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Ecology and Ecosystem Effects of Submerged and Floating Aquatic Vegetation in the Sacramento–San Joaquin Delta

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ABSTRACT

Substantial increases in non-native aquatic vegetation have occurred in the upper San Francisco Estuary over the last 2 decades, largely from the explosive growth of a few submerged and floating aquatic plant species. Some of these species act as ecosystem engineers by creating conditions that favor their further growth and expansion as well as by modifying habitat for other organisms. Over the last decade, numerous studies have investigated patterns of expansion and turn-over of aquatic vegetation species; effects of vegetation on ecosystem health, water quality, and habitat; and effects of particular species or communities on physical processes such as carbon and sediment dynamics. Taking a synthetic approach to evaluate what

has been learned over the last few years has shed light on just how significant aquatic plant species and communities are to ecosystems in the Sacramento–San Joaquin Delta. Aquatic vegetation affects every aspect of the physical and biotic environment, acting as ecosystem engineers on the landscape. Furthermore, their effects are constantly changing across space and time, leaving many unanswered questions about the full effects of aquatic vegetation on Delta ecosystems and what future effects may result, as species shift in distribution and new species are introduced. Remaining knowledge gaps underlie our understanding of aquatic macrophyte effects on Delta ecosystems, including their roles and relationships with respect to nutrients and nutrient cycling, evapotranspiration and water budgets, carbon and sediment, and emerging effects on fish species and their habitats. This paper explores our current understanding of submerged and floating aquatic vegetation (SAV and FAV) ecology with respect to major aquatic plant communities, observed patterns of change, interactions between aquatic vegetation and the physical environment, and how these factors affect ecosystem services and disservices within the upper San Francisco Estuary.

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KEY WORDS

carbon storage, ecosystem disservices, ecosystem engineer, evapotranspiration, floating aquatic vegetation, sediment dynamics, submerged aquatic vegetation, food webs, fish

INTRODUCTION

Aquatic vegetation affects ecosystem processes, physical environments, and food web interactions (Toft et al. 2003; Hestir et al. 2013, 2016; Cloern et al. 2021; Boyer et al. this issue). In the San Francisco Estuary (the estuary), floating aquatic vegetation (FAV) and submerged aquatic vegetation (SAV) communities have significantly expanded in recent decades as a few non-native species have substantially increased in abundance and distribution (Khanna et al. 2012; Santos et al. 2016; Ta et al. 2017; Khanna et al. 2018). In response to these changes, numerous recent studies have aimed to better characterize the biology and ecology of aquatic vegetation and its effect on the estuary (e.g., Khanna et al. 2012; Conrad et al. 2016; Durand et al. 2016; Hestir et al. 2016; Khanna et al. 2018; Young et al. 2018a, 2018b; Tobias et al. 2019; Moran et al. 2021).

The upstream extent of the estuary is a complex mosaic of tidal freshwater and brackish bays, marshes, and distributary river channels, incorporating the leveed canals and peripheral habitats of the legal Sacramento–San Joaquin Delta (the Delta) and adjacent up- and downstream habitats (Figure 1; see also Larsen et al. this issue). Within the Delta, the estuarine salinity gradient combines with other environmental factors and management actions (e.g., temperature, flow alteration, vegetation control treatment) to influence the survival and distribution of aquatic plant species. Today, non-native species dominate FAV and SAV communities in the Delta (Boyer and Sutula 2015) with certain species acting as “ecosystem engineers” (Jones et al. 1997), shaping the physical environment to favor their own growth and altering the habitat provided to other organisms at a range of trophic levels. For example, by altering flows and sediment dynamics, SAV can expand into low-velocity, less

turbid habitats in which SAV species then thrive (Drexler et al. 2021). Similarly, FAV can shade out or grow directly on top of other macrophytes, out-competing other species in the process (Khanna et al. 2018).

Invasions by non-native species are considered one of the greatest global threats to ecosystems (Pyšek et al. 2020), and the challenges non-native FAV and SAV present to aquatic systems are not unique to this estuary. Many, if not all, of the same species that currently dominate the Delta’s FAV and SAV communities have created similar management challenges and degraded ecosystem services in wetlands across the world (e.g., Yarrow et al. 2009; Bunch et al. 2010; Villamagna and Murphy 2010; Tanveer et al. 2018; Roberts and Singarayer 2022). As growth of non-native FAV and SAV species has substantially changed vegetation communities in the Delta, highly altered, “novel” ecosystems have emerged (*sensu* Hobbs et al. 2006). Although generally viewed as detrimental to the health of native communities, non-native species, once established, may significantly contribute to the structure and function of an ecosystem (Hershner and Havens 2008). A number of studies have explored aquatic vegetation effects on habitat quality in the estuary, particularly for at-risk fish species such as Delta Smelt (*Hypomesus transpacificus*) and Chinook Salmon (*Oncorhynchus tshawytscha*). However, the impacts of aquatic vegetation on ecosystem processes in the Delta, including evapotranspiration (ET), flow and sediment dynamics, and carbon and nutrient cycles, are just recently gaining direct attention. These effects are likely to affect not only how other species, including humans, use the region, but the distributions of aquatic vegetation itself.

Intensive study of FAV and SAV communities is critical for understanding their contributions to and effects on ecosystem functions. In a system so highly altered by anthropogenic changes to the physical landscape (Whipple et al. 2012; Robinson et al. 2014), this understanding becomes even more critical as it is essential for effective habitat management. Here, we review what has been learned over the last decade on SAV and FAV communities of the Delta (see “Aquatic

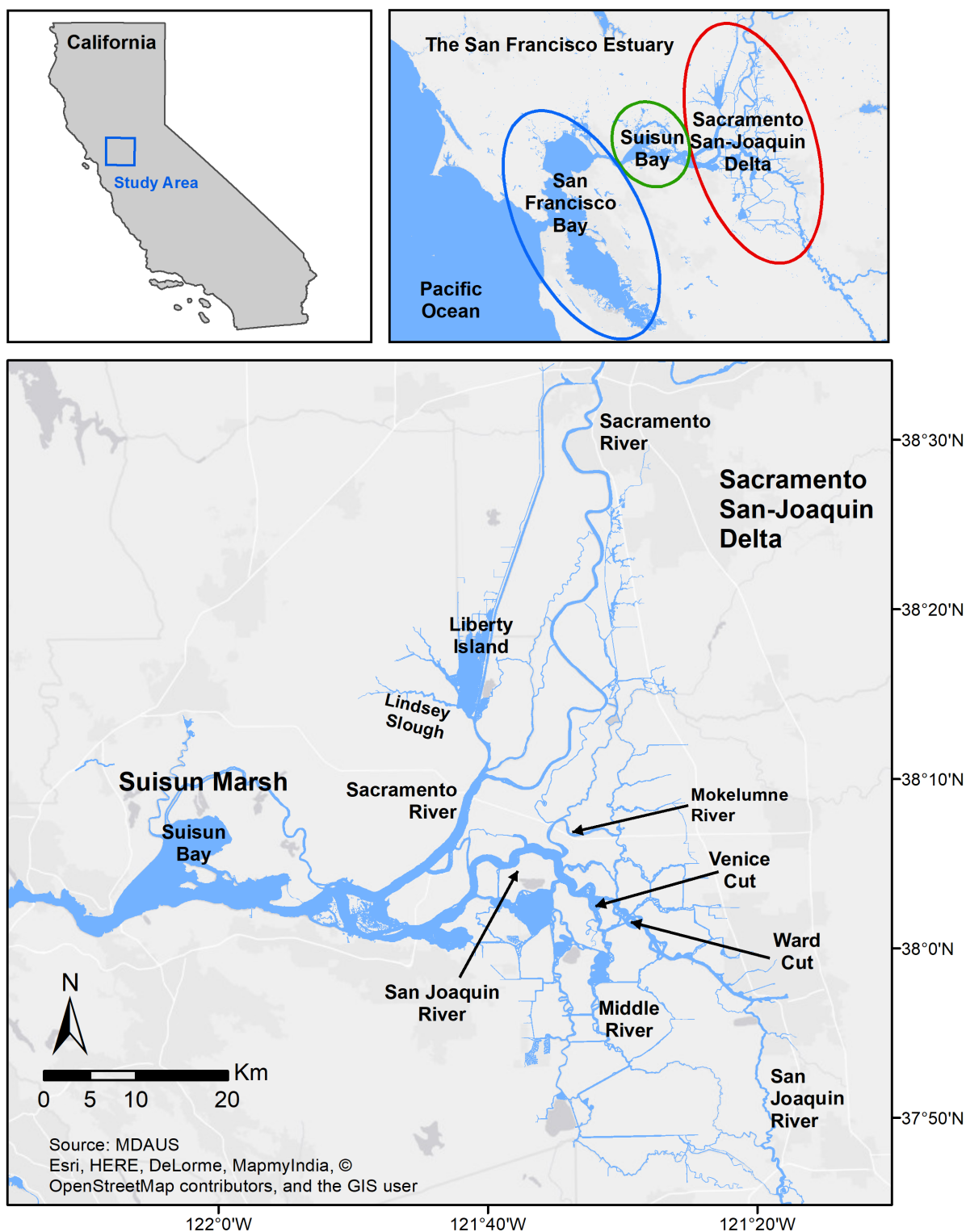


Figure 1 Maps of the upper San Francisco Estuary showing the location of the region within California (*top left*), the three major regions of the Estuary (San Francisco Bay, Suisun Bay, and the Sacramento–San Joaquin Delta, *top right*), and key locations within the Delta most relevant to this review (see *bottom image*), including study sites for Khanna et al. (2012, 2018), Drexler et al. (2021), Work et al. (2021), and Lacy et al. (2021).

Vegetation Communities of the Delta”), how these communities continue to change in response to human and natural disturbances (see “[Effects of Environmental Conditions on Plant Species](#)”), and what we know of their influences on Delta ecosystems and ecological functions (see “[Effects of Aquatic Vegetation on the Physical and Biogeochemical Environment of the Delta](#)” and “[Aquatic Vegetation and Biota](#)”). We conclude by identifying data gaps that could address critical scientific and management questions relevant to the function and ecosystem services of the Delta today and under future conditions.

AQUATIC VEGETATION COMMUNITIES OF THE DELTA

The diversity of habitats within the estuary are thought to have created an “invasion gateway” for introductions of non-native phytoplankton, plants, invertebrates, and fish species into the western US (Cohen and Carlton 1995, 1998; Light et al. 2005; Ruiz et al. 2011; Brandt et al. 2021). Saltwater, brackish, and freshwater tidal marshes; riparian corridors; and open-water habitat with varying water quality and hydrologic characteristics are all common within the region (Ruiz et al. 2011). Cohen and Carlton (1998) identified 25 non-indigenous plants in the estuary,

with 18 primarily found in freshwater habitats. A more recent and more focused assessment of the Delta region by Light et al. (2005) recorded 69 species of non-indigenous plants. [Table 1](#) summarizes the current understanding of native and non-native species that compose the FAV and SAV communities found in the Delta (Khanna et al. 2022b). Photographs of several major SAV species described in this manuscript can be found in [Figure 2](#).

A Brief History of Non-Native Species Introductions to the Estuary

For aquatic plants, the most common vectors for non-native species introductions are agricultural or aquaria releases and escaped ornamentals (Cohen and Carlton 1995; Light et al. 2005). Ballast water and dry ballast may have also been responsible for a few introductions in the estuary, though only one terrestrial plant species (*Cotula coronopifolia*, brassbuttons) is known to have been introduced to the estuary directly through ballast (Light et al. 2005). *Myriophyllum spicatum* (Eurasian watermilfoil) is suspected to have been introduced to Chesapeake Bay in the late nineteenth century through shipping ballast (Aiken et al. 1979), though its introduction to the Delta is thought to have been through aquaria

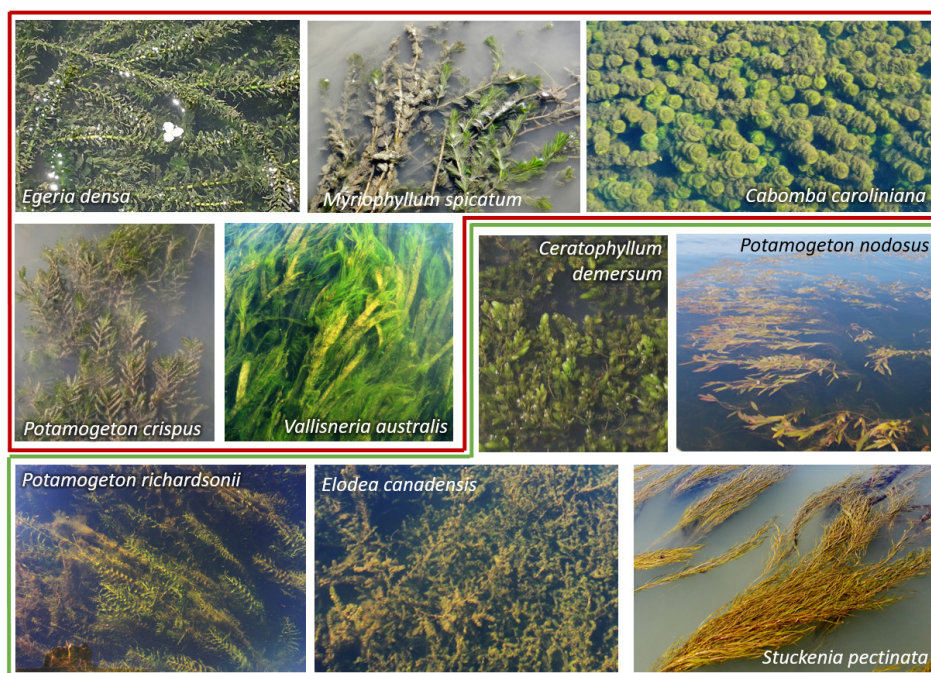


Figure 2 Photographic images of major submerged aquatic plant species in the Delta. The *red outline* indicates non-native species, and the *green outline* denotes species considered native to the estuary. Photos: Shruti Khanna.

Table 1 Native and non-native submerged and floating aquatic plant species found in the Delta, and the likely year of colonization for non-native species (Light *et al.* 2005). Relative cover of submerged aquatic vegetation (SAV) species is with respect to the entire SAV community and floating aquatic vegetation (FAV) species is with respect to the entire FAV community across the legal Delta (Boyer *et al.*, this issue; Khanna *et al.* 2022b). Canopy structure, distribution, and leaf shape denoted by *bold text* indicates that the particular trait increases the propensity of the plant to alter flow and trap sediment (see “Effects of Environmental Conditions on Plant Species and Vegetation Communities of the Delta”).

Scientific name (Common name)	Status (year of invasion in the Delta)	Relative cover of species as of 2019	Canopy structure	Distribution in water column	Leaf shape/ arrangement
SAV species					
<i>Egeria densa</i> (Brazilian waterweed)	Non-native (1946)	51.9%	dense	throughout	whorled
<i>Myriophyllum spicatum</i> (Eurasian watermilfoil)	Non-native (1979)	12.6%	medium	top-heavy	pinnate whorled
<i>Cabomba caroliniana</i> (fanwort)	Non-native (1980)	6.7%	dense	throughout	opposite fan-shaped
<i>Potamogeton crispus</i> (curly pondweed)	Non-native (1946)	3.0%	medium	throughout	alternate
<i>Hydrilla verticillata</i> (water thyme)	Non-native (1976 upstream of Delta)	0% ^a	dense	throughout	whorled
<i>Ceratophyllum demersum</i> (coontail)	Native	13.4%	dense	throughout	whorled
<i>Stuckenia pectinata</i> (sago pondweed)	Native	4.0%	low	top-heavy	long, narrow
<i>Potamogeton richardsonii</i> (Richardson's pondweed)	Native	4.0%	medium	throughout	alternate
<i>Elodea canadensis</i> (Canadian waterweed)	Native	3.2%	dense	bottom-heavy	whorled
<i>Potamogeton nodosus</i> (longleaf pondweed)	Native	<1%	low	top-heavy	short, oblong-elliptic, floating
<i>Najas guadalupensis</i> (southern Naiad)	Native	<1%	dense	throughout	short, narrow
<i>Echinodorus berteroi</i> (upright burhead)	Native (2016 in Delta)	<1%	low	bottom-heavy	long, broad
<i>Vallisneria australis</i> (ribbon weed)	Invasive (2013 in Delta)	few known locations (rare) ^b	dense	throughout	long ribbon-like
FAV species					
<i>Ludwigia</i> spp. (water primrose)	Non-native (1949)	67.5%			
<i>Eichhornia crassipes</i> (water hyacinth)	Non-native (1904)	24.4%			
<i>Limnobium laevigatum</i> (West Indian spongeplant)	Non-native (2008 in Delta)	<1%			
<i>Alternanthera philoxeroides</i> (alligator weed)	Non-native (2017)	NA ^c			
<i>Hydrocotyle umbellata</i> (manyflower marshpennywort)	Native	<1%			
<i>Lemna</i> spp. (duckweed)	Native	<1%			
<i>Azolla</i> spp. (mosquito ferns)	Native	3.9%			

a. *Hydrilla verticillata* is a potential invader, which is already present upstream of the Delta but is not in the Delta yet.

b. *Vallisneria australis* is native to Australia; the species was first observed in the Delta in 2013 in the Sacramento River near Long Island in the northwest Delta (2021 written communication from P. Gilbert, California State Parks Division of Boating and Waterways, to NR, unreferenced, see “Notes.” The species was positively identified by the California Department of Fish and Wildlife in 2021.

c. *A. philoxeroides* is a recent invader and insufficient data are available to estimate its relative cover in the Delta.

releases (Light et al. 2005). At least one SAV species, *Potamogeton crispus* (curly pondweed), was introduced accidentally with stocked fishes (Light et al. 2005).

One of the earliest aquatic macrophyte introductions to the estuary was *Eichhornia crassipes*—sometimes also referred to as *Pontederia crassipes* (Pellegrini et al. 2018) but more commonly known as water hyacinth—which arrived more than a century ago (Finlayson 1983). Although native to South America, *E. crassipes* may have been imported to California from eastern North America where it was first introduced in the US (Light et al. 2005). The most recent discoveries of non-native aquatic plant species with potential for significant impact to the Delta ecosystem include *Alternanthera philoxeroides* (alligator weed; Calflora c2022) and *Vallisneria australis* (ribbon weed; Les et al. 2008).

Most plant introductions in the estuary have been marsh and riparian species, but the few non-native SAV and FAV species have transformed the Delta in significant ways. Three of the four most common SAV species in the region are considered invasive because of their demonstrable negative effects on local ecosystem services and/or the economy (Cohen and Carlton 1995): *Egeria densa* (Brazilian waterweed), *M. spicatum*, and *Cabomba*

caroliniana (fanwort; Santos et al. 2011; Boyer and Sutula 2015). The most common native SAV species is *Ceratophyllum demersum* (coontail), which has expanded its range as a result of its association with *E. densa* (Santos et al. 2011). Non-native species comprise 74.2% of total SAV cover (Table 1; Khanna et al. 2022b). Among FAV, the two most common non-native species (*E. crassipes* and *Ludwigia* spp.) comprise most of the total FAV cover, though this may change as two more recently introduced FAV species—*Limnobium laevigatum* (West Indian spongeplant) and *A. philoxeroides*—become more established in the Delta. Additional information about historical records of some key SAV species are presented in Boyer et al. (this issue) along with how these introductions affected primary production in the estuary (also see Cloern et al. 2021).

Morphology and Canopy Architecture of Dominant Species

Most non-native aquatic macrophytes found in the upper estuary are polyploid species, which makes them highly plastic in morphology. Non-native SAV tend to have dense and evenly distributed (vertically oriented) canopies as well as wider leaf blades, greater leaf area, and higher pigment concentrations (Figures 2 and 3, Table 1). Among native SAV species, *Potamogeton nodosus* (longleaf pondweed) and *Stuckenia pectinata* (sago

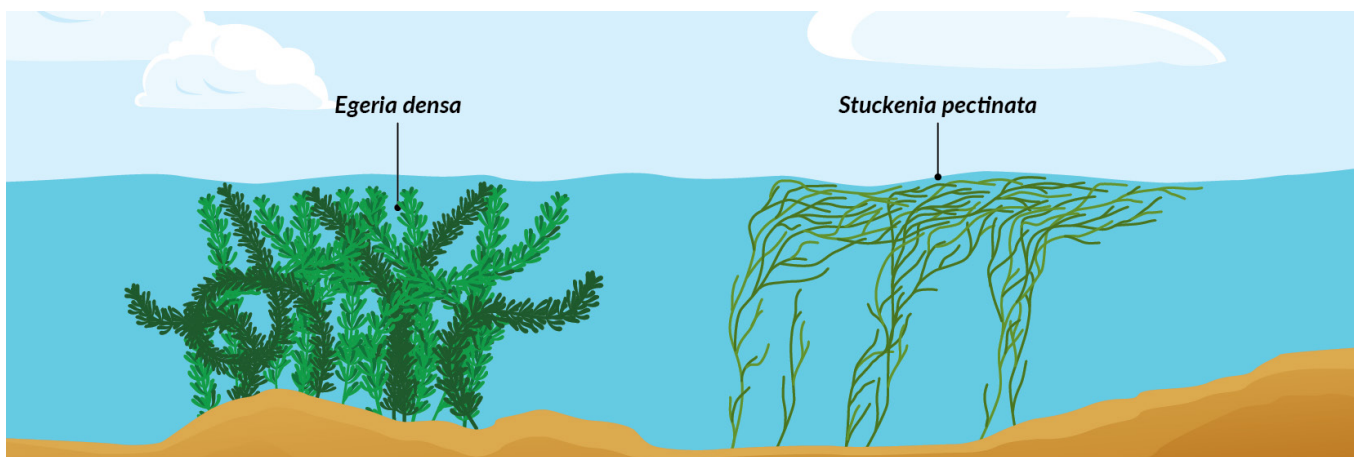


Figure 3 Illustration comparing canopy architecture and density throughout the vertical water column for *Egeria densa*, left, and *Stuckenia pectinata*, right, as described in Table 1. Both species have dense branching at the water surface, but *S. pectinata*'s long, thin leaves and branching structure result in lower-density canopy structure within the water column. In contrast, *E. densa* has dense canopy structure throughout the water column. Credit: Illustrated by Vincent Pascual with the California Office of State Publishing.

pondweed) have markedly streamlined canopies (Figure 3), while *Elodea canadensis* (Canadian waterweed; native but not very commonly found; Table 1) and *C. demersum* have more dense canopies. *C. demersum* has increased in the past 15 years, likely, in large part, from its association with *E. densa* (Santos et al. 2012), but also possibly as a result of competitive advantages conferred by its denser growth that is more similar to other dominant non-native species. For some species, optimal growth relative to available light is achieved by profusely branching shoots near the surface and sloughing lower leaves and branches (Grace and Wetzel 1978). These variable growth habits affect canopy distribution throughout the (vertical) water column and result in profound influences within SAV beds on light availability/shading (Pokorný et al. 1984; see “Light and Carbon”) and sediment dynamics (see “Effects of Environmental Conditions on Plant Species and Vegetation Communities of the Delta”).

Life-History Strategies

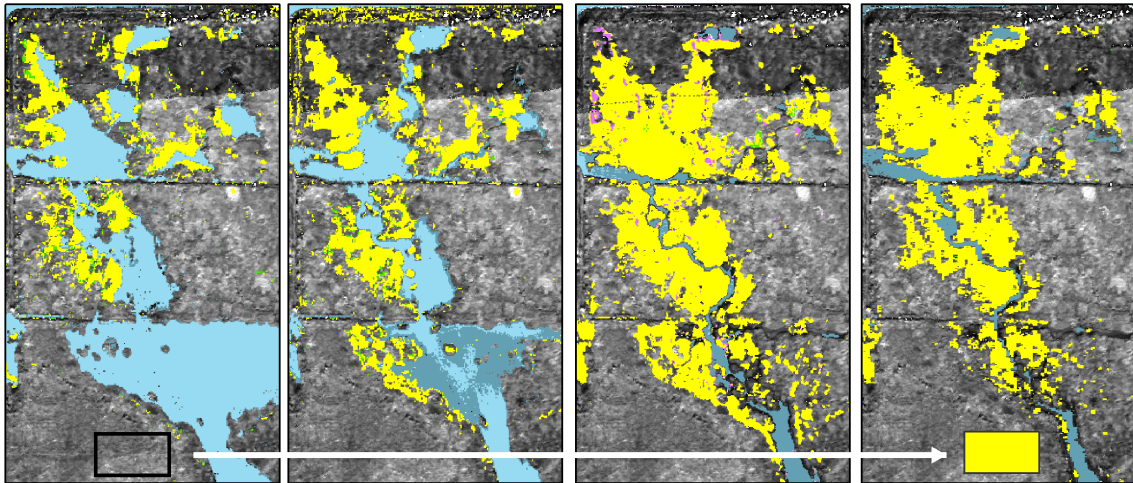
Most non-native aquatic macrophytes found in the upper estuary propagate through asexual reproduction and can spread from tiny fragments (Aiken et al. 1979; Cook and Urmi-König 1984; Malik 2007). For example, *E. densa* rarely produces seeds, does not have differentiated dispersal vegetative organs, and spreads by developing new roots from short stem fragments (double node propagation). Additionally, these species have overwintering organs that allow them to survive winters and regrow in spring. *M. spicatum* has overwintering root crowns that store carbohydrates (Aiken et al. 1979), and *C. caroliniana* produces dense turion-like structures at shoot tips at the end of the growing season (Wilson et al. 2007). *M. spicatum* and *E. densa* also maintain winter biomass and have little to no die-back (Aiken et al. 1979; Getsinger and Dillon 1984; Madsen et al. 2001). Species like *M. spicatum* also produce seeds which can survive prolonged dormancy and hence can sometimes recolonize even years after plant tissue has been eradicated (Van and Steward 1990). Collectively, these characteristics have generally assisted the persistence of these species and confounded

control programs aimed at managing them (Santos et al. 2009; Conrad et al. this issue; Rasmussen et al. 2022).

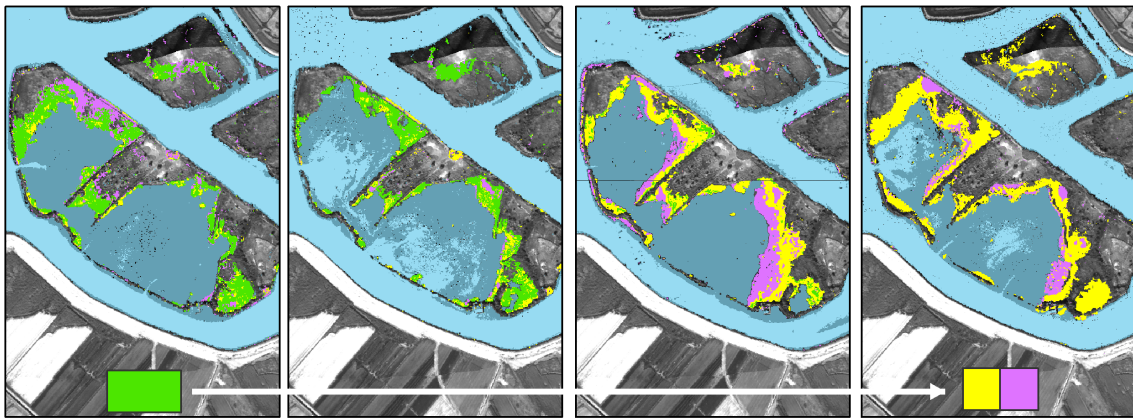
Vegetation Control Efforts

Successful management of the Delta is contingent on awareness of new invasions, responses of existing species to changing conditions, understanding the mechanisms that drive changes in distribution, and the ability of managers to respond quickly once changes are detected (see Conrad et al., this issue, for a more complete discussion of vegetation control in the estuary). While there are well-funded treatment programs for both SAV and FAV in the legal Delta, they have not proven effective in reducing overall cover of target species (Rasmussen et al. 2020; Conrad et al., this issue). However, treatment programs may lead to community turnover as cover of a particular species declines or increases (e.g., proliferation of FAV following control treatments for SAV, and vice versa; see Figure 4). Khanna et al. (2012) showed that when *E. crassipes* cover was reduced, the invaded area rarely returned to open water but instead was most often taken over by SAV growth. Similarly, in years conducive to growth, *E. crassipes* was observed to most often invade areas that already supported SAV species, possibly because SAV beds slowed water velocity and allowed *E. crassipes* mats to expand. In the case of *Ludwigia* spp., the patterns and processes of community change after control treatments were different and varied over time (Khanna et al. 2018). *Ludwigia* spp. are a threat to established marsh because they are amphibious, growing above the water column and in seasonally wet environments such as marshes and meadows (Khanna et al. 2018). Frequently, growth of different FAV species follows the same trajectory from year to year, increasing and decreasing at the same time. However, in years of aggressive *E. crassipes* treatment when *Ludwigia* spp. was not allowed to be sprayed, an increase in *Ludwigia* spp. was observed in regions previously occupied by *E. crassipes* (Khanna et al. 2012, 2018; Figure 4).

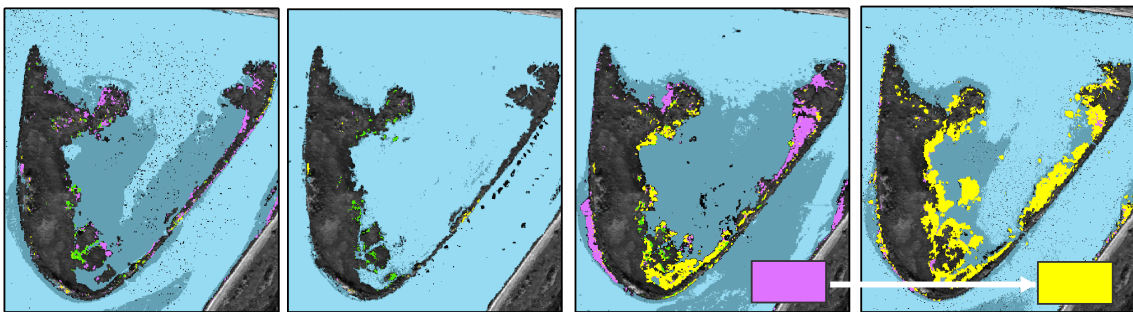
A) Expansion and marsh encroachment of *Ludwigia* spp. in LIBERTY ISLAND



B) Decline in native *H. umbellata* and increase in non-native species in WARD CUT



C) Replacement of treated *E. crassipes* by untreated *Ludwigia* spp. in VENICE CUT



June 2004 June 2008 September 2015 October 2019

Hydrocotyle umbellata
 Ludwigia spp.
 Eichhornia crassipes
 SAV
 Water

Figure 4 Class map showing observed replacement of *E. crassipes* by *Ludwigia* spp. during years that *E. crassipes* could not be treated by the California Department of Boating and Waterways. The first row shows intrusion (and establishment) of *Ludwigia* spp. into the marsh; the second row illustrates the disappearance of *H. umbellata*, a native floating aquatic vegetation (FAV) species, and replacement of niche space with non-native FAV; and row 3 illustrates the replacement of *E. crassipes* by *Ludwigia* spp. in the northeast corner of Venice cut. See Figure 1 for locations of Liberty Island, Ward Cut, and Venice Cut within the Delta. Figure presents data from Khanna et al. 2012, 2018.

Aquatic Vegetation in Restored Habitats

SAV and FAV represent a significant management challenge for restoration of Delta habitats to benefit special-status species. Generally speaking, restoration projects provide new niche space for species and lead to an increase in non-native species cover. For example, when the Prospect Island east levee was breached, *Ludwigia* spp. spread rapidly and covered hundreds of acres in the restoration site (Ustin et al. 2015). SAV has already colonized tidal marsh restoration sites throughout the Delta in varying severity (Barker Slough, Little Holland Tract, Liberty Island Conservation Bank, Decker Island, Blacklock Marsh; Farrugia et al. 2019; Young et al. 2021b; Williamshen et al. 2021). Despite SAV's success in many shallow-water habitats, planned restoration of areas already heavily colonized by non-native SAV (e.g., Franks Tract) may prove effective in reducing overall cover of SAV and FAV by creating physical habitat conditions that reduce niche space for SAV and FAV (e.g., deeper channels broken up by higher-elevation marsh areas) in combination with post-construction control efforts (Conrad et al., this issue).

EFFECTS OF ENVIRONMENTAL CONDITIONS ON PLANT SPECIES AND VEGETATION COMMUNITIES OF THE DELTA

SAV and FAV communities have increased coverage within the Delta considerably over the last 20 years, but how those changes relate to environmental drivers is poorly understood. As described above, community turnover of non-native aquatic vegetation species after control efforts has been documented (Khanna et al. 2012, 2018), but more work that connects species distributions and expansions in coverage with environmental conditions could help fill knowledge gaps. Disturbance substantially affects the successful colonization and spread of non-native aquatic species (Havel et al. 2015), and this influence will likely be exacerbated as extreme climate events increase in frequency and severity in the future (Diez et al. 2012). Within the Delta, water management actions (such as flow pulses or salinity-control measures), vegetation control treatments, and restoration efforts have the

potential to affect distributions of plant species, as do weather extremes such as floods, droughts, and extreme temperatures. This section explores impacts of the physico-chemical environment on aquatic vegetation, with an emphasis on how non-native vegetation responds to conditions and management—and sometimes helps create the conditions that favor further growth and survival as ecosystem engineers.

Light and Carbon

FAV species are generally not light or carbon limited; their leaf canopy is above the water surface, giving them direct access to sunlight and atmospheric carbon dioxide (CO₂). In contrast, SAV species have significant challenges to overcome in terms of CO₂ and light availability throughout the water column, both of which substantially affect photosynthetic efficiency and plant growth. Light availability within the water column is typically a major limiting factor for SAV to survive in deep or turbid environments, or where FAV mats cover the water surface (Nehring and Kolthoff 2011; Khanna et al. 2012; Santos et al. 2016). We have observed in rake surveys we conducted throughout the Delta that no SAV species are able to survive below dense FAV mats.

SAV species exhibit a variety of metabolic and morphological adaptations to overcome light and carbon limitations—including adjustments to leaf shape, canopy architecture, and photosynthetic pathways—and some of these differences appear to give some non-native species a competitive advantage over native species (Santos et al. 2012; Drexler et al. 2021). Several non-native species use a facultative C₄-like photosynthetic pathway to increase photosynthetic efficiency in high-light (e.g., low-turbidity) and low-light (e.g., high-turbidity or shaded) environments (Santos et al. 2012). For example, *Hydrilla verticillata* (water thyme) (Salvucci and Bowes 1981), *M. spicatum* (Van et al. 1976), *E. densa* (Casati et al. 2000), and potentially *C. caroliniana* (Salvucci and Bowes 1981) have all been found to exhibit C₄-like metabolism (Santos et al. 2012).

Temperature

The relatively mild climate of the Delta likely contributes to the presence and persistence of many non-native species. FAV species are generally more susceptible than SAV species to the number of days or nights in which temperatures drop below freezing, with *Ludwigia* spp. exhibiting the greatest tolerance to freezing of all major FAV species present in the Delta (Sainty et al. 1997; Wilson et al. 2005; Armitage et al. 2013; Thouvenot et al. 2013). Although *E. crassipes* cannot tolerate freezing temperatures or extended periods of excessively high temperatures (>34° C; Penfound and Earle 1948; Wilson et al. 2005), these temperatures are rarely experienced in the Delta.

SAV is generally more tolerant of cold temperatures than FAV. Though little is known about actual temperatures within Delta SAV beds (Borgnis and Boyer 2016), water temperatures observed in the Delta would not be considered limiting for most if not all SAV species (Aiken et al. 1979; Wilson et al. 2007; Bashevkin et al. 2022). On the other hand, *M. spicatum* (Titus et al. 1975) and *P. crispus* (Nichols and Shaw 1986) appear to benefit from the estuary's relatively warm water temperature in the summer (18 to 20 °C; Santos et al. 2011). *E. densa* growth is reduced above 30 °C (Borgnis and Boyer 2016), leading to bimodal growth pattern observations in the estuary. Peak growth occurs in the milder conditions typical of spring and fall, with dips during peak summer temperatures (Santos et al. 2011). The presence of dense SAV canopies can lead to increased water temperature in the upper water column as a result of slower water flows and increased residence time (Carpenter and Lodge 1986; Wilcock et al. 1999), although such gradients are ephemeral and mixed out with water circulation (Carpenter and Lodge 1986). While similar effects can be attributed to FAV, shading may offset slower water flows and increased residence times, making the overall effect on water temperature less clear (Tobias et al. 2019).

Average annual water and air temperatures across the region have increased during the last century (Hoerling et al. 2013; Bashevkin et al. 2022), and

this trend may continue in the immediate future, though many FAV and SAV species currently in the Delta are not likely to be affected because they are known to tolerate similar high temperature ranges in other ecosystems (Penfound and Earle 1948; Wilson et al. 2005; Wilson et al. 2007). However, under climate change, higher temperatures could affect species tolerances of other stressors (e.g., salinity) and fewer freezing events could affect species phenology. Both of these changes could alter future community dynamics.

Hydrology

Despite variability in cover by SAV and FAV across wet and dry years, FAV species have generally maintained their overall cover in the Delta while SAV species have increased in cover (Ustin et al. 2021; Khanna et al. 2022a). During the 2012–2016 drought, both FAV and SAV expanded in cover, increasing the total area of waterways invaded to up to 31% (Ustin et al. 2021; Khanna et al. 2022a). In wet years, SAV is more resistant to higher flows than FAV because most SAV species are rooted. Water depth and velocity can affect both SAV and FAV (Chambers et al. 1991; Madsen et al. 2001), while SAV is also limited by turbidity (Durand et al. 2016). During high flows in wet years, velocity, depth, and turbidity all generally rise, creating conditions which would be less favorable for SAV and FAV. In contrast, dry years generally mean lower water velocity, water depth, and turbidity, conditions that either allow SAV and FAV to proliferate in their existing niche space or to expand and colonize new areas.

Depending on the duration of the drought or dry period, positive feedbacks by SAV species can lead to continued colonization after drought conditions end. For example, extensive coverage of SAV has persisted in Big Break and Franks Tract after the emergency installation of the drought barrier (and subsequent removal) from False River in 2015 (Kimmerer et al. 2019). The drought barrier consisted of a 230-m rock barrier that was installed across the west False River channel to limit salt intrusion into the interior portions of the Delta resulting from low river flows. Although SAV was present in these areas before the drought

barrier was installed, the barrier may have helped SAV expand coverage in Franks Tract, and there was no decline in coverage of SAV in subsequent years, even with high flow events in 2017 (Kimmerer et al. 2019). Species composition within Big Break and Franks Tract also shifted after the barrier was installed, again likely as a result of altered conditions that allowed different species an opportunity to gain a foothold and become established in these areas (Kimmerer et al. 2019). Thus, even temporary disturbances that change environmental conditions can have lasting effects on the SAV community's composition and distribution.

Salinity

Increased salinity in the Delta results from a number of anthropogenic activities (e.g., flow alteration) and extreme events (e.g., levee failure, extended droughts) but is also projected to increase with sea level rise (SLR) and changes in precipitation that are projected to occur over the next few decades with climate change (Cloern et al. 2011). The dominant species in both the Delta's SAV and FAV communities are primarily freshwater plants sensitive to salinity. No major FAV species in the Delta appears able to tolerate the salinities typical of Suisun Bay or Suisun Marsh (>2 psu; Boyer and Sutula 2015) with the notable exception of the recent invader *A. philoxeroides*, which may tolerate up to 3.5 psu in lentic waters and up to 10.5 psu in lotic waters (Ensby and van Oosterhout 2012). Among SAV species, *E. densa* is particularly sensitive to salinities as low as 5 psu, and higher temperatures exacerbate the effect (>30 °C; Borgnis and Boyer 2016). As a result, lower species diversity is observed for both SAV and FAV communities in Suisun Marsh relative to the fresher waters of the Delta.

In contrast, the native SAV species *S. pectinata* tolerates much higher salinity (up to 12 psu), though optimum growth is observed at low salinity and/or in freshwater (Borgnis and Boyer 2016). In Suisun Marsh, where the distribution of *E. densa* and *S. pectinata* overlaps, salinity appears to strongly affect their interactions and competitiveness. In freshwater, *E. densa* out-

competes *S. pectinata*. However, *E. densa*'s overall range limit appears to be driven by salinity levels, which allows *S. pectinata* to dominate in areas just outside of *E. densa*'s tolerance (Borgnis and Boyer 2016).

Higher salinity during the recent 2012–2016 drought did not affect SAV extent much, although it possibly affected community composition (Kimmerer et al. 2019). Future increases in salinity and higher temperatures may limit the distribution of *E. densa* in the western end of the Delta and allow native species such as *S. pectinata* to again dominate these areas (Borgnis and Boyer 2016). However, other non-native species such as *M. spicatum*, which thrives in salinity of 10 ppt (Aiken et al. 1979), may become more competitive.

EFFECTS OF AQUATIC VEGETATION ON THE PHYSICAL AND BIOGEOCHEMICAL ENVIRONMENT OF THE DELTA

Non-native aquatic vegetation around the globe has been shown to strongly modify habitats by changing channel bathymetry, water temperature, flow velocity, turbidity, and the availability of light and dissolved oxygen (DO) in the water column (Wilcock et al. 1999; Dandelot et al. 2005; Nehring and Kolthoff 2011; Lacy et al. 2021). Through these effects, non-native aquatic vegetation has directly affected ecosystem services such as nutrient cycling, sedimentation, plant community composition (Khanna et al. 2018), and carbon storage (Cook and Urmi-König 1984; Drexler et al. 2021). Here, we review what is known about how aquatic vegetation has transformed the Delta region and how these species act as ecosystem engineers by shaping the physical environment to favor their own growth and expansion. In the following sections, recent studies conducted in the Delta that have advanced our understanding of how aquatic vegetation alters sediment and carbon dynamics are given stronger emphasis and consequently are summarized in greater detail than other studies.

Evapotranspiration

The effects of aquatic macrophyte communities on ET is poorly studied, particularly with respect to impacts of non-native FAV species. Most studies

of FAV, such as for *E. crassipes*, are based on measurements using tubs or tanks placed in fields or other areas that have very different conditions than actual wetland and aquatic ecosystems, resulting in erroneous and/or biased results. At a larger scale, much of what is known about ET in estuaries or wetlands around the world is based on field measurements or estimations of emergent marsh or riparian vegetation. A primary cause for interest in estimating water use by wetlands today—and also the basis of most historical interest—comes from the idea that natural vegetation “consumes” water that could otherwise be used for other purposes (e.g., agricultural irrigation and human drinking water; Stannard et al. 2013). Beyond consumptive use, however, accurate estimation of ET is crucial for constructing the water budget of a wetland, which controls its size, water quality, biogeochemical processes, surface water-groundwater exchange, and outflow to the greater watershed (Glenn et al. 2013). The lack of ET rates for Delta aquatic macrophytes represents a significant gap in our understanding of the true effects of these species on the ecosystems and water supply in the region.

ET is typically the largest outflow component for wetland hydrologic budgets because of the influences of temperature and air advection (Drexler et al. 2008). Despite ET constituting such a large outflow, estimates of ET are often only quantified as part of a lumped outflow term that includes other water budget components (Stannard et al. 2013). In addition, although numerous methods for estimating wetland ET exist, the complexity of surface characteristics and the diversity of wetland types often complicate its quantification (Drexler et al. 2004). For example, narrow strips or patches of wetland vegetation, which are commonly found in the Delta, prove to be challenging to study with certain field methods, such as the Bowen ratio energy method or eddy-covariance flux estimates, because these methods require relatively large fetch over a uniform vegetation type. For this reason, previous field or modeling studies to estimate ET for Delta aquatic macrophytes have primarily focused on stands of emergent vegetation in marshes (Drexler et al.

2008), with little to no data on ET in the Delta’s FAV (or SAV) communities.

A recent effort to compare crop consumptive water use in the Delta utilized several prominent methods, including estimates based on crop coefficients, water balances, energy balance using remote sensing, and field measurements (Medellín-Azuara et al. 2018). Estimated consumptive water use rates for non-agricultural land use classes—including native riparian, upland herbaceous, and FAV, which amounted to almost 88,000 acres or 13% of the Delta—averaged 247,000 acre-feet (af) in 2016. ET rates were estimated to be ~4.4 af acre⁻¹ for FAV and ~4.0 af acre⁻¹ for riparian areas, compared to an average estimated rate of 3.0 af acre⁻¹ for crop ET. However, these estimates are highly uncertain because the models used to derive them were not designed for application in wetlands. The study concluded that natural vegetation’s contribution to consumptive water use in the Delta is “non-trivial” and deserves further investigation (Medellín-Azuara et al. 2018).

In wetland systems, plant stand characteristics as well as micro-meteorological conditions have long been known to affect ET rates (Penfound and Earle 1948; Snyder and Boyd 1987). For many systems, observed water loss is typically highest during the warmer growing season, compared to winter months (Snyder and Boyd 1987), particularly when seasonal or temperature-based senescence of leaves reduces leaf area. In the Delta, summer months feature high daytime temperatures followed by cool, windy nights—conditions likely to result in strong advective forces as water temperatures warm during the day. In a study at a restored tidal marsh on Twitchell Island, Drexler et al. (2008) used the surface renewal method and observed that wind direction and the temperature of standing water in the wetland were the biggest drivers for determining ET rates. This study found mean water loss rates from the wetland to be 6 mm day⁻¹, which is higher than previous observations of similar marshes in other systems. Recent work by Hemes et al. (2018) showed for the first time that FAV can cool the water surface *in situ*—

particularly during the hot summer months—potentially reducing ET.

Discrepancies or variation in ET observed for wetland vegetation in different systems can be explained in some cases by differences in species composition, water depths, salinity, or other factors, but some studies utilized methods that did not account for the significant influence of (wind) advection that is highly typical of wetlands (Drexler et al. 2008; Glenn et al. 2013). Thus, early studies that aimed to characterize ET in open water vs. FAV patches likely have incorrect estimations that result from methods not adequately accounting for advective processes (Drexler et al. 2004). For this reason, studies dedicated to measuring and comparing ET in FAV and SAV and evaporation in open water over multiple water years are needed to fully understand how aquatic vegetation changes ET in the Delta's highly regulated water-conveyance system.

Nutrients and Water Quality

The vast amount of SAV and FAV present in the estuary today significantly affects water quality and nutrient cycling (Dahm et al. 2016), though relationships between forms and concentrations of nutrients and the growth and expansion of SAV or FAV across the Delta are poorly understood (Boyer and Sutula 2015). Much of what we know derives from studies of these species in other ecosystems, including their native habitats and other areas in which they have been introduced and proliferated. Nutrient uptake by aquatic macrophytes is thought to occur largely through roots, either floating in the water column or embedded in the sediments (Chambers et al. 1989), but strong evidence also supports shoot uptake by several SAV species, including *E. densa* and *C. caroliniana* (Feijoó et al. 2002). *C. caroliniana* has demonstrated efficiency in utilizing dissolved phosphorus (P) and nitrogen (N) directly from the water column through stem and leaf tissues, with shoot uptake rates of P exceeding that of roots (Wilson et al. 2007). Some species, such as *M. spicatum*, are able to tolerate low concentrations of nutrients like P but are also able to flourish in nutrient-rich or eutrophic

environments (Aiken et al. 1979). In the estuary, dense sub-surface mats of *C. demersum*, a native root-less species, have been observed in high-nutrient water columns as dense, monospecific canopies that lie submerged with a layer of water above them (DiTomaso et al. 2013).

SAV can have large effects on nutrient cycling in systems by mobilizing nutrients from sediments then releasing them into the water column when they senesce at the end of the growing season or in response to control treatments (Nichols and Shaw 1986). Studies have indicated that both SAV and FAV reduce DO in the water column (Penfound and Earle 1948; Grimaldo and Hymanson 1999; Dandelot et al. 2005; Nehring and Kolthoff 2011; Tobias et al. 2019), which can then mobilize P from the substrate, making it available for uptake, and changing nutrient cycling pathways in invaded areas (Aiken et al. 1979; Cook and Urmi-König 1984; Mazzeo et al. 2003). Dense growth of SAV produces strong diel patterns of DO with super-saturation at the end of the day and under-saturation at night (Anderson et al. 2017). FAV generally shades out water column photosynthetic activity and limits reoxygenation through the water surface, so FAV can lower water column DO levels, although tidal and/or river flows can minimize these effects (Tobias et al. 2019). FAV also reduces DO by increasing microbial growth from accumulation of organic matter, thus inducing anoxic conditions detrimental to aquatic life (Penfound and Earle 1948; Dandelot et al. 2005). In the Delta, Tobias et al. (2019) found that DO increased relative to baseline values for the region after patches of *E. crassipes* were treated.

The effects of nutrients on the growth and expansion of SAV and FAV in the estuary have not been documented. As was reviewed in Dahm et al. (2016), direct studies of the effects of nutrients on SAV or FAV are lacking, and thus whether proliferation of aquatic weeds over the last few decades was driven by high nutrient concentrations in Delta waters remains a subject of debate. Concentrations of N and P in Delta waters are not likely to limit plant growth (Cloern 2001), but vast and dense SAV

beds and FAV mats are likely to consume large quantities of nutrients and significantly affect nutrient dynamics throughout the region. Despite considerable attention on the effect of available N form (as nitrate or ammonium) on phytoplankton (Wilkerson et al. 2006), the importance of N form in Delta waters and sediments to aquatic vegetation has not been fully studied. In studies performed elsewhere, the estuary's dominant FAV and SAV species show higher uptake of ammonium over nitrate when both are present (e.g., for *E. crassipes*, Reddy and Tucker 1983, and for *E. densa*, Feijoó et al. 2002 and Reddy et al. 1989), but, in general, most studies show that these species readily utilize either N form, and there does not appear to be any strong relation between N form and growth (Carignan and Neiff 1992; Heard and Winterton 2000; Moran 2006). Upgrades to the Sacramento Regional Wastewater Treatment Plant will come online during the next few years, and will likely change the load and form of nutrients discharged into the Delta. Research and monitoring efforts that assess changes to SAV and FAV growth and coverage during this period could provide insights into uncertainties related to changes in loads and the forms of nutrients discharged into the Delta.

Ecosystem Engineering Ability of Aquatic Vegetation to Alter Flows, Sediment Dynamics, and Carbon Storage

The impact of non-native aquatic vegetation on flows and sediment dynamics in the Delta has until recently been a largely unstudied aspect of the ecosystem engineering capabilities of these plants. The extent to which aquatic vegetation alters flows and sediment transport depends on many variables, including the incident flow conditions, sediment flux, characteristics of the channel bed, density, phenology, architecture of the vegetation, and patch characteristics (Lacy and Wyllie-Echeverria 2011; Nepf 2012; Hansen and Reidenbach 2013; Larsen 2019; Work et al. 2021). The dominant SAV (*E. densa*) and FAV (*E. crassipes* and *Ludwigia* spp.) in the Delta have long been known to retard flows and reduce bed shear stress, allowing suspended sediment to settle out of the water column and become trapped within or below a patch of vegetation (Petticrew and

Kalff 1992; Wilcock et al. 1999; Toft et al. 2003; Hestir et al. 2013, 2016).

For several reasons, SAV generally has a greater propensity to alter sediment dynamics in channels than FAV. First, FAV is most likely to trap sediment when connected to shore in a large, contiguous mat; however, such a growth habit predominantly occurs in slow-flowing channels or along channel edges that have very low suspended sediment concentrations (SSC; Toft et al. 2003; Azza et al. 2006). Second, FAV biomass is concentrated at the top of the water column where the SSC is generally lower than near the channel bed, thus reducing the potential for trapping sediment (Garcia 2008). Finally, the presence of FAV in a channel causes an acceleration of flow around roots, decreasing the likelihood of sediment trapping due to increased flow velocity at the channel bed (Downing-Kunz and Stacey 2012). For these reasons, this section focuses primarily on the ecosystem engineering traits of non-native SAV rather than FAV on flows and sediment dynamics.

In the Delta, *E. densa* is the most common SAV species, covering ~5,000 ha, which represents 51.9% of all SAV cover (relative cover) in 2019 (Table 1). Because of its architecture, leaf shape, and stem density, *E. densa* has a particularly high propensity to trap sediment (Drexler et al. 2021; Figures 2 and 3). Two less common species of SAV—*M. spicatum* and *C. caroliniana* (12.6% and 6.7% relative cover, respectively; Table 1)—have dense architecture throughout the water column, which likely results in the trapping of sediment as well. These species stand in stark contrast to the native *S. pectinata* (4.0%; Table 1), which is one of the historically common species in the Delta (Cloern et al. 2021). *S. pectinata* likely never trapped much sediment or slowed flows due to its narrow leaves, which are most abundant near the water surface, and its low-density architecture (Table 1, Figure 3). The dramatic spread of *E. densa* and other non-native SAV species has changed how water and sediment move through the Delta's aquatic environments (Hestir et al. 2016; Drexler et al. 2021). *E. densa* has decreased water column turbidity, which increases water

clarity and light penetration, thus promoting further SAV growth and expansion (Hestir et al. 2016). This feedback loop has resulted in the build-up of a non-native aquatic vegetation sediment “sink” in the Delta. This sediment sink represents an important component in the recent Delta-wide step decrease in turbidity, which is independent of the declining trend in sediment supply in the region (Hestir et al. 2013, 2016; Schoellhamer et al. 2013).

Until just recently, little was known about how non-native aquatic vegetation alters sediment dynamics, besides promoting the formation of a new sediment sink. In particular, no data were available on the instantaneous sediment trapping by SAV, the impact of SAV on current speeds and sediment flux, and the composition

and accumulation rate of sediments under SAV. Using completely different approaches, three companion studies have recently addressed these questions as well as identified SAV as a novel form of “blue carbon” storage (organic carbon stored in coastal ecosystems; McLeod et al. 2011) on the landscape (Drexler et al. 2021; Lacy et al. 2021; Work et al. 2021). Much of the impetus behind these recent papers stems from the hypothesis illustrated in Figure 5 (top panel). Because SAV dominated by *E. densa* is known to reduce flows, this results in suspended sediment settling out of the water column. In this manner, sediment becomes increasingly trapped within or below SAV patches. This process may ultimately block sediment from reaching adjacent tidal marshes that rely on vertical accretion of both autochthonous organic production and

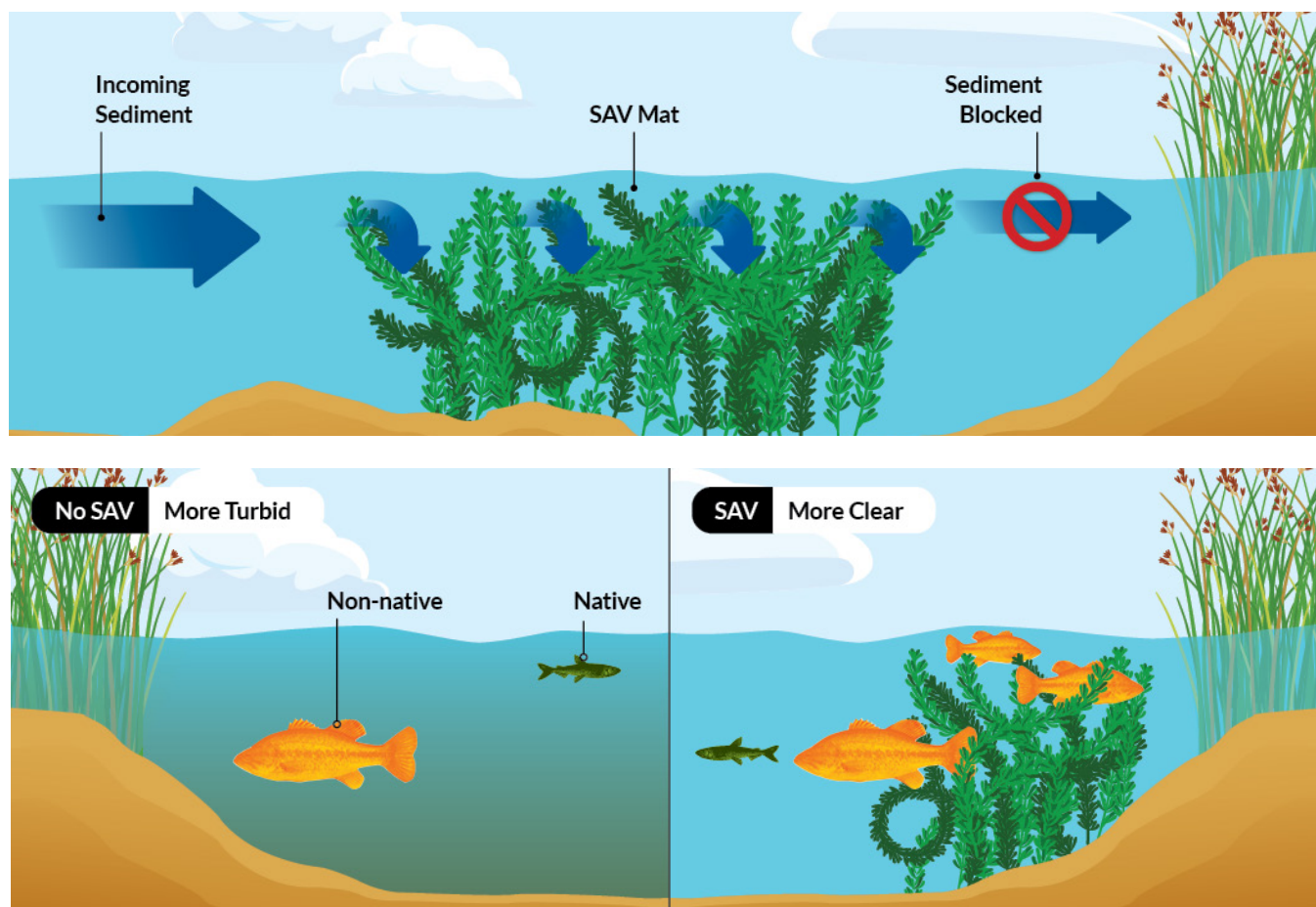


Figure 5 A schematic of a generic Delta channel showing how invasive submerged aquatic vegetation (SAV) can potentially block sediment from depositing on adjacent tidal freshwater marshes (*upper panel*) and decrease turbidity (*lower panel*). Credit: Illustrated by Vincent Pascual with the California Office of State Publishing.

allochthonous inorganic matter to build elevation and stay sustainable under SLR (Drexler 2011; Swanson et al. 2015).

In the first study, Drexler et al. (2021) collected and analyzed sediment cores from three Delta study sites with different hydrodynamics that contained marsh with adjacent SAV patches dominated by *E. densa* (Figure 1). The cores showed that non-native SAV patches had higher inorganic sedimentation rates and vertical accretion rates than adjacent marshes, but similar carbon accumulation rates (non-native SAV: 59–242 g C m⁻² yr⁻¹, marsh: 109–169 g C m⁻² yr⁻¹, $p > 0.05$). The SAV patches stored ~38% of the carbon stored annually in restored Delta marshes (~3500 ± 2200 metric tons C yr⁻¹; Drexler et al. 2019) and about 9.4% of the inorganic sediment retained by the Delta (103,000 ± 22,000 metric tons of sediment yr⁻¹) (Wright and Schoellhamer 2005; Schoellhamer et al. 2013). The carbon accumulation rates in the SAV were just slightly below the mean global rate for seagrasses (138 ± 38 g C m⁻² yr⁻¹, top 0.5 m), a major type of blue carbon ecosystem (McLeod et al. 2011). Drexler et al. (2021) acknowledged that although non-native SAV provides the valuable ecosystem services of carbon sequestration, it also provides numerous ecosystem disservices, which far outweigh any benefit it might have for reducing carbon pollution. The presence of a substantial sediment sink under non-native SAV patches represents the first line of evidence that supports the hypothesis regarding the role of SAV in trapping sediment otherwise available to marshes.

In the next study, Lacy et al. (2021) focused on how *E. densa* affects flow and sediment dynamics at the fine scale. Vegetation properties, current velocity, and SSC inside and outside of the individual patches of non-native SAV in the lower Mokelumne River and Lindsey Slough were measured (Figure 1). Lacy et al. (2021) showed that SAV with high density throughout the water column exerts strong control over flow and SSC. They found that currents were attenuated by more than 90% within patches at both sites. SAV patches reduced SSC by 20% under low discharge rates and up to 30% under high discharge rates at the

Mokelumne River site. SAV effectively reduced the cross-sectional area of channels, largely deflecting along-channel flow and sediment transport into the deeper unvegetated portion of the channel. In contrast, rising tides drove flow and sediment transport through the SAV to the adjacent marsh, so the reduction of SSC by 20% or more within SAV patches resulted in a concomitant reduction of sediment supply to the marsh.

The final study focused on instantaneous sediment trapping by SAV. Most related literature focuses on how marine SAV and a few species of freshwater SAV obstruct flow or alter sediment deposition on the channel bed (Getsinger and Dillon 1984; Sand-Jensen 1998; Lacy and Wyllie-Echeverria 2011; Jones et al. 2012; Nepf 2012). Instead, Work et al. (2021) used an acoustic Doppler current profiler deployed from a kayak to measure quasi-instantaneous sediment trapping efficiency while circumnavigating large patches of non-native SAV at the same sites as Drexler et al. (2021). Sediment trapping efficiency of patches, defined as instantaneous net trapped sediment flux divided by incident flux, averaged approximately 5%, and upscaled annual rates were quite similar to those measured with the SAV cores described above. Long-term measurements of SSC at stream gages on the Sacramento River (1963–2019; USGS station number 11447650 at Freeport, California) and San Joaquin River (1923–2019; USGS station number 11303500 at the San Joaquin River near Vernalis, California) revealed a -1.8% and -1.1% annual decline, respectively, in SSC of flow entering the Delta (USGS 2022). These results demonstrate that the extensive cover of non-native SAV, the declining sediment supply in the rivers, and the modest but chronic trapping efficiency of the SAV are likely diminishing the resilience of Delta marshes and those farther downstream to SLR. These conclusions also support the hypothesis shown in Figure 5. Overall, these findings, together with those of Drexler et al. (2021) and Lacy et al. (2021) demonstrate that chronic infestation of *E. densa* is decreasing marsh resilience to sea-level rise in the Delta and likely other tidal wetland regions infested with this globally invasive plant.

Much still remains to be learned about the ecosystem engineering capabilities of SAV on flows and sediment dynamics in the Delta and elsewhere. As mentioned above, Delta studies so far have looked at how non-native SAV is changing turbidity in the Delta at large (Hestir et al. 2013, 2016) and how SAV patches dominated by *E. densa* affect flow and sediment dynamics in channel environments (Drexler et al. 2021; Lacy et al. 2021; Work et al. 2021). However, *M. spicatum* and *C. caroliniana* are also likely to be effective at trapping sediment because of their dense architecture. Furthermore, SAV is found in flooded islands and dead-end sloughs as well as channels. A broader suite of studies that includes multiple SAV species in various environments, including flooded islands and dead-end sloughs, could be used to construct models capable of projecting the impacts of SAV on flows and sediment dynamics across the entire Delta.

In the bigger picture, what has been learned so far about how SAV affects flows and sediment dynamics stands as a cautionary tale. For several decades after infestation in 1946 (Light et al. 2005), *E. densa* did not exert a large impact in the Delta. By the 1990s, however, infestation had spread substantially, and control was initiated (USDA–ARS and CDBW 2012). It has taken until now to determine that chronic, long-standing infestation of non-native SAV affects sustainability of tidal marshes under SLR in the Delta and likely downstream in the greater estuary. Such work demonstrates that the chronic effects of non-native aquatic vegetation or any other species cannot be determined without process-level studies on an ecosystem scale. Individual studies on particular aspects of ecosystem engineering are unlikely to provide a true understanding of the full range and magnitude of ecosystem effects of long-standing plant invasions.

AQUATIC VEGETATION AND BIOTA

The effects of aquatic vegetation on biota are myriad and complex. In this section, we focus on the direct and indirect relationships between aquatic vegetation and fishes, using recent

literature from the tidal freshwater portions of the estuary. Other vegetation (e.g., emergent marsh vegetation, eelgrass) in peripheral habitats and more saline portions of the estuary provide crucial habitat functions for fishes and invertebrates (summarized in Brown 2003; Schaeffer et al. 2007; Herbold et al. 2014; with specific examples in Watters et al. 2003; Howe and Simenstad 2011; Colombano et al. 2021). Because of the complexity of the topic, vegetation beyond SAV and FAV found in the Delta are beyond the scope of this summary. In many instances it is difficult to determine the specific ecological function of different vegetation types (i.e., SAV, FAV, emergent vegetation) in areas where they co-occur; thus, the general term “aquatic vegetation” is used, with specific vegetation type noted when known.

Physicochemical Environment

Documented effects of aquatic vegetation on the physical environment include substantial impacts on habitat suitability for aquatic organisms, with perhaps the most well-studied effects on Delta fishes associated with water clarity changes. Sediment trapping (see “[Ecosystem Engineering Ability of Aquatic Vegetation to Alter Flows, Sediment Dynamics, and Carbon Storage](#)”) associated with dense SAV stands has contributed to Delta-wide declines in turbidity (Hestir et al. 2016), a noted habitat feature for Delta Smelt (Feyrer et al. 2007; Moyle et al. 2016), which are listed as threatened under the Endangered Species Act and endangered under the California Endangered Species Act. Declining turbidity can also exacerbate the negative effects of non-native piscivorous fish on native species (Ferrari et al. 2014; see [Figure 5](#)). The hydrodynamic breaks (i.e., drag) associated with SAV that contribute to sediment deposition also influence water velocities experienced by fishes. Fluvial and tidal velocities are diminished within and along SAV beds (Carpenter and Lodge 1986; Wilcock et al. 1999; Drexler et al. 2021), creating lateral gradients in velocity and turbidity which can contribute to fish microhabitat selection (Bennett and Burau 2015).

Elevated photosynthetic activity associated with SAV stands can result in large diel fluctuations in DO (see also “[Nutrients and Water Quality](#)”), and variability in DO associated with seasonal macrophyte growth and senescence can affect the suitability of vegetated habitats for species sensitive to such oxygen fluctuations (Kramer 1987; Miranda et al. 2000). In regions where vegetation cover is total and persistent, associated swings in DO concentrations may act as temporary migration barriers (*sensu* Le Pichon et al. 2020), limiting organism movement and contributing to mortality (e.g., Toe Drain, Johnston et al. 2018).

Secondary Productivity

Aquatic vegetation and the diverse array of associated microbes and epiphytic algae represent a significant component (~35–40%) of the Delta’s primary productivity (Cloern et al. 2021; Boyer et al. this issue) and thus functions as a significant contributor to the Delta’s food web. This aquatic vegetation supports a substantial community of vegetation-associated invertebrates likely both as a physical substrate and through senescence, decay, and remobilization of associated carbon and nutrients. The distribution and community composition of these invertebrates is unique to the type and species of aquatic vegetation (Toft et al. 2003; Hartman et al. 2019; Young et al. 2018a). SAV and FAV each support different densities and communities of aquatic invertebrates, and this varies with other habitat features as well, including salinity and flow.

SAV and the subtidal portions of FAV generally support non-insect invertebrates (predominately Amphipoda, Gastropoda, and Isopoda) with variable aquatic insect abundance (Toft et al. 2003; Young et al. 2018b; Hartman et al. 2019; Donley Marineau et al. 2019). Surface FAV supports higher densities of neustonic or terrestrial invertebrates, including Collembola and Insecta (Toft et al. 2003; Donley Marineau et al. 2019; Hartman et al. 2019). Microhabitat differences in vegetation-associated invertebrate communities are also apparent, with the relative abundance of various invertebrate taxa varying across epibenthic, epiphytic, and

neustonic microhabitats (Toft et al. 2003; Hartman et al. 2019).

Although poorly documented within the Delta, variation in macroinvertebrate community can occur on multiple scales, including within an individual plant or plant patch, across patches, or across sites (Schultz and Dibble 2012). Architectural differences across aquatic plant species are tightly tied to invertebrate communities, with certain plant traits (e.g., reticulate leaves, tighter leaf clusters, etc.; [Table 1](#), [Figure 3](#)) supporting higher invertebrate diversity and abundance (Cheruvilil et al. 2002; Taniguchi et al. 2003). In addition to structural differences between SAV species, observed invertebrate community differences also may reflect the propensity of certain SAV species (particularly *E. densa*) to grow in higher densities and in larger, more continuous patches than others (Santos et al. 2011). Total biomass and patch size have been shown to have a large influence on invertebrate communities across many vegetation types (seagrasses, Attrill et al. 2000; marine algae, Russo 1990; freshwater SAV, Cyr and Downing 1988a and b). It remains to be seen how Delta invertebrate communities respond to shifting vegetation distributions, although there is limited evidence to show minimal response of invertebrate communities to FAV control efforts in the short term (Donley Marineau et al. 2019).

Fish Habitat

Habitat provides specific functional needs for fish, including foraging, refuge, and spawning. In the Delta, SAV provides these functional needs for many fishes, particularly non-native species. Littoral small-bodied or invertivorous non-natives—e.g., Bluegill, *Lepomis macrochirus*; Golden Shiner, *Notemigonus crysoleucas*—rely largely on vegetation-associated invertebrates throughout their entire life cycle (Toft et al. 2003; Whitley and Bollens 2014; Young et al. 2021b), while other littoral fishes rely on these invertebrates as juveniles or as a stable food supply across seasons (e.g., Largemouth Bass, *Micropterus salmoides*; Young et al. 2018b; Weinersmith et al. 2019). In turn, the abundance of juvenile, small-bodied, and/or invertivorous

fishes associated with aquatic vegetation, particularly SAV, provides foraging opportunities for piscivorous fish (particularly for adult Largemouth Bass; Grossman 2016; Wienersmith et al. 2019), which prey upon both littoral and non-littoral species. These piscivorous fish often forage within and along vegetated margins, either ambushing or actively pursuing prey (Lehman et al. 2019).

Even though vegetation can facilitate predation, vegetated habitats provide important refuge from predation for small and juvenile fishes due to their structural complexity. For instance, Largemouth Bass largely rely on SAV-associated prey, but foraging success declines as SAV density or architectural complexity increases (Young et al. 2018a; Wienersmith et al. 2019), with decreased piscivory on SAV-associated fishes (Bettoli et al. 1992; Ferrari et al. 2014). The proliferation of plants with more dense architecture or growth habits (like *E. densa*) will thus change the availability of vegetation-associated prey items simply through impedance of movement and vision. The combination of prey availability and refuge makes SAV important for supporting juvenile life stages and are likely important factors that influence the success of littoral non-native fishes such as Largemouth Bass, Bluegill, and others (Brown and Michniuk 2007; Conrad et al. 2016; Huntsman et al. 2020). In addition to refuge, many non-native species will spawn directly on SAV (e.g., Golden Shiner and Rainwater Killifish, *Lucania parva*), or form nests in shallow-water substrates near or adjacent to SAV beds (e.g., Largemouth Bass).

Aquatic vegetation can provide benefits similar to native species, such as the SAV-associated Tule Perch (*Hysteroecarpus traskii*), which consumes vegetation-associated invertebrates (Young et al. 2021b), and Sacramento Pikeminnow (*Ptychocheilus grandis*), which can forage near SAV beds (Nobriga and Feyrer 2007; Grossman 2016). Anadromous (e.g., Chinook Salmon) and pelagic (e.g., Delta Smelt) native fishes also consume vegetation-associated invertebrates, although these interactions appear to be more opportunistic and may expose the fish to SAV-

associated predators (Toft et al. 2003; Whitley and Bollens 2014; Johnson 2018; Hammock et al. 2019; Young et al. 2021a and b). Native fish using SAV for reproduction is uncommon in the Delta, with Sacramento Blackfish (*Orthodon microlepidotus*) the only native fish species known to prefer SAV as spawning substrate (Moyle 2002), although other species have been documented to use it when preferred habitats are unavailable (e.g., Hitch, *Lavinia exilicauda*).

More broadly, the proliferation of non-native aquatic vegetation has coincided with substantial changes in fish communities. The role of SAV as nursery and refuge habitat for primarily non-native fishes has contributed to the expansion of Largemouth Bass and other centrarchids (Brown and Michniuk 2007; Conrad et al. 2016; Mahardja et al. 2017) and has facilitated changes to the littoral fish community that are resilient to many environmental perturbations (Mahardja et al. 2021). It is unclear to what extent SAV has directly contributed to commensurate native species declines, because many native species can thrive in heavily vegetated habitats. In a study of fish distributions across heavily vegetated Delta flooded islands, the native Tule Perch dominated more brackish (~1.5 PSU) and turbid regions where *E. densa* was prevalent, while non-native Bluegill and Redear Sunfish (*Lepomis microlophus*) dominated fresher (<1 PSU), clearer regions (Young et al. 2018b). This habitat response suggests that a primary distributional driver of some native fishes is prevailing environmental gradients in conjunction with the presence of non-native fish species, rather than simply the distribution of non-native SAV. Regardless, the indirect effects of SAV in conjunction with other habitat alterations (e.g., turbidity declines, non-native predators) are likely severely detrimental to native fishes.

Food Web and Ecosystem Effects

The conversion of historical tidal marshes to leveed channels dominated by non-native aquatic vegetation has resulted in net primary productivity declines, and has shifted productivity from emergent marsh vegetation to SAV (Cloern et al. 2016; Boyer et al. this issue),

making SAV a fundamental element of current ecosystem function (Cloern et al. 2021; Boyer et al. this issue). These changes have coincided with substantial changes in fish community and other ecosystem alterations. This combination has resulted in heavily modified food webs relative to what is known of historical baselines (Whipple et al. 2012), as non-native producers and consumers integrate in a novel landscape (summarized in Brown et al. 2016). SAV affects all food web components— nutrients, detritus, and organisms—across Delta and estuary habitat boundaries. SAV fuels freshwater littoral food webs Delta-wide, supporting a wide range of native and non-native fish and invertebrate species (Grimaldo et al. 2009; Young et al. 2021b). In addition, SAV also contributes variably to food webs in Suisun Marsh (Schroeter et al. 2015), other historical and restored tidal marshes (Howe and Simenstad 2011), and pelagic zones where SAV is either sparse or absent (Young et al. 2021a).

SAV may subsidize food webs across habitat boundaries in the Delta by many possible pathways (see Polis et al. 1997), but here we provide two examples: (1) direct transport of detritus and (2) organism-mediated integration. First, senescent vegetative material and related detritus can be highly mobile in a dynamic tidal environment; gravitational circulation or tidal asymmetries can result in the accumulation of this detritus in the water column and its subsequent incorporation by local consumers (Suzuki et al. 2012; Derisio et al. 2014). This accumulated detritus can subsidize pelagic food webs, as observed in the Sacramento River Deep Water Ship Channel (Young et al. 2021a). Second, mobile consumers (i.e., fishes) often serve as important integrators of multiple trophic pathways (Van der Zanden and Vadeboncoeur 2002; Petchey et al. 2008), foraging from each pathway and transferring productivity across habitat boundaries (Kneib 2002). Many Delta fish species feed generally, coupling multiple trophic pathways associated with SAV and other primary producers (Young et al. 2021b). This consumer-mediated coupling of trophic pathways is corroborated by the presence of vegetation-associated prey items in diets of non-littoral fishes

(e.g., Striped Bass, *Morone saxatilis*, Nobriga and Feyrer 2008; Delta Smelt, Johnson 2018). Together, these studies indicate the importance of SAV to both littoral and non-littoral fishes and more broadly to Delta food webs. Habitat changes that result from active management of SAV, habitat restoration, climate change, and further species introductions will modify food web dynamics and ecosystem function and require continued study and monitoring.

THE PATH FORWARD

Aquatic vegetation comprises a major functional component of Delta ecosystems through altering the physico-chemical environment and influencing biotic interactions in complex ways. Interest in better characterizing the ecology and ecosystem engineering effects of aquatic vegetation has grown in recent years, and several recent studies have made significant advances toward elucidating key roles and influences of aquatic macrophytes, particularly in the areas of sediment dynamics and carbon cycling (Drexler et al. 2021; Lacy et al. 2021; Work et al. 2021), fish habitat (Young et al. 2018a and b; Huntsman et al. 2020, Mahardja et al. 2021), and food webs (Brown et al. 2016; Young et al. 2021a and b). These recent efforts have specifically highlighted that the composition and architecture of these plant communities strongly affect physical aspects of the Delta, and that those effects, in turn, alter ecological processes and ecosystem functions at the landscape scale.

While it is evident that aquatic plants affect every aspect of the physical and biotic environment, trying to more completely understand these issues is a constantly moving target, as new species are introduced and existing species change in abundance and distribution in response to any number of natural or anthropogenic disturbances. Studies that aim to characterize specific aspects of aquatic vegetation in the Delta may not elucidate the full range or magnitude of ecosystem effects. Future studies that take a holistic approach to assessing synergistic effects could be instrumental in determining the full

extent to which aquatic vegetation provides ecosystem services and disservices in the Delta.

The following areas are highlighted as key knowledge gaps which have been historically under-studied. Research in these areas could improve understanding of the ecological roles and functions of SAV and FAV in the estuary, and inform ecosystem management and wetland restoration across the Delta region.

1. **Greater capacity for rapid detection and response to new species invasions could prevent major disruptions to ecosystem health.** Development of habitat occupancy models for SAV and FAV species is currently underway to support predictions about potential spread due to climate change and risk assessment for existing habitats. However, consistent monitoring of aquatic vegetation, which is currently lacking in the estuary, could facilitate early detection of non-native species introductions before significant spread. Ongoing monitoring could also support efforts to understand how episodic events/disturbances (i.e., atmospheric rivers, droughts, excessive summer temperatures, changes in nutrient status) affect ecological processes and key species. Simultaneously, expansion of research capacity could result in more rapid responses when such events occur, whether events are sudden and without warning (e.g., levee failure) or the result of chronic conditions (e.g., drought). Research focused on understanding competitive interactions between different non-native SAV and FAV species could improve the outcome of wetland restorations.
2. **Adaptive management of non-native aquatic vegetation requires identification of effects to ecosystem services and processes in addition to determining changes to ecosystem properties.** Major research gaps remain in the understanding of ecosystem services and disservices provided by aquatic vegetation, including SAV and FAV contributions to carbon and water balance models, the effects of SAV and FAV on sediment dynamics in flooded islands, and the effects of eutrophication on carbon and nutrient cycling in SAV and FAV. Tidal wetland restorations are planned for several large areas (Robinson et al. 2016), but the potential effects of FAV spread in these locations (particularly by *Ludwigia* spp. and *A. philoxeroides*) on marsh biogeochemistry and the resilience of infested marshes to sea level rise have yet to be investigated.
3. **A better understanding of the extent to which SAV has directly contributed to declines in native fish species could ultimately improve populations of these sensitive species.** A combination of factors likely influence native fish distributions, including proliferating vegetation and environmental gradients (e.g., turbidity, temperature, etc.), but precise relations have not been identified. Generally, shallow water and littoral habitats are under-studied, limiting the ability to predict how these habitats will change with changes to the environment. Future management of non-native vegetation, habitat-restoration efforts, climate change, and additional species invasions will likely continue to modify food web dynamics and ecosystem function. Additionally, fine-scale effects of vegetation, particularly plant architecture and growth habit, on distribution of fishes and habitat suitability (i.e., predator-prey dynamics, fish spawning habitat, vegetation-associated hypoxia) remain largely unknown.
4. **Synthesis of currently available data could support the development of models to predict which environmental conditions increase the spread of aquatic vegetation and lead to ecosystem disservices.** A wealth of data already exists on the cover, habitat requirements, food web implications, and ecosystem services and disservices of aquatic vegetation. Synthesizing these data to build statistical models that could predict the response of aquatic vegetation to varying environmental conditions could inform future adaptive management of historical and restored wetlands, reduce niche space for non-native SAV or FAV, benefit native aquatic vegetation, and provide insight into emergent effects on fish species of interest.

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