aquatic vegetation species *Eichhornia crassipes*, *Hydrocotyle umbellata*, and *Ludwigia* spp. (*based on data from Ustin et al. 2021*) in the Central Delta and Cache Slough complex (see *green boxes* in Figure 1 for covered area).

vegetation species composition and coverage described above.

**The Future Delta: Management and Climate Change**

Several types of management and climate-related changes in the Delta region could result in changes in the coverage of aquatic vegetation in the future, and thus its contributions to NPP and the greater Delta food web. Here, we

consider three management scenarios: additional treatment to control invasive FAV, tidal wetland restoration, and more variable salinity in the western Delta.

### *Treatment to Control Invasive FAV*

Methods of chemical treatment to control invasive species of SAV (including *E. densa, P. crispus, M. spicatum,* and *C. caroliniana*) and chemical, mechanical, and biological treatments for FAV (primarily *E. crassipes* and *Ludwigia* spp.) in the Delta have been practiced over several decades in the Delta, and are the subject of continuing development and testing to various degrees (Carruthers et al. 2012, 2013; CDBW 2019; Madsen 2019; Caudill et al. 2021; Moran et al. 2021; Conrad et al., this issue). However, for SAV, remote sensing time-series analyses have shown that treatment methods have limited efficacy both within years and over several years of treatment (Santos et al. 2009; Khanna et al., forthcoming), and recent field evaluations have been consistent with these findings (Rasmussen et al. 2022). Although biovolume surveys suggest some seasonal effect of herbicide treatment (Caudill et al. 2019), SAV cover generally persists across years (reviewed in Conrad et al., this issue). FAV control may show more promise; it is effective in the short-term, although it does not reduce cover permanently (Santos et al. 2009; effects can last less than 1 year: Khanna, unpublished data). It is possible that ongoing trials will lead to development of more effective methods with time (Kyser et al. 2021; Reddy et al. 2021). Also, there may be other changes in Delta conditions that could lead to greater control efficacy, e.g., a reduction in overall nitrogen and change in the form discharged from Sacramento Regional Wastewater Treatment Plant (see Figure 1 for location) could reduce the vigor of aquatic vegetation growth, although the connection between nutrient supply/form and expansion of SAV and FAV in the Delta is not well understood (Boyer and Sutula 2015). Notably, the present-day control program for SAV and FAV in the Delta does not have set targets for reduction in coverage.

Considering the above, we evaluate an alternative future scenario in which FAV can be reduced

in coverage by 20% through control measures, but with no reduction in SAV, in our additional production calculations in the section "Evaluating Alternative Scenarios: Results and Discussion." Since current efforts have no appreciable effect beyond the season the control is applied, a 20% reduction would represent a future improvement in control efficacy.

### *Tidal Wetland Restoration*

Proposed updates to the Delta Plan call for the restoration of an additional 32,500 acres (13,200 ha) of tidal wetland in Suisun Marsh and the Delta (DSC 2019). In some locations, shallow waters that support aquatic vegetation may be filled with dredged sediments to create these wetlands, such as the 550 hectares of wetland restoration proposed in the preferred concept for the Franks Tract re-design (CDFW 2020). However, in most cases, such as in the 485-ha Dutch Slough project completed in 2018, tidal wetlands are restored by breaching levees to reconnect land to tidal flows. In these latter cases, channels and sloughs embedded within tidal emergent vegetation would be expected to provide additional suitable habitat for aquatic vegetation (Figure 2).

In this scenario, we explore how meeting the proposed Delta Plan target (the restoration of an additional 13,152 hectares of tidal wetlands in the upper estuary) will increase the amount of open water in the Delta and affect Delta-wide production. To estimate the total amount of new open water in the Delta associated with this scenario (Figure A1C), we multiplied the proportion of total restoration expected to occur within the Delta (the acreage target also covers Suisun Marsh, which is outside of our study extent) by the total proportion of the restored tidal wetland area expected to consist of open water. We assumed the total area of restored tidal wetland restoration would be distributed between the Delta and Suisun in proportion to the total amount of land in each region located at intertidal elevation (0.77 of which occurs in the Delta; SFEI–ASC 2021; Figure A2), but accounted for uncertainty in this value by randomly drawing values from a truncated normal distribution (minimum = 0; maximum = 1; mean = 0.77;

standard deviation = 0.15). We multiplied the sampled proportions by the total proposed restoration area to generate estimates of the new area of restored tidal wetlands in the Delta (Figure A1A). We estimated the proportion of restored tidal wetlands consisting of open water from detailed design plans for seven tidal wetland projects either recently constructed or under planning/permitting in Suisun Bay and the Delta. For each project, we used GIS to calculate the expected areas of open water and emergent wetland, which allowed us to calculate the proportion of the total area of each project that is expected to comprise open water (Table A4). We accounted for uncertainty in this aquatic fraction by repeatedly resampling the individual proportions with replacement and calculating the resulting sample mean, yielding a bootstrapped distribution of possible values (Figure A1B).

Because species coverage and composition varies with water depth in our models, we also needed to determine the depth of the additional open-water area. We assumed most of the new open water associated with tidal wetland restorations would be relatively shallow, but accounted for uncertainty in the future depth-distribution by randomly drawing values for the proportion of water in the 0- to 1-m-depth bin from a truncated normal distribution (minimum = 0; maximum = 1; mean = 0.5; standard deviation = 0.4). The proportion of the new area in the next depth bin (i.e., 1 to 2 m) was then assigned a random proportion of the remaining area drawn from a uniform distribution. This was repeated for each successively deeper bin until all of the new area was accounted for. On average, this process resulted in a skewed distribution, with most of the area captured by the shallowest-depth bins.

### More Variable Salinity in the Western Delta

Climate change-induced sea level rise will push saltier water into the Delta, especially during droughts, without management intervention such as drought barriers. Current water-conveyance infrastructure reduces intra-annual variability in salinity so that the Delta is maintained as fresh or very low in salinity; however, with climate change it will be difficult to maintain this condition.

Alternative Delta conveyance infrastructure (e.g., tunnels) planned to deliver fresh water to southern California destinations may relieve the need to maintain the Delta as a fresh body of water for potable use, which would be expected to result in increased seasonal salinity variability in the western Delta. This could lead to a reduction in coverage of the invasive *E. densa*, which is quite sensitive to salt, and an increase in the native *S. pectinata*, which can tolerate salinities in the range of 10 to 15 ppt (Borgnis and Boyer 2016). Hence, we consider a scenario of future production that estimates the effect of this change in species extent and cover in the western Delta.

We used the maximum measured inland extent of salinity intrusion to date (the position of the 1 ppt chloride isohaline ["X1"] in 1931; CDWR 1995) to demarcate the area where *E. densa* could potentially be reduced and replaced in the future (Figure A2). This area is quite large, extending to Stockton along the San Joaquin and beyond Courtland along the Sacramento, and thus encompasses the majority of the Delta's waterways by area. For each modern reference year, we then determined the total amount of *E. densa* within the potential salinity intrusion zone by multiplying the amount of SAV mapped within the zone by the relative cover of *E. densa* within the SAV community (Table 1). Because we are uncertain what proportion of the *E. densa* might ultimately be lost from within the mapped potential salinity intrusion zone, we tested a range of values, allowing anywhere from 5% to 100% of the current mapped area (within the area subject to salinity intrusion) to be eliminated. This range of values accounts for both uncertainty and interannual variability in the extent of future salinity intrusion and the area within this zone where *E. densa* is actually reduced. Because the mapped potential salinity intrusion zone encompasses > 95% of *E. densa* in the modern system, our scenario effectively explores the loss of anywhere from just less than 5% to nearly 100% of the species' coverage in the Delta. We also allowed the proportion of lost *E. densa* that is then recolonized by *S. pectinata* to vary from 5% to 100% (see "Modeling Framework" section), reflecting uncertainty in what ultimately

limits *S. pectinata* distribution in the Delta. By propagating our uncertainty in this way, our scenario captures nearly the full range of possible changes in production via this mechanism (decreases in *E. densa* and increases in *S. pectinata* that result from different amounts of salinity intrusion and plant responses).

### Potential Future Scenarios Not Evaluated

With successful control of FAV by 20%, there is the potential that reduced FAV coverage will lead to replacement by SAV (Khanna et al. 2012). However, we have not included this possible shift in our estimates, in part because SAV would replace relatively little of the NPP lost from FAV, because SAV species have lower production rates (see Figure 5).

We also considered that climate change could prove beneficial to the FAV species *E. crassipes* and *Ludwigia* spp. because these invaders have tropical origins which makes them vulnerable to cold and especially frost (Penfound and Earle 1948; Sainty et al. 1997; Wilson et al. 2005; Armitage et al. 2013; Thouvenot et al. 2013), but such conditions are becoming less frequent with new jet-stream patterns and the weakening Arctic polar vortex (Dettinger et al. 2016; Knowles et al. 2018; Swain et al. 2018). Because we are uncertain about the rate and magnitude of increase in coverage that might result from more frequent or perpetual frost-free winters, we have not attempted to estimate a change in production through this mechanism.

Although we evaluated the potential effects of a future increase in open water associated with tidal wetland restoration, we did not analyze the effects of increases that would result from levee failures and permanent flooding of lands below sea level. This scenario is worthy of additional study because the land below sea level is quite extensive (approximately 1,400 km$^2$) and flood risks are expected to increase into the future with additional land subsidence and sea level rise (Durand 2017).

We also did not attempt to evaluate how aquatic vegetation that invades open water in restored

tidal wetlands may eventually lead to sediment trapping and the evolution of channel area into tidal marsh. The depth of the water, the aquatic vegetation species present, sediment supply, and other factors at a specific location all make the trajectory of such transformations difficult to predict.

Through time, and as climate change progresses, we can expect new invaders that will perhaps drive changes in NPP. For example, *Vallisneria australis* (ribbon weed) and *Alternanthera philoxeroides (*alligator weed) have been spreading in the Delta since at least 2015 and 2017, respectively (Christman et al., this issue). We have not attempted to include these species or others that may become more widespread in the near future in our production estimates and associated analyses.

## EVALUATING ALTERNATIVE SCENARIOS: METHODS

### Modeling Framework

We estimated annual primary production by multiplying species-specific areal production rates by the estimated area covered by each species. The area each species covered was allowed to vary between eras (historical, modern, and future) based on changes in the Delta's hydrography (Table A5). The area covered by each species was also allowed to vary within eras based on (1) interannual variability in species composition and cover and (2) the effects of specific scenarios (e.g., whether or not FAV control is implemented). We accounted for uncertainty in our production rates and other parameters using Monte Carlo simulations. We ran 950,000 simulations, with each simulation drawing a random value for each modeled parameter from a set or range of plausible values (Table 2). We implemented the scenarios described above by treating them as model parameters with random binary values (e.g., whether or not FAV is controlled is represented as a value of 1 or 0). This allowed us to assess the combined effects of non-mutually-exclusive scenarios. We generated our final estimates of production under each scenario by taking the median value from the set of relevant simulations.

**Table 2**  Parameters used to estimate primary production and the method used to assign parameter values in each simulation (n = 950,000)

| Simulation parameters | Method for assigning parameter value in each simulation |
|---|---|
| *Historical* | |
| Species-specific NPP rates | Bootstrap sample mean (Figure 5B) from literature values (Table A1) |
| *C. demersum* presence | Random binary variable (1 = present; 0 = absent) |
| *L. peploides* presence | Random binary variable (1 = present; 0 = absent) |
| Open water area by depth-bin | Constant values (Table A5). Data from Cloern et al. (2021). |
| Reference year (for species relative cover calculations) | Randomly selected from set of years with available remotely sensed data: 2004, 2005, 2007, 2015, 2019, 2020 |
| Percent cover of each FAV species within each depth bin | Derived from modern remotely sensed data (Khanna et al. 2022) based on randomly selected reference year and *L. peploides* presence/absence |
| Percent cover of SAV within each depth bin | Derived from modern remotely sensed data (Khanna et al. 2022) based on randomly selected reference year and *C. demersum* presence/absence |
| Relative cover of individual SAV species | Derived from modern field data (Table 1) based on randomly selected reference year and *C. demersum* presence/absence |
| *Modern* | |
| Species-specific NPP rates | Bootstrap sample mean (Figure 5B) from literature values (Table A1) |
| Open water area by depth-bin | Constant values (Table A5) |
| Reference year (for species relative cover calculations) | Randomly selected from set of years with available vegetation data: 2004, 2005, 2007, 2015, 2019, 2020 |
| Percent cover of each FAV species within each depth bin | Derived from modern remotely sensed data (Khanna et al. 2022) based on randomly selected reference year |
| Percent cover of SAV within each depth bin | Derived from modern remotely sensed data (Khanna et al. 2022) based on randomly selected reference year |
| Relative cover of individual SAV species | Constant values (Table 1) |
| *Future* | |
| Species-specific NPP rates | Bootstrap sample mean (Figure 5B) from literature values (Table A1) |
| FAV control: status | Random binary variable (1 = FAV control efforts implemented; 0 = FAV control efforts not implemented) |
| FAV control: proportion FAV eliminated | Constant value: 0.2 |
| Restoration: status | Random binary variable (1 = restoration occurs; 0 = restoration does not occur) |
| Restoration: total tidal wetland restoration in the upper estuary (Delta and Suisun) | Constant value: 13,152 ha (proposed Delta Plan target; DSC 2019) |
| Restoration: proportion of restoration target allocated to the Delta (vs. Susiun) | Random value drawn from a truncated normal distribution (minimum = 0; maximum = 1; mean = 0.77; standard deviation = 0.15). Distribution centered on the proportion of total land suitable for tidal wetland restoration located in the Delta |
| Restoration: proportion tidal wetland restoration that is open water | Bootstrap sample mean from individual project proportions (Table A4; Figure A1B) |
| Restoration: additional open water area depth distribution | Proportion of additional open water in 0- to 1-m-depth bin is a random value drawn from a truncated normal distribution (minimum = 0; maximum = 1; mean = 0.5; standard deviation = 0.4). The proportion in each successive deeper bin is a random proportion of the remaining area drawn from a uniform distribution. |
| Salinity shift: status | Random binary variable (1 = salinity shift occurs; 0 = salinity shift does not occur) |
| Salinity shift: proportion of *E. densa* in Western Delta eliminated | Random value between 0.05 and 1 (uniform distribution) |
| Salinity shift: proportion of eliminated *E. densa* replaced by *S. pectinata* | Random value between 0.05 and 1 (uniform distribution) |
| Open water area by depth-bin | Constant values (Table A5; modern), modified based on the restoration scenario variables |
| Reference year (for species relative cover calculations) | Randomly selected from set of years with available vegetation data: 2004, 2005, 2007, 2015, 2019, 2020 |
| Percent cover of each FAV species within each depth bin | Derived from modern remotely sensed data (Khanna et al. 2022) based on randomly selected reference year and FAV control variables |
| Percent cover of SAV within each depth bin | Derived from modern remotely sensed data (Khanna et al. 2022) based on randomly selected reference year |
| Relative cover of individual SAV species | Fixed initial values (Table 1) modified based on salinity shift variables |

**A** Literature values for annual productivity rates

**B** Bootstrap distributions for estimated mean NPP generated from literature values

**Figure 5** (**A**) Literature values for annual productivity rates of floating (FAV) and submerged (SAV) aquatic vegetation species. Dots show the literature-derived annual production rates for each species (See Tables A1 and A2). The *boxes* in the *box-and-whisker plots* show the mean value, first, and third quartiles (the 25th and 75th percentiles) of these values. The *whiskers* extend to the largest/smallest value no further than 1.5 times the interquartile range. (**B**) Bootstrap distributions for mean annual NPP derived from measured samples compiled in our literature review. Distributions shown are of 5,000 bootstrap sample means for each species. As in **Panel A**, the measured production values from the literature are plotted with *black dots*. Note the different *x*-axis scales used for SAV and FAV species. *Colors* in both charts correspond to species, which are ordered by increasing mean measured production rate within species groups (SAV, then FAV).

each simulation, the bootstrapped transfer rates for each pathway were multiplied by the NPP estimates for each scenario to yield estimates of the annual trophic transfer of primary production to detritus and herbivory. Like the NPP estimates, our final estimates of trophic transfer under each scenario were generated by taking the median value from the set of relevant simulations, with uncertainty around these estimates derived from the 2.5 and 97.5 percentile values.

**Data and Code Availability**

Data and code needed to reproduce the results of these analyses have been archived at *https://doi.org/10.5281/zenodo.6452986* (Safran et al. 2022).

## EVALUATING ALTERNATIVE SCENARIOS: RESULTS AND DISCUSSION

### Historical Estimates

Across all scenarios, we estimate historical NPP from aquatic vegetation in the Delta to have been 13.5 kt C y$^{-1}$ (95% of estimates: 7.2 to 32.5; Table A7). The majority of uncertainty in this estimate is attributable to the reference year used to determine the total proportion of available open water covered by aquatic vegetation (Figure 6). The sensitivity analysis indicated that across all simulations and scenarios the reference year explained 41% of the total variance in estimated historical productivity (Table A8). Estimates of historical NPP were much more sensitive to the area covered by each species than to the productivity rates of each species (95% of the total variance was explained by the species area variables, vs. 3% by the species productivity variables; Table A9). Note that the area covered by each species in each of the 950,000 historical estimates was determined by both the reference year and the status of the species for which presence and absence was allowed to vary (see scenarios for *L. peploides* and *C. demersum* below). When we limit our analysis to estimates under the conditions we consider to have been most likely circa 1850, with *L. peploides* absent and *C. demersum* present (the conditions assumed by Cloern et al. [2021]), our estimates of historical production (10.8 kt C y$^{-1}$ [95% CI: 6.3 to 16.8]) are slightly lower and have less uncertainty than the estimate across all historical scenarios.

Removing *C. demersum* from the historical SAV species assemblage did not dramatically alter our estimates of historical NPP; the median estimate without the species was 1% higher than the median of estimates that did include the species (Table A7; Figure 6 and 7). Across all historical estimates, the presence or absence of *C. demersum* explained <1% of the variance in estimated historical NPP (Table A8). This is largely attributable to our methods for calculating the relative cover of each native SAV species in the historical system, and the estimated productivity of the historical native species. When *C. demersum* is removed, our methods allow the other native species to increase their relative cover

to compensate (the total extent of SAV remains unchanged). Because the native SAV species in our analysis generally have similar production rates—*C. demersum*: 289 g C m$^{-2}$ yr$^{-1}$ (95% CI: 20 to 515); *E. canadensis*: 198 g C m$^{-2}$ yr$^{-1}$ (95% CI: 89 to 322); *N. guadalupensis*: 29 g C m$^{-2}$ yr$^{-1}$ (95% CI: 17 to 35) *P. richardsonii*: 130 g C m$^{-2}$ yr$^{-1}$ (95% CI: 84 to 177); *S. pectinata*: 469 g C m$^{-2}$ yr$^{-1}$ (95% CI: 283 to 673)—removal of one and replacement by the others does not meaningfully alter total NPP.

The inclusion of *L. peploides* in the historical species assemblage approximately doubled the median estimated historical annual NPP relative to all estimates that did not include the species. The sensitivity analysis indicated that across all historical estimates the presence or absence of *L. peploides* explained approximately 41% of the variance in estimated historical NPP (Table A8). Increases in NPP from the presence of *L. peploides* were most pronounced in estimates where the historical species coverage was derived from the most recent data (2015, 2019, and 2020) vs. earlier modern data (2004, 2005, and 2007; Figures 6 and 7). This is attributable to the pronounced expansion of *L. peploides* in 2015 and later years. In reference years when *L. peploides* only represented a small portion of the total area, we assumed it would have also only occupied a small portion of the area historically, so potential gains in NPP from its presence and high production rate were more limited. The overlap in the tails of our estimates of historical NPP with and without *L. peploides* is largely driven by uncertainty in the extent of open water that would have been covered by the species (driven by the choice of reference year). Overall, these results raise the interesting possibility that early species introductions dramatically increased total production from aquatic vegetation.

### Modern Estimates

Interannual variability in the extent and relative composition of aquatic vegetation species has driven significant variability in total NPP within the modern era (over the last 2 decades). Median estimates of production based on data from 2015, 2019, and 2020 are approximately double (1.7 to 2.5 times) the estimates from 2004, 2005, and 2007,
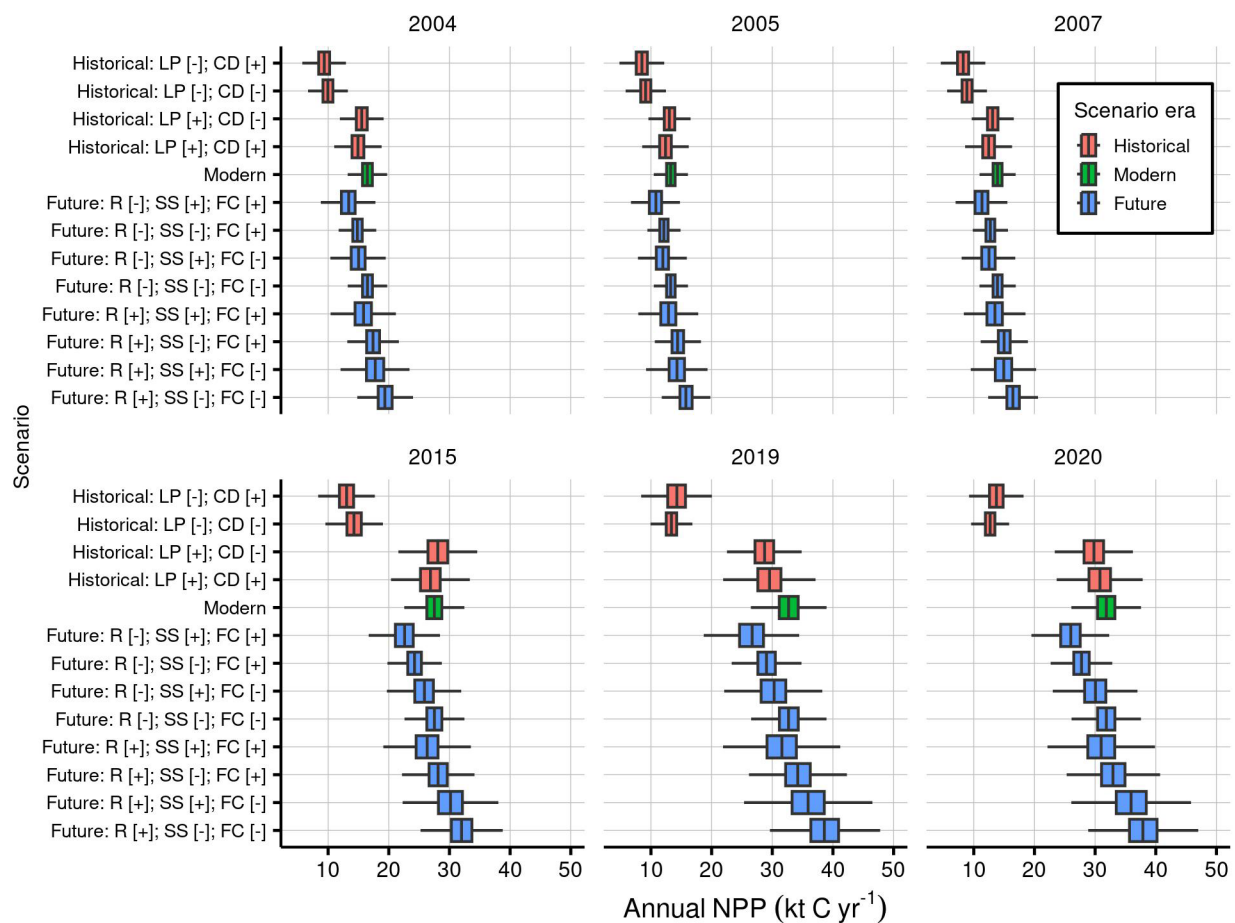
**Figure 6** Comparison of Delta-wide production associated with all scenarios, broken out by reference year used to determine relative cover of each species. In scenario names, "LP" denotes *Ludwigia peploides*, "CD" denotes *Ceratophyllum demersum*, "R" denotes restoration, "SS" denotes salinity shift, and "FC" denotes FAV control. The [+] symbol indicates the inclusion of the specified variable; the [–] symbol indicates the exclusion of the variable. For example, "CD [+]" means *C. demersum* is *present* in the scenario; "CD [-]" means it is *absent*. Similarly, "R [+]" indicates the effect of restoration is *included* in the scenario; "R [–]" indicates that the effect of restoration is *not included*. The *boxes* in the *box-and-whisker plots* show the mean, first, and third quartiles (the 25th and 75th percentiles) values of annual NPP for each scenario. The *whiskers* extend to the largest/smallest value no further than 1.5 times the interquartile range. Outlier values more than 1.5 times beyond the interquartile range are not shown in *box plots*.

with no overlap of the middle 95% of estimates from these two sets of years (Table A7; Figures 6 and 7). In total, median estimated production has varied at least 146% over the modern era (2005 v. 2019). NPP can also vary considerably between consecutive years: from 2004 to 2005, the median estimated production decreased by 19%, and from 2019 to 2020 it decreased by 3%.

Within individual years, our estimates of total modern NPP were most sensitive to the production rates of just a few species (Table A10).

*E. densa* productivity rates explained the majority (55% on average) of within-year variance in total estimated NPP. The FAV species *L. peploides* explained an average of 25% of the total variance within years; *C. demersum* and *E. crassipes* each explained ~10%. The individual productivity rates of all other species explained 1% or less of the total variance in the estimates. Future work to refine estimates in the Delta aquatic plant NPP by measuring plant productivity rates should focus on these named species (those to which total NPP is most sensitive).

**Figure 7**   Effects of alternative scenarios on estimates of Delta aquatic vegetation production. . Each set of density plots compares the distribution of annual production estimates from all simulations meeting different criteria (e.g., historical simulations in which *C. demersum* was present vs. simulations in which it was absent, which is the comparison made in the top row of figure). The bimodal distribution of many estimates relates to differences between individual simulations in the modern reference year used to determine the cover of each species, particularly the large increase in FAV-coverage in more recent years.

## Future Estimates

Differences in future estimates from differences in the reference year (which dictates the total coverage of each species) are larger than differences from modeled scenarios of FAV control, tidal wetland restoration, and salinity intrusion (Table A7; Figures 6 and 7).

Reducing the extent of FAV by 20% through simulated control measures led to a 12% reduction in estimated NPP (Table A7; Figures 6 and 7). Note that total production is reduced by less than 20% because SAV extent remains unaltered in this scenario (only FAV is reduced). If both SAV and FAV were reduced by equal percentages, our modeling framework would result in an equivalent percent reduction in total NPP. Although the level of FAV control evaluated here (20%) has the potential to reduce NPP, the magnitude of this change is less than recently observed interannual variability in NPP. In other words, control efforts would need to be more extensive than modeled in this version of the scenario to have a greater impact on NPP than normal year-to-year differences.

Our models suggest that tidal wetland restoration meeting Delta Plan habitat restoration targets will appreciably increase aquatic plant NPP (Table A7; Figures 6 and 7). Across all scenarios of future conditions, the inclusion of tidal wetland restoration increases median estimated NPP by 19%, from 18.7 kt C yr$^{-1}$ (95% of estimates: 9.7 to 34.0) to 22.3 kt C yr$^{-1}$ (95% of estimates: 11.6 to 41.2). While this difference is small compared to the full range in production estimates attributable to interannual differences in the extent and composition of species (i.e., the 146% increase in estimated NPP between 2005 and 2019), its magnitude is equal to or greater than interannual differences in NPP between more-recent pairs of years (i.e., the 19% increase between 2015 and 2019 and the 3% decrease from 2019 to 2020).

We estimated the total amount of new open water associated with the ~13,200 ha (32,500 acres) of tidal wetland restoration proposed under the Delta Plan. Across all simulations with restoration, the median amount of restored tidal wetland located in the Delta (vs. Suisun) was 9,988 ha (95% of estimates: 6,210 to 12,826), of which 20% (95% CI: 13 to 26) was assumed to be open water. This yielded a median modeled increase in Delta open water of 1,976 ha (95% of estimates: 1,068 to 2,960). Note that this area is much smaller than the extent of diked land currently below sea level, so levee failure and

polder flooding have a much greater potential to increase the total extent of aquatic vegetation in the Delta than the restoration of tidal wetlands. The sensitivity analysis indicated that across all future estimates the effect of restoration explained only 5% of the variance in estimated NPP (Table A8). Interannual variability in the extent and species composition of aquatic vegetation (captured by the reference year variable) explained a much larger percentage (84%) of the variance in future estimates.

Loss of *E. densa* and subsequent replacement by *S. pectinata* (one possible effect of more frequent/extensive salinity intrusion in the western Delta) did not dramatically affect our estimates of NPP (Table A7; Figures 6 and 7). Across all scenarios of future conditions, the median of estimates with a salinity-shift-induced change in the extent of these species was 9% lower than the median of estimates without salinity-shift-induced changes. Across all future estimates, the effect of a salinity shift on *E. densa* and *S. pectinata* explained only 1% of the variance in estimated NPP (Table A8).

One reason for the relatively small effect of a salinity shift on total NPP is that *E. densa* and *S. pectinata* have similar mean production rates (*E. densa*: 464 g C m$^{-2}$ y$^{-1}$ (95% CI: 336 to 620); *S. pectinata*: 469 g C m$^{-2}$ y$^{-1}$ (95% CI: 283 to 673), so replacement of one by the other has only a modest effect on total NPP. Although *E. densa* has a slightly lower mean NPP rate (meaning replacement by *S. pectinata* would be expected to increase production), our model allows for incomplete recolonization of areas by *S. pectinata* where *E. densa* has been eliminated (each simulation allows for somewhere between 5% and 100% of the area to be recolonized). This partial replacement drives the decrease in estimated total median NPP under our salinity-shift scenario. Note that estimates of NPP were more sensitive to the magnitude of eventual *S. pectinata* replacement than to initial *E. densa* loss. When reference year was held constant and scenarios were limited to those with a shift in salinity (no FAV control or restoration), *S. pectinata* recolonization explained an average of 27% of

the variance in estimates, vs. 21% explained by *E. densa* loss.

## Trophic Transfer Potential: All Scenarios

Table A7 summarizes how our estimates of potential NPP from aquatic vegetation translate to carbon flows to detritus production and herbivory. Roughly 79% (95% CI: 70 to 85) of NPP is expected to flow to detritus production and 22% (95% CI: 13 to 36) to herbivory, based on bootstrapping rates from the freshwater macrophyte values in the meta-analysis of Cebrian and Lartigue (2004) 5,000 times. Our estimates of carbon flows mirror the variation in NPP described in previous sections, because they are multiplicative of the NPP values. We estimate that 10.6 kt C yr$^{-1}$ (95% CI: 5.6 to 26.0) went to detritus production in the historical Delta across all scenarios. Detritus production may have nearly doubled after introduction of *Ludwigia peploides* (Table A7); however, this still would have represented a small fraction of the detrital production historically, when marsh plants (emergent freshwater macrophytes) were contributing 1,000 kt C yr$^{-1}$ and all producer groups together were estimated to contribute 1,100 kt C yr$^{-1}$ in detrital production (Cloern et al. 2021). Similarly, we estimate that historical flows of aquatic vegetation carbon to herbivory amounted to 3.0 kt C yr$^{-1}$ (95% CI: 1.3 to 9.0), a small fraction of the 88 or 170 kt C yr$^{-1}$ contributed by marsh plants or all producer groups together, respectively (Cloern et al. 2021).

Detritus production in the modern period (over the last 20 years) ranged from approximately 10 to 26 kt C yr$^{-1}$, depending on the year, with an average of 16.7 kt C yr$^{-1}$ (95% CI: 9.3 to 28.6) across the 6 years sampled (Table A7). The interannual variation in our estimates would have been inconsequential relative to total production in the historical era, but it is important to recognize this variation in the modern era when marsh plants are estimated to contribute only 21 kt C yr$^{-1}$, and all producer groups together are estimated to contribute only 62 kt C yr$^{-1}$ to detrital production (Cloern et al. 2021). Similarly, the range of carbon that we estimate flows to herbivores across years in the modern era—2.9 kt C yr$^{-1}$ (95% CI: 1.7 to

4.8) in 2005 to 7.2 kt C yr$^{-1}$ (95% CI: 4.2 to 11.9) in 2019—is substantial, considering total flows to herbivores were estimated to be 18 kt C yr$^{-1}$, with only 2 kt C yr$^{-1}$ coming from marsh plants (Cloern et al. 2021).

Across all the potential future scenarios we modeled, estimated median detritus production from SAV and FAV (16.3 kt C yr$^{-1}$; 95% CI: 8.0 to 31.3) is comparable to that of the modern period. Slightly lower detritus production was estimated with 20% FAV control and salinity intrusion into the Delta, and slightly higher with wetland restoration projects leading to more open water. The highest detritus-yielding scenario is wetland restoration combined with no salinity intrusion and no FAV control, at 20.2 kt C yr$^{-1}$ (95% CI: 10.8 to 34.8) (Table A7). As with our NPP estimates from which we derived these carbon values, the scenarios we modeled for future conditions made relatively little difference in carbon available to the food web from detritus production, compared to the interannual differences for the modern period. The same was true for carbon flowing to food webs via herbivory (Table A7).

## KEY FINDINGS AND CONCLUSIONS

A 75% increase in open water area that occurred with the Delta's reconfiguration over the last century or so created opportunity for SAV and FAV to expand in coverage. We estimate that the NPP of SAV and FAV during the historical period before the large increases in open water was approximately half that of today. In general, SAV productivity rates are an order of magnitude lower than those of FAV, and assuming the SAV *C. demersum* was present or absent historically made little difference overall. However, assuming that *L. peploides* was abundant by the early 20th century approximately doubles our estimates of historical NPP because of the roughly three times higher productivity rates compared to the only other FAV species presumed present at that time, *H. umbellata*. Hence, this early introduction of *L. peploides* may have dramatically increased total production from aquatic vegetation early on, just as it exerts strong control over production

patterns (though now mixed with *L. grandiflora* and *L. hexapetala*) in the modern Delta.

In recent years, high interannual variability in the extent and relative composition of aquatic vegetation species has driven significant variation in total NPP, which is perhaps our most striking finding. Expansion of SAV from 14% to 16% of Delta waterways in 2004 to 2005 to 25% to 27% in 2018 to 2019 (Ustin et al. 2021) drove a large increase in NPP Delta-wide. A steady increase in SAV cover at Liberty Island is largely responsible for this change; reasons for this expansion are not fully understood but may relate to the extended drought of 2012 to 2016 creating an opportunity for SAV to establish, followed by positive feedback of wave dampening and finer sediment accumulation by the plants, which favored further spread. A reduction in strong tidal pumping and water flow at Franks Tract after the installation of the temporary salinity barrier at False River in 2015 probably favored SAV colonization throughout the previously sparsely covered central rib. Large, lake-like areas in the modern Delta are a defining feature of its hydrography in contrast to the historical Delta; clearly, the presence or absence of SAV in these large open-water areas strongly influences Delta-wide patterns in NPP from aquatic vegetation. In addition, and importantly, generally comparable production rates among the submersed species lead to similar NPP, regardless of their native vs. introduced status; by our estimates, the largely native SAV assemblage currently in Franks Tract produces approximately the same NPP as does an assemblage dominated by the introduced *E. densa* elsewhere in the Delta. This by no means suggests that other ecological functions of these native vs. non-native SAV species are equivalent, including habitat provision for introduced vs. native fish (e.g., Ferrari et al. 2014; Conrad et al. 2016) and feedbacks to water clarity (e.g., Hestir et al. 2013, 2016) that may influence predator-prey and other species interactions.

The high variation in FAV coverage during the modern period, and especially the step increase in very recent years, is in part a result of winter temperatures remaining above freezing, which allows the invasive FAV *E. crassipes* and *Ludwigia* spp. to persist through the winters and continue to expand the following spring and summer seasons (Penfound and Earle 1948; Sainty et al. 1997; Wilson et al. 2005; Armitage et al. 2013; Thouvenot et al. 2013). In addition, multiple years of drought and a paucity of large winter storms help to keep the fully floating *E. crassipes* from becoming dislodged and transported out of the region. With climate change increasing extremes in weather patterns (e.g., Swain et al. 2018), "levers" to control abundances of these species are largely out of reach for managers. This may change to some degree as control measures continue to be an active area of research and management pursuit (see Conrad et al., this issue). Further, the recent large reduction in nutrient inputs from the Sacramento Regional Sanitation District's Wastewater Treatment Plant may shed light on the poorly understood relationship between nutrients and the spread of aquatic vegetation (Boyer and Sutula 2015), though causation will remain speculative.

The high temporal variation in aquatic vegetation NPP in recent decades dwarfs the small changes attributable to the projected future drivers of change we evaluated, including the possibility that FAV can be controlled by 20%, that SAV and FAV will colonize channel areas of planned wetland restorations, and that salinity variability will increase with climate-warming-induced sea level rise and influence the composition of aquatic vegetation in the western Delta. Large swings in NPP of SAV and FAV from year to year in the modern era cascade to determine the flow of carbon to food web support provided primarily through detrital pathways.

Along with the 77% loss of emergent wetlands with human transformation of the Delta since the mid-1800s, the 94% loss of NPP and similarly dramatic loss of carbon flowing to detritus production and herbivory (Cloern et al. 2021) has elevated the importance of SAV and FAV production to the Delta's food web. However, the large interannual variation in this contribution that we document indicates inconsistency in this source of carbon to Delta consumers from year to

year. This volatility and interannual inconsistency make achieving wetland restoration goals for the Delta, which could recover a portion of the NPP lost since historical times (Cloern et al. 2021), even more imperative.

## RECOMMENDATIONS

**Measure productivity rates of individual FAV and SAV alone vs. in mixed assemblages, under current and predicted future conditions.** Although our literature search compiled 138 productivity rates for twelve species across 35 studies, we had difficulty finding rates for some of the species found in the Delta; many studies report productivity rates of mixed field assemblages and thus could not be used in our workflow seeking individual species' rates. In fact, mixtures of aquatic species are common, especially for SAV, and interactions with neighbors surely shape the productivity rates of a species within a particular vegetation assemblage. For example, *Ceratophyllum demersum*, which does not root in the sediment, is often associated with *Egeria densa* in Delta surveys (Santos et al. 2011); this association may result in improved access to light in the upper water column, which could lead to higher productivity rates than what could be achieved by *C. demersum* growing alone without physical structure. Species interactions are also mediated by the abiotic conditions in a particular location; for example, *E. densa* is a superior competitor to *Stuckenia pectinata* in freshwater, but loses this advantage at higher salinities; thus, both biotic and abiotic conditions influence the rates of each species' production (Borgnis and Boyer 2016). We recommend field and lab measures of productivity rates of local species alone and in mixtures over a range of conditions in the current and predicted future Delta. This would permit refinement of model predictions of production and food web support within a particular region where surveys indicate a specific aquatic species composition.

**Incorporate additional climate-related changes into predictions of NPP.** We considered salinity intrusion into the Delta with sea level rise as a potential scenario, but other effects of climate change should be evaluated in future iterations of

modeling efforts like ours. For example, climate warming is likely to increase coverage of FAV species with tropical origins that are vulnerable to frost. Predicted changes in average conditions, and frequency and magnitude of extreme conditions should be incorporated into future endeavors to model NPP as the responses of aquatic vegetation to these changes become better understood.

**Consider other scenarios of increased open water besides tidal marsh restoration.** We did not model increases in open water that could result from permanent flooding of the ~1,400 km$^2$ of Delta lands that are below sea level. Modeling both incremental (e.g., a single levee breach that could result from a flood event, rodent burrowing, etc.) and catastrophic (e.g., multiple levee failures at once from an earthquake) changes in aquatic acreage would help to support our understanding of future production and trophic transfer potential.

**Anticipate effects of recent invaders on primary production.** Very recent introductions (last 5 to 7 years) of the rapidly spreading aquatic species *Vallisneria australis* and *Alternanthera philoxeroides* illustrate the continuing potential for invasion of the Delta. We suggest compiling production rates from the literature for recently introduced species (as we did for established Delta species in this study), to anticipate ecosystem-level effects to NPP under possible future scenarios in which these species increase in abundance.

**Conduct annual, Delta-wide monitoring of FAV and SAV.** We expect that NPP from aquatic vegetation will continue to be largely driven by variability in overall cover and relative abundance of highly productive species. Annual monitoring, including remote sensing and point sampling of species composition, is needed to track localized and Delta-wide changes in distribution and the relative abundance of aquatic plants, including new invaders.

**Refine understanding of food web contributions of SAV and FAV species.** Aquatic vegetation now produces the largest fraction of NPP across all producer groups in the Delta (Cloern et al. 2021), and a growing

body of literature recognizes the importance of this production in supporting both nearshore and pelagic fishes (see review by Brown et al. 2016). Recent stable isotope analyses showed that a substantial proportion of the diets (up to two-thirds) of all 28 species of Delta fishes studied could be traced to SAV (Young et al. 2021). Although there have been few studies of food web roles of aquatic vegetation species separately, a Suisun Marsh study traced native pondweed (*S. pectinata*) carbon in the diet of the amphipod *Gammarus daiberi* along a trophic path to higher-level consumers (Schroeter et al. 2015). Another noted little difference in abundance or composition of invertebrate prey items in invaded (*E. densa*-dominated) vs. native (*Elodea canadensis*- and *C. demersum*-dominated) SAV beds (Young et al. 2018), which could mean carbon transfer to fishes would also be similar. However, invertebrate abundance and species composition on a single SAV species can vary substantially among locations (e.g., on *S. pectinata;* Patten and Boyer 2023), which suggests that trophic transfer may vary with abiotic conditions across a species' range. We recommend additional comparisons of individual aquatic vegetation species' contributions to the food web. Such investigations would entail measuring carbon transfer for each SAV or FAV species (and from multiple locations across Delta abiotic gradients), as opposed to utilizing composited literature values as we did here (Table A6). Assessments of how large swings in interannual differences in aquatic vegetation NPP translate to the abundance and composition of consumers could also help us to understand the implications of the results presented here.

**Consider other functional differences between aquatic vegetation species.** The relatively small range in productivity rates among SAV species and thus their similar potential to supply carbon to fuel food webs is notable, considering the large range in standing biomass among species. Clearly, standing biomass is not a proxy for carbon produced over time, i.e., the net rate of biomass/carbon production can be similar among species despite variation in growth form as well as patterns of senescence vs. biomass retention. Though we have shown that SAV

species are largely interchangeable in their NPP contributions, morphological differences between plant species are relevant to their provision of habitat for consumers as well as differences in how species affect abiotic conditions that can feed back to habitat. SAV species in the Delta range from a pillar-type morphology, with comparable biomass throughout the water column (e.g., *Myriophyllum spicatum*, *E. densa*) to canopy-forming, with biomass concentrated at the surface (most pondweeds; Wychera et al. 1993). Such characteristics are expected to matter to fish, including several species of concern in the Delta; for example, the endangered Delta Smelt (*Hypomesus transpacificus*) may use turbid water as a visual refuge from predators (Johnson 2016; Hobbs et al. 2019), and may find the more open canopy-forming *S. pectinata* better habitat than a densely packed water column of *E. densa* that traps sediment and clears the water (Hestir et al. 2016; Drexler et al. 2020). FAV species also differ in habitat value, e.g., *H. umbellata* supports higher dissolved oxygen and invertebrate abundances than *E. crassipes* (Toft et al. 2003). That we found FAV species differ greatly in NPP further recommends against lumping species together into groups for management purposes. Finally, although not well-studied in the Delta, there are numerous species of aquatic herbivores (particularly insects) that have specialized relationships with a small number of aquatic plant species (Newman 1991). These species-specific interactions could also drive functional differences between individual SAV and FAV species that are otherwise similar in their NPP.

**Use tidal marsh restoration as a tool to even out extreme swings in Delta-wide NPP.** The high variation in aquatic vegetation NPP over recent decades (146% difference between the extremes of 2005 and 2019) makes reliance on this source of carbon for Delta food webs a risky proposition. Variation in production from this group of producers may now be more pronounced than historically, with the dominant, non-native species less resilient to fluctuations in conditions than better-adapted native species. But even if aquatic vegetation NPP in the historical Delta varied 3-fold decadally as today, that variation

would have been inconsequential relative to the 10- and 30-fold-greater carbon that flowed from tidal marshes to detrital and grazing food webs, respectively (Cloern et al. 2021). Recovering even a small percentage of lost tidal marshes through restoration actions could help balance the temporal volatility of NPP and food web contributions of aquatic vegetation in the Delta. In addition, our estimates that new channels included in the tidal marsh restorations will increase aquatic vegetation NPP enough (median of 19%) to offset the differences in production between recent pairs of years (i.e., the 19% decrease from 2004 to 2005) further support tidal marsh restoration (with channels) as a means of building resiliency into Delta food webs.

## ACKNOWLEDGEMENTS

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