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SPECIAL ISSUE: STATE OF BAY-DELTA SCIENCE 2022

Ecosystem Services and Disservices of Bay-Delta Primary Producers: How Plants and Algae Affect Ecosystems and Respond to Management of the Estuary and Its Watershed

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ABSTRACT

The Sacramento–San Joaquin Delta (Delta) is a case-study of the Anthropocene "great accelerations," with exponentially increasing temperatures and sea level over time, leading to rapid change in other ecosystem components. In nearly all these interconnected changes and across scales, primary producers play a major role, with diverse effects that mitigate or exacerbate the rapid change induced by climate or other human-driven perturbations. Through this anthropocentric lens, primary producers can be viewed as performing numerous ecosystem services—which ultimately benefit humans—as well as ecosystem disservices, which negatively affect human communities. For example, through carbon sequestration, wetlands can perform ecosystem services of mitigating warming at a global scale and combating relative sea-level rise at a local scale, while generating food that supports regional food webs and fisheries. On the other hand, invasive aquatic vegetation (IAV) can trap sediment before it reaches wetlands, exacerbating local subsidence and relative sea-level rise while incurring great costs to recreation, fishing, and agencies tasked with its control. Effectively managing these ecosystem services and disservices requires understanding how they are connected. For example, wetland restoration often creates opportunities for IAV, which may inhibit sediment deposition on the wetland and out-compete native species. As the Delta science community works toward a more integrative understanding of how different components of the Delta interact as a whole and across scales, the pervasive effects of the ecosystem services and disservices of primary producers serve as foundational knowledge. In this topically themed edition of State of Bay–Delta Science, we review these effects. Individual contributions focus on the historical ecology of the primary productivity of aquatic vegetation, the ecology and control of invasive aquatic vegetation, harmful algal blooms, carbon sequestration and subsidence reversal by wetlands, and remote sensing methods

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for quantifying the ecosystem services and disservices of Delta primary producers.

KEY WORDS

Primary productivity, harmful algal blooms, ecosystem services, ecosystem disservices, invasive aquatic vegetation, carbon sequestration, subsidence reversal, remote sensing

The Sacramento–San Joaquin Delta

The Sacramento–San Joaquin Delta ("Delta") marks the confluence of the Sacramento River flowing from northern California, the San Joaquin River flowing from southern California, and the San Francisco Bay (Figure 1). Collectively, the San Francisco Bay and the Delta comprise the largest estuary on the western coast of North and South America (DSC 2013). Because the Sacramento and San Joaquin rivers converge inland, in the low-lying Central Valley, their sediment load is deposited inland of the Coastal Range, giving the estuary a rare, inverted geometry, with tidal distributary channels diverging from the ocean inland (Figure 1). This network of waterways historically supported extensive tidal and non-tidal wetlands and riparian woodlands (Whipple et al. 2012; Boyer et al., this issue).

Now, as a leveed and channelized patchwork of agricultural land, urban and rural settlements, and with 99% loss of historical wetlands (Robinson and Safran 2014), the Delta is one of the most highly altered landscapes in California. Nevertheless, it sustains one of the West Coast's biodiversity hotspots, with over 750 plant and animal species that currently use the Delta, including 102 federally- and state-listed species of concern (Healey et al. 2016). Prominent physical gradients—arranged longitudinally, laterally, and vertically—underlie this biodiversity, including gradients in salinity, tidal influence, temperature, elevation, oxygen, and redox potential.

The Delta's watershed encompasses nearly 40% of California's land area, but its influence on human communities extends far beyond its boundaries. Fresh water is pumped from the central Delta southward via the Central Valley Project (CVP) and State Water Project (SWP; Figure 1), ultimately to the taps of two-thirds of Californians (Lund 2016). It irrigates approximately one-quarter of the agricultural produce grown in the US, helping to sustain the state's economy, which ranks fifth of economies in the world (Winkler 2021). The Delta also supports multiple life stages of anadromous Chinook Salmon and Steelhead Trout, which help sustain Pacific Ocean fisheries (Perry et al. 2016). It also supports a thriving sport fishing industry that focuses primarily on Largemouth Bass and Striped Bass, several species of catfish, native salmon, steelhead, and sturgeon (Mount et al. 2012).

STATE OF BAY-DELTA SCIENCE

All of the world's major estuaries are imperiled by rising sea level and temperatures (Cloern et al. 2016), and in the Delta—given the importance and political implications of managing freshwater supply, threatened and endangered species, and recreational/cultural uses— management challenges are particularly acute (Luoma et al. 2015). To address these challenges with decision-making designed to be firmly grounded in science, the Delta Plan, mandated under the 2009 Delta Reform Act, tasks the Delta Stewardship Council (DSC) with creating a Delta Science Plan, which identifies priorities for establishing a robust science governance structure. The Delta Science Plan (DSC 2019), in turn, requires the Delta Science Program (1) to regularly update the Science Action Agenda, which prioritizes science actions (on the 4- to 5-year time-scale) and aligns them with the most urgent management needs, and (2) to regularly report on the state of the science through the State of Bay–Delta Science (SBDS) report.

The two previous SBDS editions, published in 2008 and 2016, focused on a wide range of topics, but future editions will be published more frequently (approximately biennially), with each edition focused on a theme related to priority management needs on which substantial progress has recently been made. Based on the urgency of management needs to understand and quantify primary productivity processes

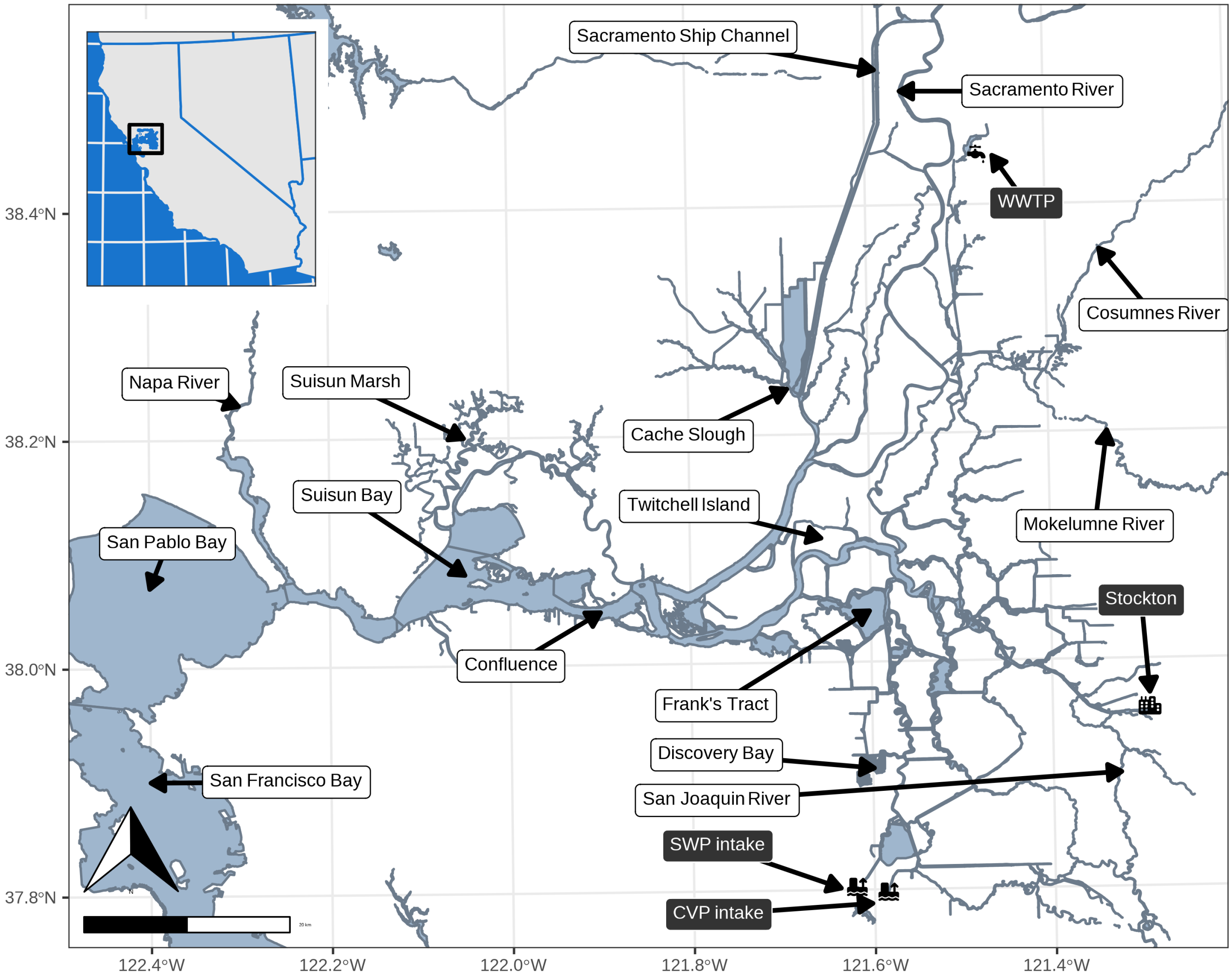

Figure 1 Map of the upper San Francisco Estuary. The Delta includes all areas upstream of the confluence. "WWTP" refers to the Sacramento Wastewater Treatment Plant, "SWP" refers to the State Water Project, and "CVP" refers to the Central Valley Project.

in the Delta (see "Conclusions"), together with a critical mass of recent progress on the topic, the theme of this edition is "Ecosystem Services and Disservices of Bay–Delta Primary Producers: How Plants and Algae Affect Ecosystems and Respond to Management of the Estuary and its Watershed." We frame this edition through the lenses of the Anthropocene and the ecosystem services and disservices concepts (see "The Delta and the Study of Primary Producers as a Case Study of the Anthropocene"), highlighting how primary producers both respond to and influence humans. Social-ecological feedback is an integral component of this framing, with humans serving as direct and indirect drivers of primary producer abundance and composition, and primary producers serving as drivers of management responses, economic effects, and human health. Though the individual papers in this edition are topically focused, here we extract the findings that connect them (see "Scope, Highlights, and Synthesis"). From this exercise a more complete view of the characteristic feedback emerges, together with insights about implications for management and remaining knowledge gaps (see "Conclusions").

THE DELTA AND THE STUDY OF PRIMARY PRODUCERS AS A CASE STUDY OF THE ANTHROPOCENE

Great Accelerations: Hallmarks of the Anthropocene

The Anthropocene is commonly referred to as the "Great Acceleration," alluding to a series of iconic time-series graphs on socio-economic indicators and Earth system effects that show exponential growth from about 1950 on (Steffen et al. 2006). The Great Acceleration is characterized by interacting trends driven by multiple local and global human disturbances. Of these accelerating trends, the best known include global temperature and sea level, which mirror trends observed in the Delta (Figure 2A–2C). Globally and locally, these climate drivers interact with anthropogenic drivers such as drainage and filling of wetlands (Figure 2D) to produce accelerating challenges for resource management. For example, rising temperatures and sea levels contribute to losses or shifts in habitat, and may facilitate species invasions, which have had an economic effect of over one trillion dollars

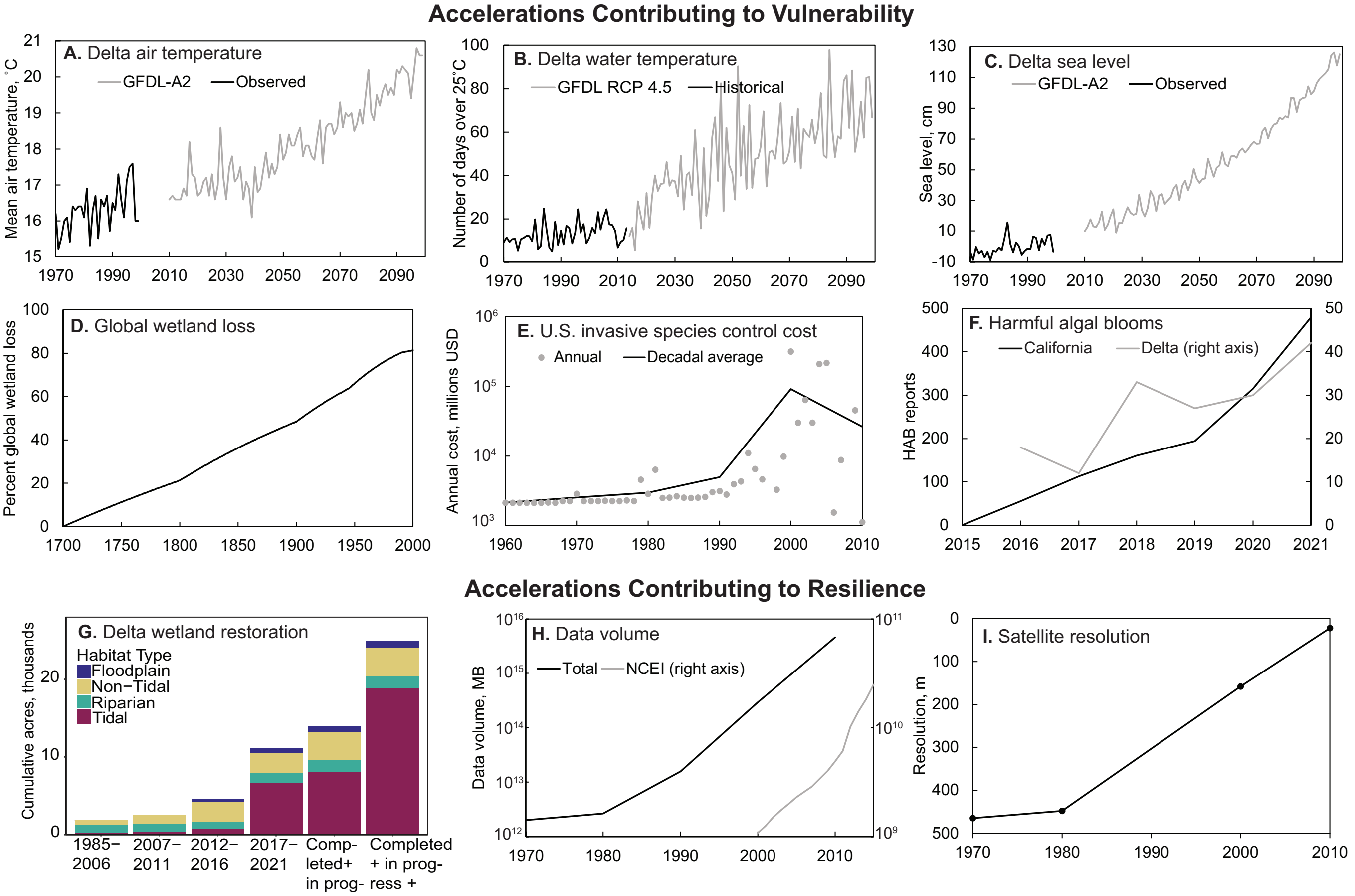

Figure 2 Cross-scale great accelerations relevant to this edition of SBDS. Note that the *x*-axis scale differs among plots. Data sources and additional information for figure panels are as follows: (**A**) Observed and projected (using the GFDL climate model with the A2 emissions scenario) annual mean Delta air temperature, modified from Cloern et al. (2011); (**B**) Observed and projected (using the GFDL climate model with the RCP 4.5 emissions scenario) days per year with mean Delta water temperature that exceed 25 °C, from Wulff et al. (2021); (**C**) Observed and projected (using the GFDL climate model with the A2 emissions scenario) mean Delta sea level, modified from Cloern et al. (2011); (**D**) Estimated global wetland loss since 1700 AD, extrapolated from average rates of wetland loss, modified from Davidson (2014); (**E**) Annual and decadal average costs of invasive species control in the US, modified from Crystal-Ornelas et al. (2021); (**F**) Reports of harmful algal blooms in the Freshwater Harmful Algal Bloom Reports database (SWRCB 2022); (**G**) Cumulative acres of wetland habitat restoration in the Delta, with the final two bars also showing in-progress and planned restoration projects as of January 1, 2022, from Chapple et al. (2022, unreferenced, see "Notes"); (**H**) Growth of total data volume, from Runting et al. (2020) and environmental data volume stored at NOAA's National Centers for Environmental Information (NCEI; modified from Peng et al. 2016); (**I**) Decadal changes in satellite resolution, from Runting et al. (2020).

in control and damage costs in North America alone between 1960 and 2017 (Crystal–Ornelas et al. 2021; Figure 2E). Meanwhile, temperature changes, changing patterns of precipitation, and nutrient enrichment interact in complex ways to produce widespread increasing trends in freshwater harmful algal bloom (HAB) occurrence (Paerl and Paul 2012; Ho et al. 2021), as well as localized increasing trends in marine HAB occurrence (Gobler et al. 2017; Hallegraeff et al. 2021).

Ecosystem Services and Disservices: Quantifying Effects on Human Communities

While great accelerations are useful for visualizing drivers or symptoms of environmental change, ecosystem services and disservices are useful for quantifying how those changes affect human communities. The first widely popularized use of the term "ecosystem services" dates to the Millennium Ecosystem Assessment summary reports (MEA 2003), which defined ecosystem services as "the benefits people obtain from ecosystems." This definition, in turn, had its roots in earlier descriptions that recognized ecosystem services as originating from both highly human-modified and highly unmodified ecosystems (Costanza et al. 1997) and encompassing both tangible and intangible benefits (Daily 1997), including maintenance of biodiversity and production of ecosystem goods. Defining and categorizing ecosystem services (e.g., mitigation of the effects of floods and droughts, reduction of erosion along riverbanks and coastlines, soil formation and maintenance of soil fertility, and maintenance of a diverse gene pool; Harte 2001) effectively established a framework for consistently recognizing, classifying, quantifying, and monetizing them in a wide range of environments (Fisher et al. 2009; Gómez–Baggethun et al. 2010; Shapiro and Báldi 2014). Essentially, the concept of ecosystem services provides a Western-centric, capitalistic means of quantifying the value of ecosystem functions to human communities (Gómez–Baggethun and Ruiz–Pérez 2011; Silvertown 2015), which, though widely criticized (e.g., McCauley 2006; Lyytimäki et al. 2008; Carpenter et al. 2009), has proven useful in the assessment of trade-offs and effects of alternative human actions (or inaction) in ecosystems, as well as in the development of integrated models (White et al. 2012; Boumans et al. 2015; Costanza et al. 2017). In particular, Granek et al. (2010) opine that for coastal ecosystems that lie at the interface of marine and terrestrial ecosystems and provide diverse functions that affect humans and non-humans, ecosystem services serve as a "common language" for ecosystem-based management.

"Ecosystem disservices," defined in Table 1, is a concept that addresses one of the reigning critiques of the ecosystem services concept: that it focuses only on how ecosystems positively affect human communities while blindly ignoring ecosystems' negative or hazardous effects (some of which arise from the very provisioners of ecosystem services; Rasmussen et al. 2017), which should be accounted for and monetized in environmental decision-making (Lyytimäki and Sipilä 2009; Dunn 2010; Schaubroeck 2017). Commonly invoked examples of ecosystem disservices include eutrophication (Swain et al. 2013), invasive species (Shackleton et al. 2016; Milanović et al. 2020; Tebboth et al. 2020), and HABs (Shackleton et al. 2016). Although the term "ecosystem disservices" focuses on how these phenomena affect human communities, it is widely recognized that many of these disservices have their ultimate origins in human actions or modifications to ecosystems (Lyytimäki and Sipilä 2009).

Table 1 Definitions of "ecosystem disservices"

Definition	Source
Absence or diminishment of valued ecosystem service or biodiversity	Chapin III et al. (2000)
Negative effects of ecosystem change	Balmford and Bond (2005)
Functions or properties of ecosystems that cause effects perceived as harmful, unpleasant, or unwanted	Lyytimäki (2015)
Ecosystem goods and services that undermine or harm human well-being	Shackleton et al. (2016)
The processes and functions that affect humans in "negative" ways, causing damages and costs	Costanza et al. (2017)

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In addition to providing an organizational framework to quantify trade-offs of actions or inaction for ecosystems (e.g., Zhang et al. 2007; Escobedo et al. 2011; Campagne et al. 2018), the concept of ecosystem disservices can be useful for understanding human behavior patterns. Specifically, Blanco et al. (2019) claims that ecosystem disservices may often serve as a stronger motivator of human behavior than ecosystem services, and that, under certain circumstances, reducing ecosystem disservices may be more effective than enhancing ecosystem services to promote nature-friendly behavior. For example, in many circumstances, managing invasive species is economically preferable to paying for habitat restoration (Shackleton et al. 2016). Ecosystem disservices have likewise provided a useful framework for measurement in the environmental justice movement (London et al. 2018; Calderón–Argelich et al. 2021). The concept has been found to be particularly relevant in the urban setting, where ecosystem disservices disproportionately affect disadvantaged communities (Escobedo et al. 2011; von Döhren and Haase 2015; von Döhren and Haase 2019).

Like ecosystem services, the concept of ecosystem disservices has been critiqued (see Shapiro and Báldi 2014; Villa et al. 2014; Shackleton et al. 2016; Saunders 2020). Many of these critiques acknowledge how the term “ecosystem disservices” implies a causal origin in the ecosystem, which displaces attention—potentially harmfully (from a conservation perspective)—from the human activities that may provide the root cause of the disservice. Additionally, the binarization of ecosystem functions into services and disservices may impede recognition of their dynamism; indeed some functions and characteristics commonly shift between services and disservices, or simultaneously both benefit and burden human communities (Rasmussen et al. 2017).

How Ecosystem Services and Disservices Modulate Great Accelerations in the Delta

The Delta literature is rich in its discussion of ecosystem services and disservices. Examples of ecosystem services include carbon sequestration in restored wetlands (Valach et al. 2021), water supply and hydropower (Roe 2011), detrital and algal material fueling food webs that ultimately sustain commercial fisheries (Sobczak et al. 2002), and modulation of water quality by restored and constructed wetlands (O’Geen et al. 2007; Kasak et al. 2020). Meanwhile, examples of disservices include methane release by constructed wetlands (Kasak et al. 2020) or flooded agricultural fields (Anthony and Silver 2021) and the spread of invasive submerged aquatic vegetation (SAV; Santos et al. 2016), such as water hyacinth (*Eichhornia crassipes*), which further limits ecosystem services (Hopper et al. 2017).

Much discussion of ecosystem services and disservices in the Delta focuses on primary producers and how they serve as drivers or symptoms of great accelerations at the local and global scale. Approximately equivalent to the global-scale level (Figure 2D), wetland loss within the Delta (i.e., an estimated 77% of hydrologically connected habitat) translates into a 94% reduction in net primary production (Cloern et al. 2021). Further reductions in energy supply to food webs result from extensive replumbing of the Delta, upstream effects from dams and gold mining, water diversions, alterations of the seasonal hydrograph, and non-native species invasions, including that of the clam *Potamocorbula amurensis* in the 1980s, which nearly eliminated phytoplankton blooms in the lower estuary (Alpine and Cloern 1992). The cascading and compounding effects of this transformation are enormous. Loss of phytoplankton blooms in the lower estuary caused zooplankton populations to plummet (Kimmerer and Orsi 1996; Moyle 2002). The clearing water column, in turn, opened niches for IAV, facilitating its expansion within open-water habitats (Conrad et al., this issue), where it provides rearing habitat for non-native predatory fish (Conrad et al. 2016). The decline in food supply from wetland habitat loss and loss of phytoplankton blooms, together with declining habitat suitability, are considered to be important contributors (Winder and Jassby 2011; Kimmerer et al. 2012) to the phenomenon termed the Pelagic Organism Decline, which describes the step-like decline in four pelagic fish species observed in

2002, including the federally endangered Delta Smelt (Sommer et al. 2007). Meanwhile, as a separate symptom of the great accelerations, warming temperatures and anthropogenically-altered seasonal inflows have contributed to the increasing incidence of HABs observed in the Delta (Figure 2F; Paerl et al. 2018; Kudela et al., this issue). Once established, these blooms appear resilient to interannual variability in climatic conditions (Lehman et al. 2020) and increasingly affect human communities through effects on food sources (e.g., fishery closures), recreation, and health.

However, because of the ecosystem services they provide, the Delta's primary producers will also play a key role in mediating great accelerations both locally and globally. "Nature-based solutions" such as wetland restoration, which are themselves on an accelerating trajectory (Figure 2G), can reverse the anthropogenically-caused loss of key ecosystem services in the Delta (Sloey et al. 2015). Broadly, wetland restoration and hydrologic reconnection can provide meaningful subsidies for estuarine food webs; in the Delta, meeting wetland restoration targets could result in recovery of 12% of the lost historical net primary production, equating to a doubling of carbon flow to herbivores and a tripling of detritus production (Cloern et al. 2021). Additionally, carbon sequestration in the soils of created or managed wetlands (Windham–Myers et al. 2018; Wang et al. 2021; Windham–Myers et al., this issue) has been proposed as a strategy to ameliorate excess CO_2 in the atmosphere globally and within the Delta. Another strategy that focuses on primary producers to mediate great accelerations is to stimulate phytoplankton blooms through managed flow pulses at times critical for recovery of endangered fishes (Williams et al. 2009; Sommer et al. 2020; Frantzich et al. 2021).

In addition to the increasing deployment of nature-based solutions, other human-driven accelerations may contribute to management of primary producers for resilience in the Delta. The technological revolution has produced an exponential growth in environmental data resources and sensing capabilities both globally (Figures 2H–2I) and within the Delta (Hestir and Dronova, this issue). These technological advances have fueled opportunities to assess the landscape-scale effects of restoration and other management actions (Taddeo and Dronova 2019), visualize rapidly changing bloom conditions (Ryan et al. 2014; Fichot et al. 2016; Bracher et al. 2017), and develop operational ecological forecasts (Dietze et al. 2018) for phenomena such as HABs.

This edition of SBDS is timely, because the ecosystem services and disservices of primary producers are interwoven into many of the biggest contemporary management topics, questions, and projects in the Delta. For example, prevention and control of invasive species remains one of the costliest (Conrad et al., this issue) and biggest management issues in the Delta, with early detection and rapid response an increasingly prominent need as climate change brings new invaders (DISB 2021). The California EcoRestore project, which proposes 121 km^2 of habitat restoration in the Delta and Central Valley, and the Delta Plan's targeted 274 km^2 of habitat restoration, will serve as large-scale experiments on how humans can promote ecosystem services of food web supplementation and carbon sequestration while minimizing trade-offs and disservices, such as creating opportunities for invasive species (Christman et al., this issue) or generating methane (Windham–Myers et al., this issue). Meanwhile, the Delta recently underwent a major change in nutrient loading when the new tertiary treatment system for the Sacramento Regional Sanitation District's wastewater treatment plant (Figure 1) came online in 2021. The foundational information provided in this edition of SBDS—about how ecosystem services and disservices of primary producers in the Delta interact, respond to changes and environmental drivers, and affect human communities—will provide a basis for anticipating the effects of these and other planned management actions.

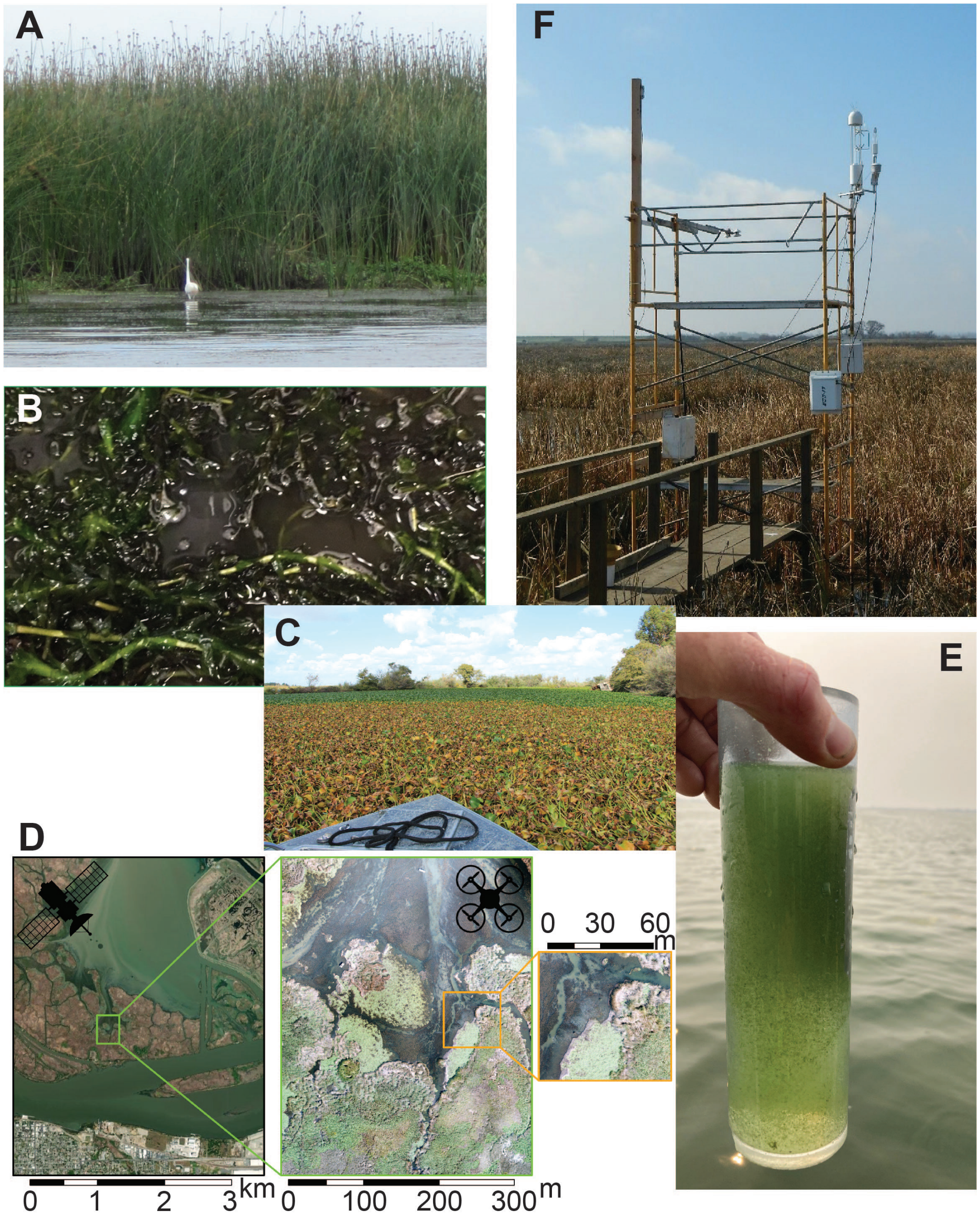

Figure 3 This edition of SBDS in pictures (*counterclockwise, from upper left*): (**A**) Historical ecology (*Boyer et al., this issue*): A glimpse into a typical historical Delta landscape, with tule in the background and pennywort and sago pondweed in the foreground. *Photo: Katharyn Boyer*. (**B**) Ecology of invasive aquatic vegetation (*Christman et al., this issue*): Submerged aquatic vegetation (SAV) like the depicted *Egeria densa* traps sediment effectively, with effects on wetlands that range from the local to the estuary scale. *Photo: Judy Drexler*. (**C**) Control of invasive aquatic vegetation (*Conrad et al., this issue*): Treated (*foreground*) and untreated (*background*) water hyacinth (*Eichhornia crassipes*). *Photo: Maggie Christman*. (**D**) Remote sensing of primary producers (*Hestir and Dronova, this issue*): Remote sensing at multiple scales can enrich the mapping, modeling, and measurement of primary producers. Here, a tule marsh complex with water primrose infestation in the Sherman Island Wildlife Area is seen from space-based satellite sensors (*left*) and from a camera mounted on an unoccupied aerial system (*right*). *Aerial photos and insets: Bailey Morrison*. (**E**) Harmful algal blooms (*Kudela et al., this issue*): A water sample extracted from Franks Tract shows evidence of a cyanoHAB event. *Photo: Keith Bouma-Gregson*. (**F**) Carbon sequestration and subsidence reversal (*Windham-Myers et al., this issue*): A flux tower with sensors for monitoring carbon fluxes at Twitchell Island, a long-term research site for wetland carbon sequestration. *Photo: Dennis Baldocchi.*

SCOPE, HIGHLIGHTS, AND SYNTHESIS

Topics and Cross-Cutting Themes

The State of Bay–Delta Science for 2022 reflects both the timely management needs and the topical areas that have seen the most scientific research progress over the past decade. Specifically, in this edition we review the ecosystem services of subsidence reversal and carbon sequestration (Windham–Myers et al., this issue) and primary production supply to food webs (Boyer et al., this issue). We examine the ecosystem disservices of HABs (Kudela et al., this issue), evaluate the ecology (Christman et al., this issue) of aquatic vegetation, and describe the history and science of management and control (Conrad et al., this issue) of invasive aquatic plants (Figure 3). Last, we survey the emerging remote sensing methods employed to quantify the spatial distribution and magnitude of many of these ecosystem services and disservices (Hestir and Dronova, this issue).

The most important findings from these reviews (see also Box 1) highlight themes that cut across the individual papers and the ecosystem services and disservices that they profile. One theme pertains to how these ecosystem services and disservices feed back to and influence other parts of the Delta social-ecological system, with climate as a common driver–response variable (Figure 4). Related to these connections, other key findings disrupt conceptual paradigms about and deepen our understanding of the ecosystem services and disservices themselves, including their interactions. A third and fourth theme are the importance of scale for the Delta and the importance of understanding geographic connections to the watershed and lower estuary. These connections are important for predicting species invasions (Christman et al., this issue) and tracking the down-estuary movement of cyanotoxins and up-estuary movement of potential HABs-forming organisms (Kudela et al., this issue).

Here, we take a deeper dive into the insight that emerges when looking across contributions, specifically focusing on the first two themes (feedback, with climate as a governing variable, and disruption of conceptual paradigms), to better understand the connections between the primary producers' ecosystem services and disservices in the Delta (Figure 4). Using Figure 4 as a guide, we discuss the connections that emerge from each major topic (*boldface* in the figure), relating the emergent insight to the cross-cutting themes. The state of the science is such that these connections are generally understood at a conceptual level (i.e., existing research points to the existence of the connections and the direction of influence), though, despite progress that is underway, important gaps remain in quantifying these interactions. As will be discussed, these knowledge gaps constitute an important direction for future research that may be critical for Delta management under future climate extremes.

Climate as a Governing Variable

Climate is a central variable at both a local and global scale, which offers both positive and negative feedback as part of the ecosystem services and disservices of primary producers. Changing climate locally creates new opportunities for IAV to invade (Christman et al., this issue) and HABs to proliferate (Kudela et al., this issue), and it may threaten planned wetland restoration with inundation (Stralberg et al. 2011). However, at the global scale, climate is not purely a driver but could also respond to human–ecological actions in the Delta, as planned wetland restoration sequesters carbon from the atmosphere (Windham–Myers et al., this issue). As Windham–Myers point out, however, these actions may also, at least initially, participate in a positive global feedback loop with climate warming through releases of methane (i.e., double-sided red arrows connecting CH_4 to climate, Figure 4), a more potent greenhouse gas than CO_2 on a per-molecule basis. Speaking to the ecosystem service critique that binarization of ecosystem functions into services and disservices ignores their dynamism (Rasmussen et al. 2017), this finding disrupts the paradigm that wetland restoration chiefly generates ecosystem services. Windham–Myers instead discuss how restored wetlands may shift from net methane sources to sinks over multi-decadal time-scales. Notably, though, even immediately after restoration, the

BOX 1

Key Findings in the State of Bay-Delta Science for 2022

Historical ecology of aquatic vegetation: Boyer et al.

- Increases in open water and proliferation of invasive aquatic vegetation in the last 20 years led to a doubling of the net primary production of floating and submerged aquatic vegetation relative to the historical period (circa 1850).
- Projected future changes will alter net primary production by floating and submerged aquatic vegetation and thus food web support, but effects will be minimal compared to recent interannual variability in their net primary production.

Ecology of invasive aquatic vegetation: Christman et al.

- Invasive aquatic vegetation affects every aspect of the physical and biotic environment, including both ecosystem properties and processes.
- Invasive submerged aquatic vegetation stores carbon on the landscape but can also block sediment from accreting in marshes, reducing their resilience to sea-level rise.
- Key remaining knowledge gaps in understanding invasive aquatic vegetation's effects on Delta ecosystems include their roles in nutrient cycling, evapotranspiration, carbon and sediment dynamics, and fish populations and distributions.

Control of invasive aquatic vegetation: Conrad et al.

- Control efforts for submerged and floating aquatic vegetation have been ongoing in the Delta since 1983 and rely primarily on herbicides, with mixed results because of the tidal dynamics of the Delta. Parallel investment in biological control agents has yielded no appreciable control benefit, and control efforts for emergent aquatic vegetation invaders have been uncoordinated.
- The science assessing target and non-target effects of control efforts in the Delta is nascent, and further advancement requires continued collaboration between regulating entities and those leading and innovating control measures.
- Setting quantitative targets for IAV control informed by social and ecological assessments of acceptable levels of IAV coverage is critical for strategic planning and must be accompanied by a robust monitoring program.

Remote sensing of primary producers: Hestir and Dronova

- Remote sensing supports monitoring the distribution and biomass of primary producers and modeling Delta primary productivity.
- Maximizing the benefits offered by a growing deluge of open and accessible new sensor data—including unoccupied aerial vehicle imaging, space-based imaging spectroscopy, dual-band synthetic aperture radar and LiDAR—requires investment and greater capacity-building, coordination, and standardization of data-management and data-sharing protocols.

Harmful algal blooms: Kudela et al.

- Harmful algal blooms and associated toxins have emerged as a concern relatively recently in the Bay–Delta, and toxins from marine and freshwater are often co-located.
- There is increasing evidence for chronic and acute accumulation of a variety of toxins at low trophic levels, with likely transfer to higher trophic organisms, including humans, through the food web.
- Monitoring and mitigation in a changing climate require better coordination among researchers and agencies and a focus on restoring/maintaining ecosystem resilience.

Carbon sequestration and subsidence: Windham-Myers et al.

- Restoring aquatic habitats can reduce current greenhouse gas emissions while providing additional ecosystem benefits to wildlife and water management.
- Hydrologic management (through agriculture, subsidence reversal, and tidal reconnection) is the dominant pathway to increased carbon sequestration and reduced methane emissions.
- The largest uncertainties in estimating the contributions of restored wetlands to market-based climate mitigation estimates lie in projections of aquatic habitat type, as affected by climate- and operations-driven changes in water flows.

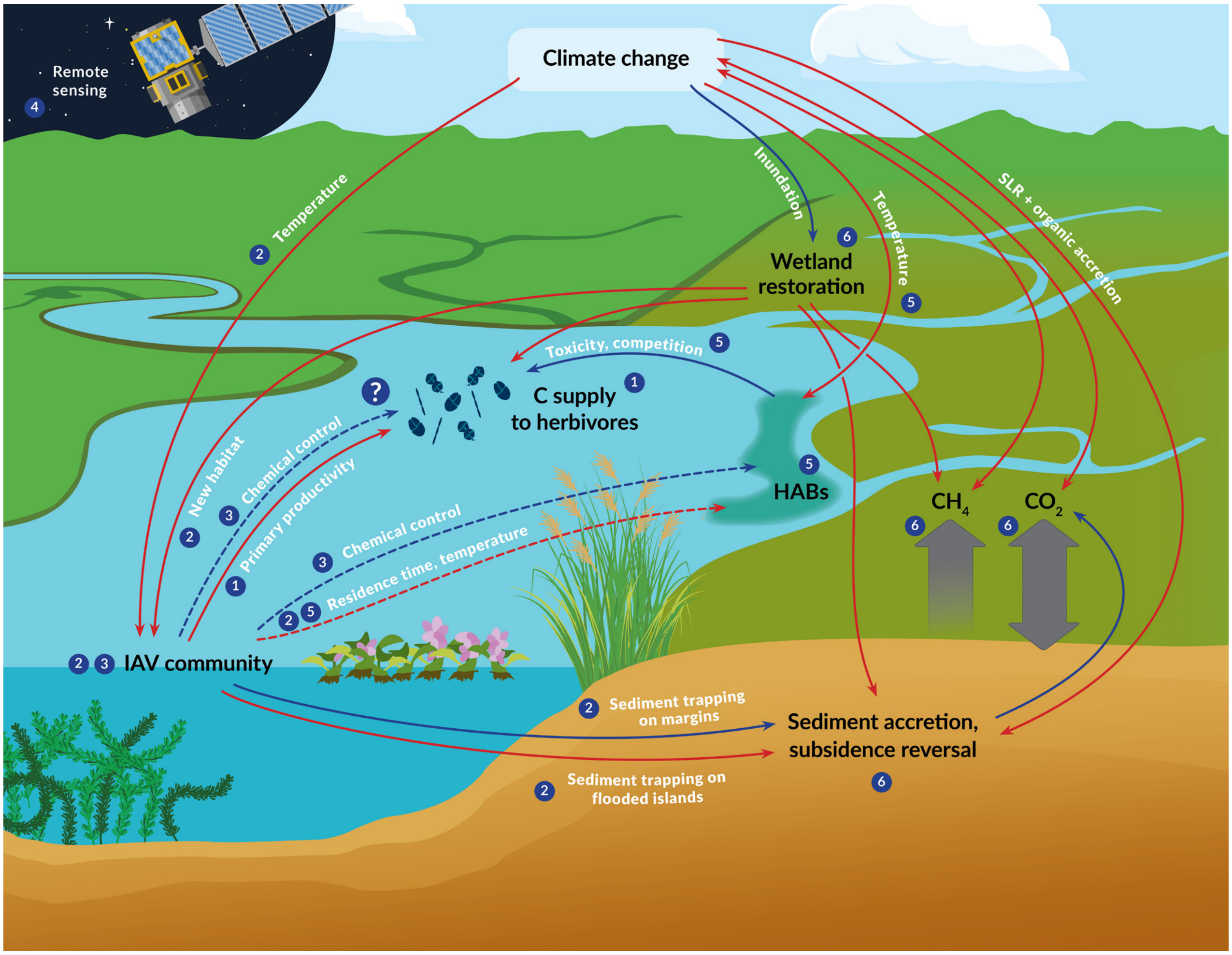

Figure 4 Oblique view of a Delta landscape, depicting the primary producer communities, functions, and processes addressed in this edition of SBDS. *Labeled entities* are topics discussed in the collection of papers, and the graphic is not interpretable as a comprehensive conceptual model of the system. The *arrows* depict feedbacks and relationships among the depicted entities, with *red arrows* indicating a positive relationship (i.e., whereby an increase (or decrease) in the driver results in an increase (or decrease) in the response) and *blue arrows* indicating a negative relationship. *Dashed arrows* indicate a hypothesis/knowledge gap. Where needed for clarification, the mechanism behind the depicted driver/response relationship is indicated on the *arrow*. The *circled numbers* indicate the chapter or chapters in which the depicted relationship, process, or primary producer community is discussed: (1) Boyer et al.; (2) Christman et al.; (3) Conrad et al.; (4) Hestir et al.; (5) Kudela et al.; (6) Windham–Myers et al. *Credit: Illustration by Vincent Pascual, California Office of State Publishing.*

magnitude of the warming contribution of these greenhouse gas releases (GHG) is most commonly smaller than that of the previous (i.e., non-restored) land type.

IAV as a Disruptive Agent in Concepts of Ecosystem Services and Disservices

Proliferation of IAV has pervasive and diverse effects on the Delta (Figure 4) that further underscore the disruptive theme that agents of ecosystem disservices may also provide ecosystem services, and vice-versa. For example, wetland restoration projects may create opportunities for IAV to proliferate (Christman et al., this issue). IAV traps sediment efficiently and may curtail sediment deliveries to wetlands, potentially threatening the persistence of wetland restoration sites. A clear next step is to evaluate whether sediment budgets will be sufficient to sustain proposed restoration projects under future sea-level-rise scenarios (e.g., Ganju 2019), and whether external (e.g., dredged, biosolids) supplementary sediment inputs may be needed, as in the San Francisco Bay (Foster–Martinez and Variano 2018; Boyd et al. 2019). On the other hand, SAV on flooded islands may promote carbon sequestration and subsidence reversal, given appropriate sediment management (Christman et al., this issue). Meanwhile, with the widespread historical loss of wetlands in the Delta, floating and aquatic vegetation has become a much more important contributor of carbon to food webs (Boyer et al., this issue). Specifically, with the proliferation of IAV, contributions of SAV and floating aquatic vegetation (FAV) communities to overall primary productivity and Delta food webs have doubled over the past 20 years (Boyer et al., this issue). Control of IAV may diminish these contributions (Conrad et al., this issue), but the effect is likely to be small relative to the high interannual variability in the primary productivity of FAV and SAV (Boyer et al., this issue). An ancillary benefit of controlling IAV with fluridone or other herbicides may be a local reduction in the rate of growth of HAB-forming cyanobacteria, though desirable phytoplankton taxa may also be affected (Lam et al. 2020; Conrad et al., this issue). Intact patches of SAV, however, may slow velocities and increase residence times (Christman et al., this issue), potentially creating more favorable conditions for HABs (Kudela et al., this issue).

The potential connection between IAV, associated residence times, and HABs (Figure 4) is arguably an important interaction to quantify through further modeling and empirical studies. An illustrative anecdote is that of Franks Tract during drought conditions. During the drought of 2015, a rip-rap salinity barrier was erected on the West False River, just downstream of Franks Tract, to minimize saltwater intrusion into the Central and South Delta. The resulting longer residence times in Franks Tract were associated with the proliferation of *Egeria densa* and other IAV that persisted once the salinity barrier was removed, but no HABs were observed (Kimmerer et al. 2019). When the salinity barrier was installed for a second time in 2021, however, a HAB event was triggered (Hartman et al. 2021). An important difference between 2015 and 2021 is that a bed of IAV was established in 2021, which possibly contributed to increased residence time and more favorable conditions for HABs in 2021, though this hypothesis was not tested. Broadly, improved understanding of the connections between IAV, residence times and temperatures, and HAB potential may help to prioritize IAV control and to mitigate adverse human and ecological effects of managing salinity during droughts.

Connections Affecting Delta Food Webs: Wetland Restoration, HABs, and Carbon Supply to Herbivores

Of all the connections depicted in Figure 4, the best quantified are the connection between wetland restoration and carbon supply to herbivores at the base of the food web (see Cloern et al. 2021) and that between IAV and carbon supply. Boyer et al. (this issue) estimate that controlling FAV would diminish carbon supply from aquatic vegetation to herbivores by a median of 11%, though response of FAV to control measures has yet to be well quantified (Conrad et al., this issue). As wetlands are restored and associated IAV is controlled system-wide, it will be possible to verify these estimates with remote-sensing-derived computations of gross primary productivity (Hestir and Dronova, this issue). Meanwhile, Kudela et al. (this issue) describe how long-term, Delta-wide increases in the dominance of cyanobacteria diminish food quality for herbivorous grazers (Winder et al. 2017) and are associated with less productive food webs, though there are knowledge gaps in quantifying the causal effects of HABs on food web productivity. How HABS may negatively affect Delta food webs is also consistent with other [negative] mechanisms observed elsewhere (reviewed in Burkholder et al. 2018), including shading of the water column, competitive exclusion of preferred taxa, and reduction in the abundance of herbivores through toxic effects or anoxia.

Feedback Between Primary Producers and Human Communities

Interactions with humans pervade the system depicted in Figure 4, although human communities are not explicitly shown. In this issue, Conrad et al. discuss the economic costs and target and non-target effects of controlling IAV, while Windham–Myers et al. discuss the quantitative role of different types of agricultural or wetland management interventions within different land-use/-cover categories in carbon-mitigation markets, pointing out that gains are likely to be small unless conventional agricultural practices in the Delta are fundamentally changed. Meanwhile, Kudela et al. review what is known about the health effects of HABs while acknowledging salient gaps in this understanding. In general, however, many of the social-ecological connections remain under-explored. More broadly, Shackleton et al. (2016) highlight a pervasive need to consider trade-offs between ecosystem services and disservices at multiple scales.

In addition to experiencing effects, humans can also strongly control the ecosystem services and disservices considered here, such as, for example, manipulating water levels to control the release of methane or nitrous oxide from managed wetlands (Windham–Myers et al., this issue). However, experimental tests of innovative new approaches are needed. For example, IAV chemical control techniques used in lentic systems have, at best, ephemeral success in the Delta, particularly for SAV, underscoring the need for innovation (Conrad et al., this issue). Similarly, techniques used to mitigate HABs elsewhere may not be scalable to the Delta (Kudela et al., this issue), and hence a combination of innovation, synthesis of lessons learned from other systems, and targeted experimentation are needed to develop HAB mitigation plans. On the other hand, the proliferation of environmental data made possible through technological advances can help minimize adverse effects on humans by facilitating the development of HAB forecasts that would support the timeline to deploy health advisories or modify drinking-water intakes, or that could inform early detection and rapid response actions to manage invasive species (Hestir and Dronova, this issue). These data sets may also be used to document changing habitat in response to sea level rise and management actions, and to predict gross primary productivity and net ecosystem exchange across the scale of the Delta via remote sensing (Hestir and Dronova, this issue). How different stakeholder and community groups use these data, and how decisions on managing and controlling these ecosystem services and disservices are made, given uncertainty, remains another open question that underlies a more complete understanding of this social-ecological system.

Knowledge Gaps

While Figure 4 reflects the current state of understanding reviewed in this edition of SBDS, some clear gaps (i.e., dashed lines) emerge, many of which relate to the role of primary producers in Delta food webs. One of these gaps is understanding detrital contributions of primary producers from the Delta and its watershed to food webs and how the quality of organic matter that originates from different species of wetland macrophytes, FAV and SAV, and algal species affects these contributions. Given that heterotrophic energy supplied to the estuary is over five times that supplied autochthonously (Durand 2015), this knowledge gap is potentially significant, which is further underscored by findings from isotopic food web models that detrital energy transfer plays a substantial role (Howe and Simenstad 2011). In general, drivers of the estuarine food web are poorly understood in the Delta, leading to prominent calls for food web modeling (DISB 2021) and synthesis (Brown et al. 2016). Such food web modeling would help planners anticipate how proposed wetland restoration at large scales may affect fish populations, and could aid in the design of flow actions (e.g., Frantzich et al. 2021) intended to increase food resources for fish.

CONCLUSIONS

In this edition of SBDS, we have focused on those aspects of Delta primary producers that are most aligned with management needs by framing the issue through the lens of ecosystem services and disservices. Primary producers in the Delta infuse energy into the food web; regulate carbon balances at multiple scales; provide habitat; and influence human health, recreation, and livelihoods for better (services) or worse (disservices). They are subject to a wide array of physical, biological, and social drivers, and also shape the physical (i.e., as "ecosystem engineers"; Christman et al., this issue), biological, and social environment in a complex set of interactions and bi-directional feedbacks. As a result of this web of drivers and feedbacks, primary producers in the Delta have undergone long-term, interannual, and intra-annual change in abundance and community composition (Boyer et al., this issue), making their management a continuously moving target (Christman et al., this issue). Managing primary producers for desired outcomes, therefore, requires adopting a complex-systems approach that considers feedbacks and multiple scales.

This edition makes several key contributions to providing a scientific underpinning for managing the ecosystem services and disservices of primary producers. **First**, it helps untangle the web of complex controls by defining the key drivers that must be considered in estimating or forecasting ecosystem services (e.g., carbon sequestration; Windham–Myers et al., this issue) or disservices (e.g., HABs; Kudela et al., this issue). It also highlights the emerging technology and analyses that could be used in models that quantify these services or disservices (Hestir and Dronova, this issue). **Second**, through new syntheses presented here, it is now possible to assess the cumulative effects of wetland restoration, IAV management, or alternative strategies for managing wetland and agricultural land on Delta-wide carbon balances and carbon inputs to food webs—a necessary step toward trade-off assessment and Delta-wide planning for carbon neutrality and species recovery (Windham–Myers et al., this issue; Boyer et al., this issue). **Third**, this edition also lays a conceptual foundation for estimating the cumulative effects of wetland restoration and IAV management on Delta sediment balances and sea-level-rise resiliency strategies (Christman et al., this issue). **Fourth**, it compiles specific science-based management recommendations that include the following:

1. Establishment of quantitative targets for IAV controls (Conrad et al., this issue) and HAB toxins (Kudela et al., this issue),

2. Development of more effective monitoring strategies for HABs (Kudela et al., this issue) and IAV (Conrad et al., this issue),

3. Expansion of the use of specific techniques to limit CO_2 and CH_4 emissions, for example:
    - Flooding agricultural fields,
    - Intermittently draining rice fields,
    - Developing new impounded wetlands for subsidence reversal, tidal restoration to impounded wetlands, and expanding riparian forest. (Windham-Myers et al., this issue)

Finally, this edition highlights key research and implementation gaps. Some of these gaps are specific to individual ecosystem services and disservices, such as carbon flux data gaps in freshwater tidal marshes and SAV and FAV habitats (Windham–Myers et al., this issue) or the need to test new techniques for managing IAV (Conrad et al., this issue). However, many of the gaps lie in system-level understanding, including the need to understand the effects of Delta-scale sediment and vegetation interactions on wetland persistence (Christman et al., this issue), to model how changing detrital and autochthonous inputs affect all levels of the food web (see "Knowledge Gaps"), to quantify how changing Delta inflows drive HABs (Kudela et al., this issue) and primary productivity in general (Boyer et al., this issue), and to evaluate effects and trade-offs of different suites of management actions on human communities (see "Feedback between Primary Producers and Human Communities"). Such multifaceted understanding will ultimately enable the community of Delta scientists and managers to address questions like the following:

> *"What is the relative value in investing in IAV control for fish vs. promoting wetland restoration?"*

> *"How might alternative strategies to restore wetlands affect Delta sediment and carbon balances, IAV coverage, and economic and recreation opportunities for human communities?"*

The fundamental research advanced in this edition of SBDS is foundational to such a trade-off assessment and will help meet related research priorities in the 2022–2026 Science Action Agenda (DSC 2021).

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