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# Briefing Paper: Exploring scientific and management implications of upper trophic level food webs in the Delta

An assessment of the scientific needs  
to inform management actions



**Delta  
Independent  
Science Board**

DELTA STEWARDSHIP COUNCIL

Created by the Delta Reform Act of 2009 and appointed by the Delta Stewardship Council, the Delta Independent Science Board is a standing board of nationally and internationally prominent scientists that provide oversight of the scientific research, monitoring, and assessment programs that support adaptive management of the Sacramento-San Joaquin Delta through periodic reviews.

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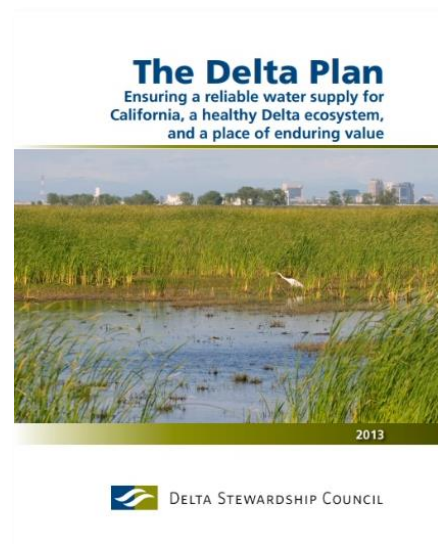
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*Juvenile Salmonid Collection System. Photo Credit: DWR.*

## Background and Purpose

California's Sacramento-San Joaquin Delta (the Delta) is expected to experience significant environmental modifications in the coming decades. The modifications are largely driven by climate change, sea level rise, major flooding and storms, non-native species, water supply diversions, shifts in land use, restoration actions, and a host of other influences originating from a growing human population (Norgaard et al. 2021). Understanding and predicting how those drivers affect the abundances of fish species and ecosystem sustainability are at the core of Delta policy and management, and are critical to achieving the Delta Plan's coequal goals of providing a more reliable water supply and protecting, restoring and enhancing the Delta ecosystem in a manner that protects and enhances the Delta as a place (Delta Stewardship Council and Delta Science Program 2022).



Understanding food-web interactions and developing food-web models for the Delta are key recommendations from both the Strategic Science Needs Assessment (DPIIC and Delta ISB 2021) and the Delta Independent Science Board's (Delta ISB) Non-Native Species Review (Delta ISB 2021). A quantitative understanding of food-web interactions is needed to evaluate the impact of management actions aimed at supporting fish populations under climate and other system-wide changes. The Delta ISB food web review aims to evaluate existing information on Delta food webs, to identify informational gaps impeding progress, and to link the resulting knowledge to inform management actions. The Delta ISB contends that a better understanding of trophic processes will not only improve management actions and the assessments of management impacts on individual species; it is essential for multispecies and ecosystem management for the Delta.

The Delta ISB is reviewing the contemporary and emerging science underpinning the current management and understanding of food webs in the Delta. This review is focused on food-web interactions at upper trophic levels (primarily fishes) to elucidate connections that can benefit individual-species and ecosystem-based management of the Delta. As part of this review, the Delta ISB is hosting a two-day workshop November 8 and 9, 2023 in Sacramento, California (see [Save-the-Date](#)). The workshop will bring together scientists, managers, and many other members of the Delta community with extensive experience in food-web dynamics, ecology, and species management. Workshop participants will assess the importance of food-web interactions in the Delta, and identify where improved understanding and tools (e.g., food-web models) might substantially improve predictions of an individual species' responses to environmental drivers and to management actions.

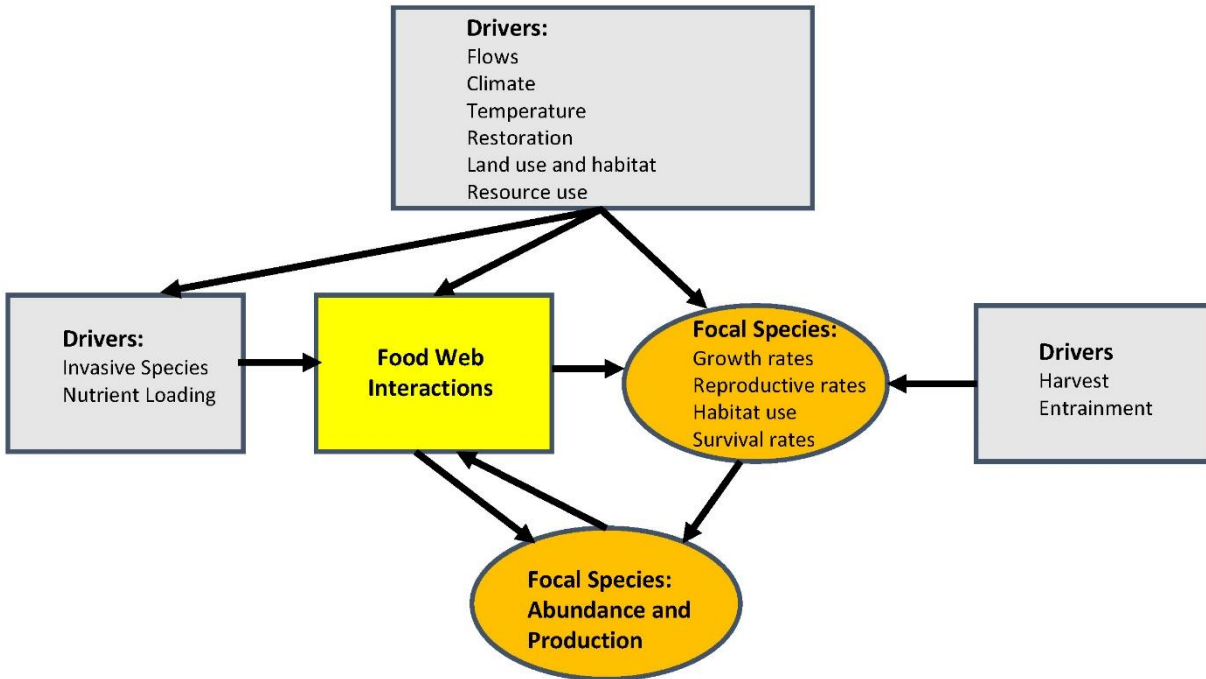
The workshop will inform a Delta ISB review on how a contemporary understanding of upper trophic levels dynamics could add new capabilities to anticipate fish population changes in response to management and environmental drivers. Specifically, the review will evaluate the degree to which the inclusion of food-web interactions across trophic levels might benefit and facilitate ecosystem management in the Delta, and whether available data and science can support the development of such tools. This briefing paper is intended to introduce this topic relative to the Delta and to provide workshop attendees with a common baseline of information. The briefing paper is not intended to be a comprehensive review of the literature on this topic.



*Person fishing along a section of the San Joaquin River near Webb Tract. Photo Credit: DWR.*

## Importance of Food Webs to Management

Food webs describe the trophic (feeding) relationships and flows of energy and nutrients among species in an ecosystem. Food-web processes have long been recognized to affect ecosystem functions and link species abundances, ecosystem dynamics, and energy cycling across time and space (e.g., Lindeman 1942). Traditional fish management in the Delta is generally focused on how an individual driver or a combination of drivers (e.g., flow and temperature) directly affects the abundance of a single species. However, a dynamic understanding of food-web interactions is critical to predicting how environmental drivers or management actions might affect an individual species (Figure 1) since these drivers might affect abundances of other species and thus food web dynamics as well (Wootton 1994; Lathrop et al. 2002; Jordán et al. 2006; Vander Zanden et al. 2006; Naiman et al. 2012; Bunnell et al. 2014; de Mutsert et al. 2016; Townsend et al. 2019; Naman et al. 2022). Food-web interactions shift abundances of species since predation causes direct mortality of prey species, and the availability of prey resources affects growth, reproductive capacity and, ultimately, production of the predator population. Food webs are also important components of ecosystem-based management (Korpinen et al. 2022).



**Figure 1:** Conceptual diagram showing the importance of food web interactions (yellow box) to the abundance, function, and biological functions of focal species (orange ovals). Traditional Delta management normally considers both direct and indirect drivers (gray boxes) to a species' population but does not typically consider the effects of drivers to food web interactions, which are necessary for fully understanding changes to a species' abundance and production.

Predicting the impacts of habitat restoration, fisheries, changes in environmental drivers (e.g., climate, changes in nutrient loading, invasive species) and the bioaccumulation of contaminants on species or the ecosystem requires an understanding of food web processes. The degree that food webs need to be understood or quantified depends on the management applications (e.g., see boxes 2-5). Food web interactions can be quantified and visualized in a variety of different ways (see review by Naman et al. 2022). For example, investigations may determine the connections among different species in the ecosystem (structural food web), examine the flow of energy through the ecosystem (bioenergetics), or focus on dynamics that affect abundances of species within an ecosystem (dynamic or functional food webs; Embke et al. 2022).

Information on food-web interactions can be collected through direct sampling of diets, such as stomach (gut) contents, using tracers (e.g., stable isotopes), or through behavioral observations. The specific method employed depends on the scientific or management questions of concern (Box 1; Zale et al. 2013). Many food web studies begin with a conceptual diagram to identify the trophic connections among individual species or taxa groups.

#### **Box 1. Methods to describe food web interactions**

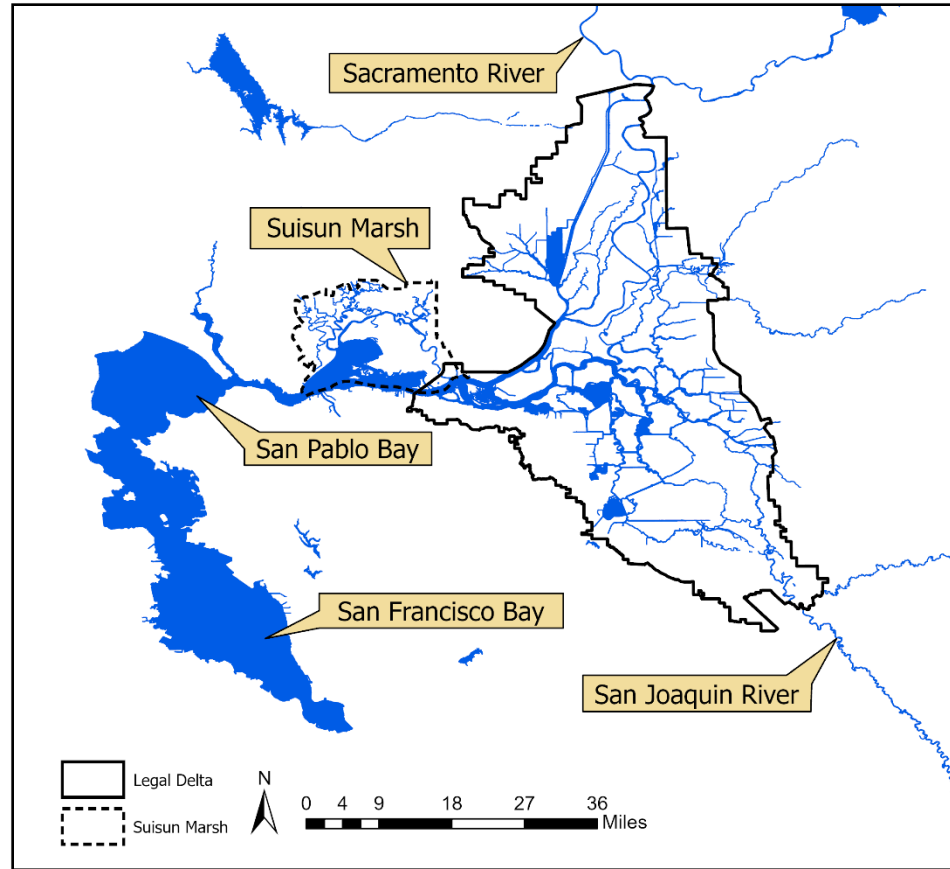
**Stomach content analysis:** Sampling diets of consumers is a way to directly measure what animals are eating and can often be done non-lethally for fish. Presence/absence of prey can either be done by dissecting and identifying stomach contents, or by analysis using eDNA. This method can be time consuming, but can be done without specialized equipment.

**Stable isotope analysis:** Stable isotope analysis relies on the presence of isotopes (primarily of carbon and nitrogen), which are elements that have different numbers of neutrons and are differentially taken up in the transfer of energy through food webs. Stable isotopes are often used to determine the basal source of the food web and to identify the trophic level(s) the animal feeds at. This method requires specialized analytical equipment.

**Behavioral observation:** Behavioral observation of food web dynamics can be done without needing to collect samples of animals or tissues. They can be done actively/visually or determined by placing cameras in set locations for passive measurement. Behavioral

Modeling food web processes encompasses a broad range of approaches (Naman et al. 2022). Approaches range from simple linear models to complex spatially and temporally explicit assemblages of data inputs of species and environmental conditions. Food web modeling has been used to evaluate the effects of environmental drivers (such as salinity, contaminant levels, nutrient loading, and temperature) on species abundance and interactions. Food web models can also reveal the effects of the drivers on species' abundances, predation risk, and contaminant loads, and how they respond to future changes (e.g., Osakpolor et al. 2021; Naman et al. 2022). Importantly, quantitative models with predictive capabilities are especially useful, as they evaluate the influence of environmental and management changes on multiple future scenarios (e.g., Trifonova et al. 2017).





*Map of the Sacramento-San Joaquin Delta and Suisun Marsh. Credit: Delta ISB*

## Food Webs in the Sacramento-San Joaquin Delta

The Delta, as the largest estuary on the west coast of the United States, provides water for communities and agriculture within California while supporting many biodiverse ecosystems. Prior to extensive system-wide modification (e.g., mining, levee creation, draining/filling wetlands, damming), the Delta consisted of connected flood basins, tidal islands, freshwater emergent wetlands, and river distributaries (Whipple et al. 2012). The historic Delta was highly productive and supported diverse food webs; many resources were regularly harvested by Indigenous peoples (SFEI-ASC, 2016). Currently, the Delta is a highly modified and structured ecosystem consisting of agricultural land, tidal channels, and a patchwork of managed wetlands subjected to altered flow regimes and reduced hydrological connectivity and heterogeneity (SFEI-ASC, 2016).

The Delta is a complex ecosystem characterized by multiple food webs that vary in time and space. Physical modifications, in addition to the introduction of non-native species and the changing climate, have challenged management and significantly altered food webs over time (Brown et al. 2016). Historical and ongoing changes in the relative species composition of the Delta have certainly altered the food web; yet many of the observed alterations may have been caused by human-induced changes to the food web by management actions and policy decisions.

Fortunately, the Delta is a well-studied and monitored system, and previous investigations provide a foundation for understanding food-web processes. Past investigations primarily focused on the effects of bottom-up processes and lower trophic levels in sustaining populations of individual species (Jassby et al. 2003; Cloern et al. 2016, 2021). However, recent investigations have demonstrated that top-down effects can also drive food web dynamics (Rogers et al. 2022). Generally, primary productivity in the Bay-Delta is lower than in similar estuaries (Bauer 2010; Cloern and Jassby 2012; Kimmerer et al. 2012). For example, net primary productivity in the modern Delta (e.g., via photosynthetic and bacterial processes) has decreased an estimated 94% since historical times (Cloern et al. 2021). Phytoplankton are considered the primary base of food webs in existing Delta food web models and reduced primary productivity/food availability is thought to inhibit the native fish populations (Jassby, Cloern, and Müller-Solger 2003; Bardeen 2021; Slater and Baxter 2014). Some models suggest that detrital food webs may also be important (Bauer 2010; Durand 2015; Kendall et al. 2015).

Other environmental changes have altered Delta food webs, including the largescale decline of pelagic organisms (primarily fishes) (Sommer et al. 2007; Baxter et al. 2008). The pelagic organism decline (POD) was considered to be an ecosystem tipping point (regime shift) complicated by the shifting baseline of climate change (Brown et al. 2016). Early studies attributed the decline of four pelagic fish species [Delta Smelt (*Hypomesus transpacificus*), Longfin Smelt (*Spirinchus thaleichthys*), Threadfin Shad (*Dorosoma petenense*), and Striped Bass (*Morone saxatilis*)] to a combination of factors, including (but not limited to) predator-prey relationships, increases in water exports from the Delta, abiotic factors (e.g., temperature), and the effects of a non-native clam species (*Potamocorbula amurensis*) on water clarity and food availability for fishes (Baxter et al. 2008; Mac Nally et al. 2010). Collectively, the POD illustrates the crucial role

that food webs play in understanding the abundance of individual species in the Delta, one complicated by human management, non-native species introductions, and climate change.

Uncertainty around the POD, the role of invasive clams and the need to improve management and understanding of protected species spurred research that contributed to an improved understanding of lower-trophic level dynamics in the Bay-Delta region (Kimmerer et al. 2008; Brown et al. 2016). Previous reviews of food web science (Kimmerer et al. 2008; Brown et al. 2016) highlighted several gaps, including the need for long-term monitoring, understanding the effects of harmful algal blooms on the ecosystem, conducting interdisciplinary analysis and synthesis, and a better understanding of the causes for the POD (Brown et al. 2016). A key suggestion from these reviews was to establish continued development of conceptual food web models and frameworks, ones that could be used to guide large-scale restoration and to address the spatiotemporal complexity of the system.

Various components of species interactions have been previously examined in the Delta. Results from these studies show conflicting results, for instance, regarding the role of striped bass as a predator of native fishes (e.g., Delta smelt and juvenile Chinook salmon). While some studies point to striped bass as a generalist predator (Grossman et al. 2013; Grossman 2016), others show that during specific seasons and environmental conditions, striped bass feed primarily on native species (Brandl et al. 2021). Prey switching is evident in several fishes across seasons and habitat gradients, such as between densely or sparsely vegetated sites (Whitley and Bollens 2014), but the frequency of prey-switching across the food web has been challenging to quantify. Moderate densities of non-native, submerged aquatic vegetation was shown to increase the habitat for juvenile largemouth bass but larger fish were found at all densities of vegetation (Conrad et al. 2016), indicating the importance of including life history parameters in examining food web interactions.

There are still additional, and important, gaps in food web knowledge for the Delta. While several studies identified aspects of upper trophic species interactions (e.g., Grossman, 2016; Appendix 2), the higher trophic levels are hard to quantify, in part, due to a lack of long-term data on large piscivorous fishes and the impact of population decreases from water exports (Mac Nally et al. 2010; Rogers et al.,

2022). Knowledge of prey preferences and anti-predator behavior are important to supplement long-term studies on diet and prey availability and to fully represent upper-trophic level interactions (Grossman 2016). Generally, the roles of avian, reptilian, and mammalian predators in upper-trophic level species interactions in Delta food webs are not well known, but may be important sources of predation, especially at predator hot spots or hatchery release sites (Bauer 2010; Grossman 2016). Similarly, the role of tidal marsh restoration in restoring food webs has potentially contributed to an increase in San Francisco Bay tidal marsh birds (Dybala et al. 2020), which suggests a concomitant increase in avian predation on upper trophic levels. Overall, multispecies food web interactions at upper trophic levels need to be better understood in order to incorporate them into models guiding management actions (Brown et al. 2016; Sturrock et al. 2022), as the management focus has been primarily on single species' responses to environmental drivers.



*Steelhead hatchery release. Photo Credit: DWR*

## Food-web Modeling in the Delta

There have been several food web models developed for the Bay-Delta (e.g., Durand 2008, 2015; Bauer 2010; Mac Nally et al. 2010; Rogers et al. 2022). Each represents an examination of different temporal and spatial aspects of the Delta food web, as well as a distinct modeling method (e.g., conceptual models, Ecopath with Ecosim, structural equation models, and so forth). These efforts have focused primarily on the role of bottom-up processes structuring food webs and have relied heavily on long-term monitoring in the Bay-Delta conducted by state and federal agencies and academic institutions.

Many of the more comprehensive Delta models are limited in spatial/temporal coverage or are conceptual in nature (e.g., Durand 2015; Brown et al. 2016); however, a quantitative evaluation of the effects of management or species population changes requires quantitative modeling. For example, an Ecopath with Ecosim model of 1982 Bay-Delta food webs showed that mid-upper trophic levels (comprised primarily of fishes) contributed to 37% of food web biomass. Phytoplankton and detritus contributed to 55% of the total biomass. The remaining 8% was comprised of primary consumers and apex predators (Bauer 2010). This model considered phytoplankton and detritus together as the base of the food web and suggested that future studies may want to differentiate pathways of energy obtained from phytoplankton and energy obtained by detritus, as well as separate the roles of the pelagic and littoral food webs (Bauer 2010). A second example is from the Delta Regional Ecosystem Restoration Implementation Plan (DRERIP). DRERIP developed a series of conceptual food web models for each trophic level to determine the impacts of restoration activities (Durand 2008, 2015). These qualitative models focused on a variety of drivers (e.g., temperature, hydrology, habitat, depth, contaminants, water diversions, and more) and their effects on food web dynamics. Additionally, these models portrayed several key characteristics of contemporary Delta food webs: a decoupled phytoplankton and detrital food web base and the role of non-native benthic grazers (e.g., *Potamocorbula amurensis*) on phytoplankton abundance and turbidity (Durand 2015). A related series of conceptual models showed spatial differences in Delta food webs based on habitat type, such as tidal wetlands, submerged aquatic vegetation, floodplains, and benthic vs. pelagic processes (Brown et al. 2016).

A more recent food-web model differentiates the role of bottom-up, top-down, and environmental drivers in shaping pelagic food webs. Using structural equation models, this model showed that for zooplankton and estuarine fishes, bottom-up effects were stronger in upstream, freshwater regions, but top-down effects were stronger in downstream, brackish water regions (Rogers et al. 2022). However, the authors mention that there were no long-term data on large-bodied piscivorous fishes to add into the model and, as a result, upper-trophic level food web interactions may not have been accurately represented (Rogers et al., 2022). Additionally, they showed several novel relationships that were not identified in another multivariate food web model (Mac Nally et al. 2010), including the direct impact of chlorophyll on zooplankton biomass since the *Potamocorbula* clam introduction, unique trophic relationships among zooplankton groups, and the effects of flow, salinity, and temperature on different regions of food webs across the Delta (Rogers et al. 2022).

Highly altered conditions within the Delta amplify the difficulties in predicting outcomes associated with changing baselines of food web interactions and the ecosystem-scale effects of management activities (Brown et al. 2016). A key challenge in the maintenance of complex and highly altered systems is identifying management strategies that support native and/or desirable fish species. Integrating food web dynamics into management can offer insights into species interactions, trophic relationships, and the flow of energy throughout the system that collectively impact survival, growth, and reproduction (Naman et al. 2022).

There is a massive amount of science being conducted in the Delta (e.g., Appendices 1 & 2), and topics of current research relating to food webs (identified through the Delta Science Tracker) range from studies on water quality impacts on species, USGS isotope studies (e.g., Kendall et al. 2015), quantifying phytoplankton and zooplankton communities, energy flow through the system, and the effects of environmental drivers on food webs. Additionally, the importance of developing comprehensive knowledge of food webs for the Delta is mentioned in both the 2019 Delta Science Plan (Delta Stewardship Council and Delta Science Program, 2019) and the science priorities developed for the 2022-2026 Science Action Agenda (Delta Stewardship Council and Delta Science Program 2022). One objective of the food webs workshop will be to identify science gaps that complement historic and

current research in the Delta and contribute to an improved understanding of upper trophic level food web interactions.

## Food-web applications in other large ecosystems

The Delta's aquatic food webs experience many stressors similar to those in other complex and highly altered ecosystems. Management actions incorporating food web processes have been used successfully in other large, spatially complex ecosystems including the Great Lakes, the Columbia River Basin, the Gulf of Mexico, Chesapeake Bay and the Everglades (e.g., Smith et al. 2023); we provide relevant examples in select locations (see Boxes 2, 3, 4, and 5).

### **Box 2. Gulf of Mexico: Managing nutrient inputs**

Runoff from agricultural fields in the Mississippi River watershed brings nutrient-rich waters to the Gulf of Mexico, waters that promote the formation of extensive zones of hypoxia. These oxygen-depleted zones are known to affect fish by decreasing feeding and growth rates, altering activity level, and causing avoidance behavior as well as mortality (Zhang et al. 2009; Lewitus et al. 2009; de Mutsert et al. 2016). However, separating the effects of nutrient loading and the effects of hypoxia on the system allows for a greater understanding of the effects of different drivers on ecosystem processes. An ecosystem model that incorporated species interactions (including food web interactions), spatial distribution, and changes in species biomass was successfully used to simulate the impact of hypoxia levels on fish harvest and biomass. Results indicate that reductions in biomass and harvest of fishes due to hypoxia alone were an order of magnitude lower than the increases due to nutrient loading. These conclusions suggested that seasonal hypoxia was not sufficiently important to incorporate into species management plans and, as well, demonstrated the importance of food web interactions for management, such as managing for specific levels of nutrient addition (de Mutsert et al. 2016).

As with many other locations, the National Oceanic and Atmospheric Administration (NOAA) and other regulatory agencies are moving toward ecosystem-based management for fisheries resources through the establishment of the Gulf of Mexico Integrated Ecosystem Assessment. This program is designed to balance the needs of nature and society by conducting integrated science in the Gulf of Mexico, similar to the co-equal goals in the Delta (Integrated Ecosystem Assessment 2023). Several projects in the Gulf of Mexico include food web interactions as a key piece of information, including developing a multi-species harvest control rule (using an Atlantis model; Kaplan et al. 2021) and establishing ecosystem support for fisheries. An understanding of food web interactions has aided NOAA in managing the natural and socio-economic benefits that the Gulf of Mexico provides.

**Box 3. Great Lakes: Non-native species and the balance of predator-prey populations**

The Great Lakes, a series of interconnected freshwater lakes (Superior, Michigan, Huron, Erie, and Ontario), contain 84% of North America's surface freshwater and ~21% of the world's freshwater supply (EPA 2023). The Great Lakes support a wide diversity of plants and animals and understanding food webs has long been a major part of state, federal and international management goals to maintain water quality, mediate impacts of invasive species, and support an economically important sports fishery.

Like the Delta, the Great Lakes struggle with the impacts of non-native species on the ecosystem (Delta ISB 2021). The invasion of non-native dreissenid (zebra and quagga) mussels have drastically reduced the biomass of primary producers and have had major impacts throughout the food web (Bunnell et al. 2014; Madenjian et al. 2015; Fera et al. 2017; Ives et al. 2019; Li et al. 2021). Findings suggest that, in concert with declining total phosphorus inputs, dreissenid mussels exert strong bottom-up regulation on phytoplankton populations, which subsequently affects zooplankton populations and reduces the food supply for important fishes (Bunnell et al. 2014). Mussels also affect water quality, nutrient cycling, and bottom structure. Similar invasions by non-native round goby (*Apollonia melanostomus*) and copepods have serious consequences for energy flow. Newer food-web modeling approaches are being used to predict the impact of potential new invaders like the Asian carp species (Robinson et al. 2021).

The Great Lakes are also using a combination of bioenergetics models, predator/prey ratios and population dynamics to try to balance the productivity of stocked salmonids to available prey resources (Bunnell et al. 2014; Tsehaye et al. 2014; Fitzpatrick et al. 2022). Pacific Salmon were first introduced into the Great Lakes to try to control the burgeoning population of the exotic alewife (*Alosa pseudoharengus*). Salmon occupy the same regions as alewife and serve as predators to keep their populations down. The program was so successful that stocking was expanded to support an economically important sports fishery valued at \$7 billion (Great Lakes Fishery Commission 2023). Ultimately, overstocking of salmon reduced population levels of prey to such an extent that salmon populations and growth was reduced, which impacted the sports fishery. As a result of the improved understanding of food-web processes, fisheries management in the Great Lakes evolved toward an ecosystem-level focus in order to capture natural and human modifiers to fish production (Ives et al. 2019) and to protect the Great Lakes fisheries.

Examples from the Great Lakes demonstrate that incorporating food webs into water quality and fisheries management is achievable. Recent syntheses also demonstrate that a conceptual framework based on energy and nutrient flows, species interactions within



**Box 4. Columbia River Basin: Food web impacts to habitat restoration**

Dam construction, water storage infrastructure, and water withdrawals have fundamentally altered the hydrology and the fisheries in the Columbia River Basin. The last several decades have seen complex and expensive hatchery and restoration programs focused on sustaining viable environmental conditions, especially for the fisheries. While some in the scientific community do not believe that the efforts have been generally successful (e.g., Jaeger and Scheuerell 2023), the broader community appreciates that the efforts have generally maintained the return of salmon in the face of unusually poor ocean conditions over the last 30+ years. Further there are complex legal treaty obligations for mitigation using a mix of hatchery and wild fish as well as competition with the broader responsibilities of co-managers to maintain a viable ecosystem (Rieman et al. 2015).

There is widespread agreement that three priority food web-related issues impede fully successful restoration: 1) uncertainty about habitat carrying capacity, 2) proliferation of chemicals and contaminants, and 3) emergence of hybrid food webs containing a mixture of native and non-native species. Like the Delta, there is the need to place these food web considerations in an evolving temporal and spatial framework by understanding the consequences of altered nutrient, organic matter (energy), water, and thermal sources and flows; reconnecting critical habitats and their food webs; and restoring for a changing environment (National Research Council 1996; Stouder et al 1997; Naiman et al. 2012; Rieman et al. 2015). Integrating a food web perspective is key to improving restoration outcomes and preventing unanticipated consequences. For instance, an important commonality between the Columbia River and the Delta is that better food-web knowledge could identify reasonable carrying capacity for target species while an improved knowledge could help determine the key components of productive and resilient food webs, those with the capacity to withstand unanticipated changes (Naiman et al. 2012).

**Box 5. Chesapeake Bay: Multi-species management**

The Chesapeake Bay is the largest estuary in the United States connecting ~150 rivers to the Atlantic Ocean. In addition to supporting several species under state and federal protection, the Chesapeake Bay watershed provides drinking water for over 18 million people, and underpins several commercial fisheries (Chesapeake Bay Program 2023). Like the Delta, managers in the Chesapeake Bay contend with non-native species introductions, runoff and water contamination, population growth, land use conflicts, and declining native species populations.

A key management dilemma in the Chesapeake Bay is how to reduce nutrient loading to improve water quality and also to maintain healthy fish populations. Historical fisheries management in Chesapeake Bay relied on single-species modeling (Maryland Sea Grant 1995). However, growing recognition of the need to represent critical predator-prey dynamics led to the development of multispecies monitoring programs and multi-species models (Chesapeake Bay Fisheries Ecosystem Advisory Panel 2006; Anstead et al. 2021). Some of the foundational work underlying the ability to use food webs include detailed studies of the diets of the major predators and prey, bioenergetics models of the key predators and dominant pelagic prey such as anchovies (*Anchoa mitchilli*) and menhaden (*Brevoortia tyrannus*), linking growth and production of menhaden to a three-dimensional hydrodynamic model and detailed distributional studies (Hartman and Brandt 1995; Luo et al. 2001; Brandt and Mason 2003).

The Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) began in 2002 with the goal of filling data gaps and to support stock assessment modeling activities for both single- and multi-species modeling approaches (VIMS 2023). Data from this fisheries-independent survey estimates population sizes and geographic and temporal distributions for priority species, determines major links of the food web through stomach content analysis, and determines the age structure of populations through otolith (inner ear bones in fishes) sampling. The establishment of this program has contributed to improving the stock assessment for both single species models and multi-species models in the Chesapeake Bay. Since then, the model has undergone several changes, including the development of several Ecopath with Ecosim models for menhaden in the Chesapeake Bay (Link et al. 2008; Christensen et al. 2009) and including their broader geographic range in the Atlantic Ocean (Buchheister et al. 2017).

Developing multi-species management in the Chesapeake Bay has been an adaptive process that is centered around understanding the dynamics of food webs in and outside of the Bay; this change in management evolved with a greater understanding of human and climate impacts on the system and allowed for more sustainable management of important species such as menhaden.

While there are differences between systems, such as the non-native species or local regulations, the need to understand species interactions and the effectiveness of different management actions remains similar across locations. The selected examples showcase complementary research and management approaches that might be applied in the Sacramento-San Joaquin Delta to address issues related to non-native species, predator interactions, and habitat restoration by incorporating food web knowledge into policy and management actions. A recurring theme across these ecosystems, including the Delta, is the strong need to understand the fundamental structure and bioenergetics of food webs (including for detrital-based energy pathways) to adaptively manage fish populations (Naiman et al. 2012; Ives et al. 2019; Lewis et al. 2022).

## Initial ideas for applications of improved understanding of upper food webs

A key workshop focus is to evaluate how improved science and understanding of food-web interactions can inform individual species and ecosystem management in the Delta. Here, we introduce some initial ideas as an introduction to a more in-depth exploration of needs at the workshop. These initial ideas were derived from the literature, past Delta reviews, and from a series of discussions with members of the Delta science and management community. Collectively, they explore

1. the current management needs and how knowledge of food web interactions might be employed in the Delta, and
2. current gaps or barriers to understanding food-web interactions.

Information from these discussions was used to plan the scope of the food web workshop. The Delta ISB conducted 14 discussions during summer 2023, with 35 participants from a combination of federal agencies, state agencies, local/regional agencies, non-governmental organizations, and academic institutions (Table 1).

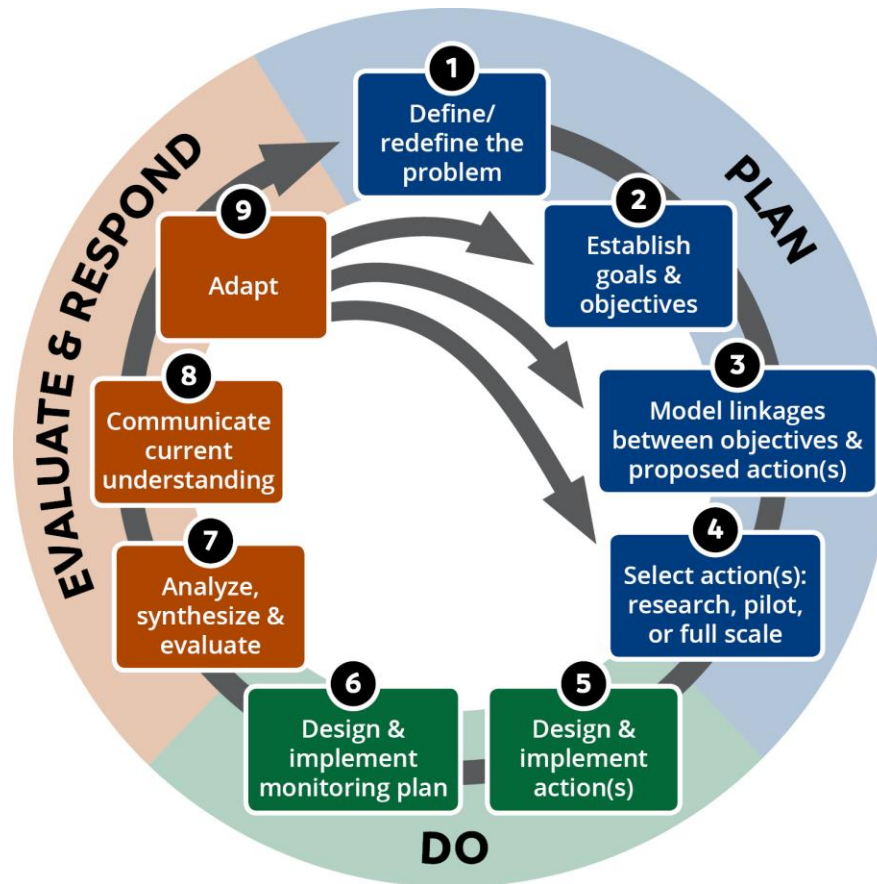
**Table 1.** Demographics of Delta management and science community discussions on the role of food webs and upper trophic level species interactions conducted by the Delta ISB in 2023.

Participant Category	Number of Participants
State Agency	12
Non-Governmental Organization	3
Local/Regional Agency	5
Federal Agency	9
Academic Institution	6

Our objective was to receive informal and diverse input from the science and management communities on the topic of incorporating knowledge about upper trophic level food webs into management. We were unable to schedule discussions with all rights-holder groups and interested parties; however, we expect the workshop and public comment sessions will provide opportunities for further and broader input on these same topics.

#### Establish an adaptive management approach

Establishing an adaptive management approach in the creation and use of food web models for upper-trophic level management would be advantageous. Adaptive management is a science-based, structured approach to decision making that has been built into regulations for several state and federal agencies, including in the Delta. The Delta Reform Act of 2009 mandates the Delta Stewardship Council to use the best available science and include a transparent, science-based adaptive management strategy for ecosystem and water management in the Delta. Adaptive management is an iterative process, which requires periodic re-evaluation of the key management problem or goals, knowledge acquisition, and monitoring (Wiens et al. 2017). Food webs in the Delta are both spatially and temporally dynamic, and likely require regular updates to monitoring programs and any associated management strategies. An understanding of the dynamics of food webs will be vital for creation of adaptively managed ecosystem-based management strategies in the Delta.



*The nine-step adaptive management cycle. Credit: Delta Plan and Wiens et al. (2017). Modified for accessibility.*

Individual species management and effects of environmental drivers

Agencies can often be restricted to conducting science that addresses impacts to listed species, and so they naturally focus on single-species management (Rieman et al. 2015). It is well recognized that food webs can play an important role in the abundances of individual species. Key ecosystem drivers such as climate change, restoration efforts, and water flows can affect a species directly and indirectly through the food web.

Ecosystem-based management

The concept of ecosystem-based management is to manage water, land, and organisms *together* to develop a desired ecosystem with benefits for both biodiversity and humans, and is aligned with the Delta's coequal goals (Delta Reform Act 2009). Ecosystem-based management, along with multispecies management have emerged as crucial for spatially diverse and evolving landscapes

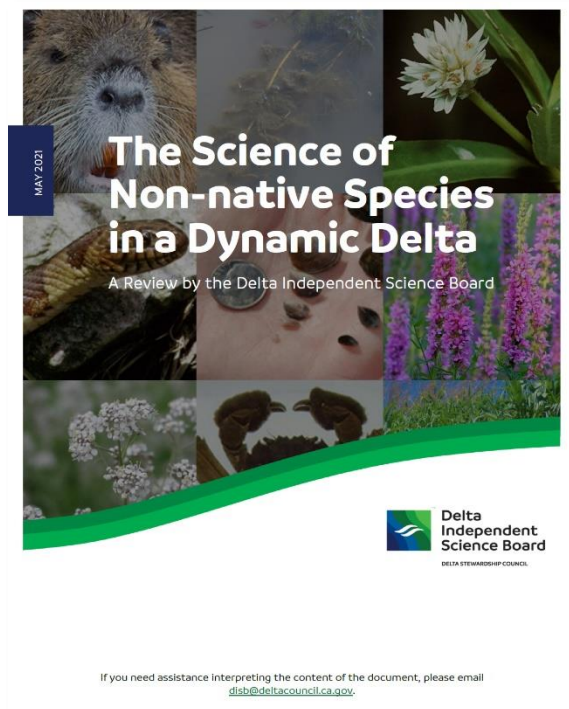
and contributes toward a more holistic view of ecosystem health, within the limits of existing regulations (e.g., Rieman et al. 2015; Delta Stewardship Council and Delta Science Program 2019; Mount et al. 2019). An important component of both ecosystem-based and multispecies management is an understanding of food web interactions. For instance, the carrying capacity (abundance or biomass of species a particular habitat can support) largely depends on food availability and food web interactions, in combination with other biotic and abiotic conditions. Improving carrying capacity is essential for successful restoration of fish or migratory birds or species managed for harvest. A poor understanding of food webs can impact the outcome of management actions, yet food-web science is not often included in natural resource management (Naiman et al. 2012; Naman et al. 2022).

### Non-native species

The San Francisco Estuary is one of the most invaded aquatic ecosystems in the US. A key management challenge is to predict the impacts of new species introductions. In a review by the Delta ISB of the science of non-native species in the Delta, a key recommendation was to

*“...develop a comprehensive, spatially explicit, food-web model that is Delta-wide in scope and tied to environmental driving forces and conditions.”*

One of the universal impacts of a new non-native species is to alter the food web. A comprehensive food-web model for the Delta would improve our understanding of non-native species currently in the Delta and help guide decision-making and management solutions. Such a model could also predict potential impacts of new non-native species on ecosystem structure, function and services, and how potential threats would be altered by climate change (Delta ISB 2021).”



## Restoration

Ecosystem restoration is a key component of management to support species. Regulatory requirements mandate the restoration of tidal wetland and floodplain habitat. The focus of this restoration is to promote lower trophic level food production, which will then support at-risk species (e.g., smelt and Chinook salmon). It is vitally important to be able to assess which species benefit directly from ecosystem restoration and understand the impacts of restoration efforts throughout the Delta food webs.



*Dutch Slough Tidal Marsh Restoration Project. Photo Credit: DWR*

## Temporal and spatial scales

Delta heterogeneity was frequently mentioned as a topic of concern in the science and management Delta community discussions. The spatial diversity of habitats and the prevalence of seasonal and short-term changes in the system underpin many food web interactions (e.g., Nobriga and Feyrer 2007; Young et al. 2021). Additionally, a wide variety of spatiotemporal scales of environmental and anthropogenic drivers impact Delta species. Understanding how these drivers affect resource availability, predation, competition, and other food-web interactions is critical. The science and management communities stressed that an appropriate food-web model (or set of models) would help incorporate the spatiotemporal variability in the system and the associated dynamics of food webs.

An ideal food-web model (or models) would also be able to connect to species life cycle models (to provide information about species interactions across ontogeny) and help elucidate bottlenecks in habitat use. Similarly, a model with predictive capabilities that could forecast the effects of management decisions on species would be especially useful for managing State and Federally listed species.



*Sandhill Cranes. Photo Credit: DWR.*

#### Contaminants and impacts to species interactions

Contaminants and their role within Delta food webs were mentioned across multiple discussion groups. Contaminants are a concern at all trophic levels, but especially so at upper trophic levels due to bioaccumulation and potential to impact human health. Some community members articulated that there had been sufficient research on the physiological effects and lethal limits of some contaminants (e.g., heavy metals) but that the ecosystem effects and sublethal effects of contaminants were largely unknown. In addition, it was noted that sublethal impacts from contaminants on species and how they may impact feeding behavior or predator avoidance are important informational gaps. Assessing bioaccumulation of contaminants requires a quantitative understanding of food webs.

#### The role of behavior in food web interactions

Understanding the impact of behavior on the movement of energy through the system was viewed as a significant science gap in Delta's food web knowledge base. This may include changes to migration patterns or habitat use, predator avoidance tactics, prey switching, or other behaviors. Behavior is challenging to quantify and incorporate into models, but having increased understanding of the role of behavior in food web interactions will be useful for effective system management.

#### Understanding components of Delta food webs

The importance of detritus and benthic invertebrates for supporting Delta food webs is not empirically well-established. Detritus, such as dissolved organic carbon, is gaining recognition as an important component of Delta food webs (Jeffres et al. 2020). Initial food web models combined the pelagic and detrital aspects of food



webs, but suggested that detrital pathways be considered separately in future studies (Bauer 2010). Detrital components can be challenging to quantify and are essential for understanding the movement of carbon through the system. Coupling the pelagic and detrital pathways, especially the role of benthic invertebrates (clams) in interrupting the transfer of detrital energy to the system, may be paramount in understanding carrying capacity (Durand 2015). Much concern has been placed on food availability for listed fish species, and additional research could clarify the role of the detrital pathway throughout ontogeny in these species. Benthic invertebrate communities in the Delta have changed over time, primarily due to the introduction of non-native species.



*The Overbite Clam. Photo Credit: United States Geological Survey*

For example, the non-native clam, *Potamocorbula amurensis*, changed the availability of phytoplankton and altered turbidity patterns in the Delta (Kimmerer et al., 1994; Kimmerer and Orsi, 1996; Kimmerer and Thompson, 2014; Durand 2015). The food web effects of other benthic invertebrates have been explored less, such as the role of the non-native red-swamp crayfish as prey for upper trophic level species (e.g., Durand 2015; Weinersmith et al. 2019). Similarly, aquatic insects and benthic microfauna are often overlooked, and may not be well represented in the contemporary understanding of Delta food webs.

Data management, data and information sharing, and synthesis

Science and management community members identified several gaps in data collection and availability, including information on trophic linkages, community-level species interactions, sub-lethal effects of drivers, and behavior. Some identified issues associated with the quality and consistency of data. For example, data collection is often centered around presence/absence and timing, which

cannot always be translated into species abundance. More intentional data collection (i.e., not just opportunity-based), establishing the spatiotemporal scales of monitoring, and determining Delta-wide data priorities may help.

Data users shared that continuing to improve data accessibility, transparency, and digitizing older data records would make Delta data more user-friendly. Often data sharing and accessibility are not the highest priorities for agencies, and data users mentioned it was challenging to understand the full breadth of data that does exist.

Another frequent comment was that the Delta scientific community possesses an incredible amount of science, data, and experts but that the community is lagging in producing syntheses of the knowledge gained. This is especially true for upper trophic levels. The synthesis of data and existing research is crucial to evaluate the state of the science, and to be able to adapt and change management, monitoring, and science moving forward. Synthesis of science is also a key step toward open data and science communication.

## Moving Forward: Linking Food Webs to Management Actions

Through this review, the goal is to determine whether incorporating food web interactions into management is a feasible option for moving the Delta toward better solutions. Fortunately, there is a wealth of knowledge and key examples from other large ecosystems that share common challenges with the Delta. There has been extensive research by an active science community, and there is a wealth of data available on the Delta. Focusing future efforts on understanding some of the science gaps of upper-trophic level food web interactions, and prioritizing collaboration and synthesis of science, will be key to implementing effective management guided by food web interactions.

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## Appendix 2: List of current food web research projects in Delta Science Tracker

Title	Lead	Science topics	Updated	PI(s)	Contributors
<a href="#">Examining the relationship between Longfin Smelt, zooplankton, and flow in the San Francisco Bay Delta</a>	UNIVERSITY OF CALIFORNIA - BERKELEY [UC BERKELEY]	Fish, Flows, Longfin Smelt, Zooplankton	30-Nov-22	Saffarinia, Parsa; Ruhi, Albert	
<a href="#">Fish Diet and Condition</a>	CALIFORNIA DEPARTMENT OF FISH AND WILDLIFE [CDFW]	None specified	29-Apr-22	Burdi, Christina	
<a href="#">Biomass and Toxicity of a Newly Established Bloom of the Cyanobacteria <i>Microcystis aeruginosa</i> and its Potential Impact on Beneficial Use in the Sacramento-San Joaquin Delta</a>	CALIFORNIA DEPARTMENT OF WATER RESOURCE [DWR]	None specified	29-Apr-22	Lehman, Peggy	
<a href="#">Phytoplankton Communities in the San Francisco Estuary: Monitoring and Management using a Submersible Spectrofluorometer</a>	CALIFORNIA DEPARTMENT OF WATER RESOURCE [DWR]	None specified	29-Apr-22	Muler-Solger, Anke	
<a href="#">Nitrogen cycling and ecosystem metabolism before and after regulatory action</a>	STANFORD UNIVERSITY	<a href="#">Nitrogen / ammonia</a>	29-Apr-22	Volaric, Martin; Monismith, Stephen	Senn, David
<a href="#">An Open-Source, Three-Dimensional Unstructured-Grid Model of the Sacramento/San Joaquin Delta: Model Construction and Application to Delta Hydrodynamics and Temperature Variability</a>	STANFORD UNIVERSITY	<a href="#">Water temperature</a>	29-Apr-22	Monismith, Stephen	

Title	Lead	Science topics	Updated	PI(s)	Contributors
<a href="#">Quantifying Biogeochemical Processes through Transport Modeling: Pilot Application in the Cache Slough Complex</a>	UNIVERSITY OF CALIFORNIA - DAVIS [UC DAVIS]	None specified	18-Nov-22	Holleman, Christopher	
<a href="#">Operation Baseline Project 2A2: USGS Pilot Studies - Isotopes</a>	U.S. GEOLOGICAL SURVEY [USGS]	Algae, Floating aquatic vegetation, Food webs, Nitrogen / ammonia, Open water, Other discharge contaminants, Phytoplankton, Submerged aquatic vegetation, Wastewater discharge, Water operations / exports, Wetlands, Zooplankton	14-Dec-22	Kendall, Carol; Young, Megan	
<a href="#">Operation Baseline Project 2A1: USGS Pilot Studies</a>	U.S. GEOLOGICAL SURVEY [USGS]	Algae, Floating aquatic vegetation, Food webs, Nitrogen / ammonia, Open water, Other discharge contaminants, Phytoplankton, Submerged aquatic vegetation, Wastewater discharge, Water operations / exports, Wetlands, Zooplankton	14-Dec-22	Kraus, Tamara; Bergamaschi, Brian	Parker, Alex; Kimmerer, Wim
<a href="#">Operation Baseline Project 1: Conceptual Framework</a>	DELTA STEWARDSHIP COUNCIL	Algae, Floating aquatic vegetation, Food webs, Nitrogen / ammonia, Open water, Other discharge contaminants, Phytoplankton, Submerged aquatic vegetation, Wastewater discharge, Water operations / exports, Wetlands, Zooplankton	14-Dec-22	Senn, David	
<a href="#">Simulating methylmercury production and transport at the sediment-water interface to improve the water quality in the Delta</a>	UNIVERSITY OF CALIFORNIA - MERCED [UC MERCED]	Bioaccumulation, Chemistry, Hg and methyl mercury	17-Nov-22	Helmrich, Stephanie; O'Day, Peggy	Alpers, Charles
<a href="#">Operation Baseline Project 2C: Zooplankton, Romberg Tiburon Center, SFSU</a>	SAN FRANCISCO STATE UNIVERSITY [SFSU]	Algae, Floating aquatic vegetation, Food webs, Nitrogen / ammonia, Open water, Other discharge contaminants, Phytoplankton, Submerged aquatic vegetation, Wastewater discharge, Water operations / exports, Wetlands, Zooplankton	14-Dec-22	Kimmerer, Wim	
<a href="#">Operation Baseline Project 2B: Phytoplankton, CSU Maritime Academy</a>	CALIFORNIA STATE UNIVERSITY MARITIME ACADEMY	Algae, Floating aquatic vegetation, Food webs, Nitrogen / ammonia, Open water, Other discharge contaminants, Phytoplankton, Submerged aquatic vegetation, Wastewater discharge, Water operations / exports, Wetlands, Zooplankton	14-Dec-22	Parker, Alex	



Title	Lead	Science topics	Updated	PI(s)	Contributors
<a href="#">Soil type as a driver of agricultural climate change response in the Sacramento-San Joaquin Delta</a>	UNIVERSITY OF CALIFORNIA - BERKELEY [UC BERKELEY]	Agriculture, Carbon, Nitrogen, Phosphorous, Soil	17-Nov-22	Anthony, Tyler; Silver, Whendee; Deverel, Steven	
<a href="#">Delta Landscapes Primary Production Project</a>	SAN FRANCISCO ESTUARY INSTITUTE [SFEI]	Primary production, Phytoplankton, Emergent macrophytes, Epiphytic algae, SAV/FAV	29-Apr-22	Cloern, James; Grenier, Letitia; Safran, Sam	Vaughn, Lydia; Robinson, April
<a href="#">Restoring tidal marsh foodwebs: assessing restoration effects on trophic interactions and energy flows in the San Francisco Bay-Delta</a>	UNIVERSITY OF CALIFORNIA - BERKELEY [UC BERKELEY]	Food webs, Wetlands	30-Nov-22	Pagliari, Megan; Ruhi, Albert	
<a href="#">Directed Outflow Project [DOP] - Paired Habitat Sampling</a>	U.S. BUREAU OF RECLAMATION [USBR]	Flows, Water management	29-Apr-22	Nelson, Ben	
<a href="#">Food Temperature Optimization Model for CVP</a>	U.S. BUREAU OF RECLAMATION [USBR]	None specified	29-Apr-22	VanNieuwen huysse, Erwin	
<a href="#">Fish Restoration Program Monitoring</a>	CALIFORNIA DEPARTMENT OF FISH AND WILDLIFE [CDFW]	Nitrogen/ammonia, Phosphorous, Carbon, Chlorophyll A / B, Phytoplankton, Other zooplankton, Salinity, Water temperature, Dissolved oxygen, pH, Turbidity, Submerged aquatic vegetation, Chinook Salmon, Steelhead Trout, Green sturgeon, White Sturgeon, Delta Smelt, Longfin Smelt, Sacramento Splittail, Insects, Mollusks, Crustaceans, Invertebrates	29-Apr-22	Sherman, Stacy	
<a href="#">Suisun Marsh Salinity Control Gate Study</a>	CALIFORNIA DEPARTMENT OF WATER RESOURCE [DWR]	<u>Salinity</u>	29-Apr-22	Sommer, Ted	

Title	Lead	Science topics	Updated	PI(s)	Contributors
<a href="#">The Role of Microcystis Blooms in the Delta Foodweb: A Functional Approach</a>	SAN FRANCISCO STATE UNIVERSITY [SFSU]	<a href="#">Harmful algal blooms HAB</a>	29-Apr-22	Parker, Alex	
<a href="#">Phytoplankton and cyanobacteria growth and response to stressors</a>	UNIVERSITY OF CALIFORNIA - DAVIS [UC DAVIS]	Phytoplankton, Cyanobacteria	29-Apr-22	Lam, Chelsea; Teh, Swee	Lehman, Peggy