Advancing Scientific Understanding and Management of the Delta Through a Food Web Perspective

An assessment of the scientific needs to inform aquatic management actions in the Delta, with an emphasis on upper trophic levels

Delta Independent Science Board

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Executive Summary

The Sacramento-San Joaquin Delta (the Delta) is characterized by a diversity of ecological processes and food webs that vary greatly in time and space. Food webs are important because they mediate the flows of energy and nutrients through ecosystems, via interactions among species (competition, predation) as well as interactions of the species with the environment (e.g., Paine 1980). Physical modifications, non-native species and changing environmental drivers have significantly altered the structure and energetic pathways of food webs in the Delta for decades. Predicting the impacts of water routing, habitat restoration, fisheries, contaminants, and changes in environmental drivers (e.g., climate, nutrient loading, invasive species) on the ecological carrying capacity, productivity, and population dynamics of species of interest of the Delta requires an understanding of food web interactions and processes.

This review examines the scientific requirements and management implications of achieving a better understanding of food webs, especially the upper trophic levels, in the Delta. A quantitative understanding of food web interactions, via analysis of empirical data and development of food web models, allows managers to evaluate the impact of their actions aimed at supporting fish species under climate and other system-wide changes. This review evaluates existing information on Delta food webs in the context of advancing food web modeling of upper trophic levels, identifies scientific gaps to advance progress, and links the resulting knowledge to inform management actions.

Upper trophic levels include fish, and particularly those (e.g., salmon) being actively managed. The intentions of this report from the Delta Independent Science Board (Delta ISB) are to provide information that would help agencies assess how to better incorporate and advance a food web understanding in managing the Delta ecosystem and to identify what tools are available or could be developed. The Delta ISB undertook this activity with the goal of assisting natural resource managers in improving the vitality of individual fish species/populations through new management actions, ecosystem-based management (currently not employed), and adoption of relevant performance measures for Delta lands and waters. **Overall, the review explores the benefits of moving away from a reliance on conceptual and species-centric models and toward greater reliance on a**

quantitative framework that explicitly incorporates food webs into data analyses and modeling.

Our recommendations reflect lessons largely learned from elsewhere in North America, where a basic understanding of food webs has greatly improved ecosystem-scale management and the restoration of aquatic systems that support fisheries (e.g., Columbia River, Chesapeake Bay, Great Lakes). Examples presented in this report strongly suggest that an understanding of food web interactions is essential for sustaining a healthy Delta ecosystem and is key to fulfilling recommendations from both the Strategic Science Needs Assessment (DPIIC and Delta ISB 2021) and the Delta ISB's Non-Native Species Review (Delta ISB 2021).

The Review Process

The effort is based on an initial evaluation of the literature (Brandt et al. 2023), open public comments on a prospectus and public suggestions during Delta ISB board meetings, community engagement through a series of interviews, and a focused two-day workshop. The workshop was held in Sacramento, California, on November 8 and 9, 2023, and convened over 100 scientists, managers, and other members of the Delta scientific and management community, most with extensive experience in food web processes, ecology, and species management.

The workshop and community conversations emphasized how a contemporary understanding of upper trophic level structure and dynamics, viewed in the context of a food web, could augment new scientific capabilities, especially to anticipate fish population changes in response to management and environmental drivers. Specifically, the review process evaluated the degree to which an enhanced focus on food web processes across all trophic levels might benefit and facilitate ecosystem management, and whether available data and science can support the development of such tools and models.

Current Food Web Science in the Delta

The Delta is a well-studied and monitored system, and previous investigations provide a solid foundation for understanding food web processes. The Delta ISB affirmed that past food-web investigations primarily focused on selected bottom-up pathways and lower trophic levels in sustaining populations of individual species. The various food-web models that have been developed for the Bay-Delta region are generally conceptual and differ in methods and goals, but most do not represent both lower and upper tropic levels or, if they represent multiple upper trophic level species, they have coarse temporal and spatial resolution limiting their application to important management questions. The conceptual models that document the Delta's food webs, and the single species conceptual models that include food web interactions, could be improved by generating quantitative predictions of how fish are likely to respond to management.

There are a few food web models, with associated monitoring, that have led to recent progress in understanding fish population dynamics in a multi-species context in the Delta. However, they do not fully represent an important perspective emerging from recent investigations elsewhere. Specifically, that top-down effects (e.g., predation) and evolving environmental conditions can strongly influence food web processes and fish abundance. For instance, these investigations show that species interactions, such as prey preferences and prey behaviors to avoid predators, is important for supplementing the existing long-term studies on diet and prey availability to fully understand the roles of upper trophic level interactions in food web dynamics. A major challenge will be to improve food web models in a manner that enables them to be realistic under the novel (never previously observed) conditions that occur under plausible futures.

The workshop, interviews with Delta scientists and managers, and comments received on the prospectus and an initial draft of this report highlighted the variety of approaches that could be employed for understanding food webs. At the most basic level, food web models reveal the diets of the prey and predators and identify dominant energy pathways that govern dynamics within trophic levels and link lower and upper trophic levels. A common application of food web models is the evaluation of the effects of environmental drivers (e.g., drought, salinity, contaminants, nutrients, and temperature) and altered biological conditions (e.g., invasive species, changes in food base) on species' abundances that include inter-specific interactions (e.g., predation risk). There are several widely used modeling approaches available that vary in complexity, spatiotemporal scales represented, assumptions and limitations, and types of questions they can answer. The review illustrates examples of commonly used types of food web models that should have applicability in the Delta.

Applying Food Web Science to Management

The Delta's aquatic food webs experience many drivers like those in other complex, highly altered and evolving ecosystems. The review provides relevant examples where incorporating food web processes have been used to help inform management in large, spatially complex ecosystems. These include the Great Lakes, the Columbia River Basin, the Gulf of Mexico, and the Chesapeake Bay.

The review identifies several direct applications of food web models to the Delta's most pressing natural resource management issues. Five applications are addressed: 1) the effects of environmental drivers on individual species management, 2) ecosystem-based management, 3) invasion of non-native species, 4) ecosystem (habitat) restoration, and 5) contaminant exposure and cycling. For each, the review documents the fundamental management questions, potential benefits of using a food web strategy, data collection and modeling priorities, and provides key examples. Additionally, the report addresses the importance of establishing an effective adaptive management process to apply knowledge gained from a food web perspective.

Food Web Science Gaps in the Delta

Data management, data and information sharing, and synthesis are the pillars of a well-functioning science-management system. The science and management community of the Delta – through the interviews, comments on the prospectus and the workshop – noted that a wealth of information is available for food web analyses but also identified several key gaps in knowledge and data availability. These gaps include lack of sufficient information on the different energetic pathways of trophic linkages, the many possible community-level interactions, sub-lethal effects of single and multiple environmental drivers, and species' behavior related to feeding, predation risk and reproduction that determine movement and spatial distributions.

Some community members identified issues associated with the quality and consistency of food web data, and with monitoring activities. For instance, the current monitoring enterprise of the Interagency Ecological Program (IEP) focuses on smaller fishes or the early life stages of larger fish species (e.g., striped bass) rather than the abundance and distribution of larger individuals; other predators, such as birds and marine mammals, are either not regularly monitored or are not integrated with the IEP. Collectively, these informational gaps can limit our understanding of the implications of management actions by hindering analyses that explicitly include the food web responses of the upper trophic levels.

The Delta ISB found that, as aids to improving management, *intentional* data collection (i.e., not opportunity-based), establishing the ideal spatiotemporal scales of monitoring for each management issue, and determining Delta-wide data priorities are essential for enhancing an understanding of food web processes. The Delta ISB feels that it may be beneficial for new quantitative food web models to initially focus on a small number of species (i.e. multi-species models) that comprise the highest proportion of biomass in the Delta. Therefore, initial food web models may include many non-native species, small-sized fishes, large predatory fishes, freshwater clams and macrophytes, whose collective food web interactions have received less attention in previous studies. Once trends in the dominant aquatic species are determined, food web models can be revised to focus on specific regions of the Delta and expanded to include more lower trophic level species and represent the population dynamics of species that have high management importance.

Nearly all users of food web information – through interviews, formal comments on the prospectus, and the workshop – shared that continuing to improve data accessibility, meta-data documentation, and digitizing older data records would make the Delta's data more useful. The findings related to synthesis and data accessibility are not new and have been documented in previous Delta ISB reviews on fish and flows (2013), water quality (2018), the Interagency Ecological Program (2019) and the monitoring enterprise (2022). The need for increased capacity, dedicated time for coordinated syntheses, along with data accessibility, is included as actions in the Delta Science Plan, Science Action Agenda, and Interagency Ecological Program Science Strategy.

Recommendations

The key finding from this review is that an improved mechanistic understanding of food webs, especially the inclusion of upper trophic levels, is essential for predicting the impacts of biophysical drivers (e.g., climate, flow, nutrients, contaminants, invasive species) and management actions (e.g., habitat restoration) on individual fish species as well as on ecosystem-level processes relevant to agencies, Indigenous Tribes (Tribes), and the public. Given the potential for providing management relevant insights into aquatic ecosystem management, the Delta ISB recommends that a focused and adequately funded scientific collaboration among agencies, academia, Tribes, and the public be established to design and implement a food web science strategy. The food web strategy – guided by science priorities – should include: 1) formal scientific coordination and funding mechanisms, 2) flexible monitoring that includes emerging methods, 3) knowledge-based food web models, and 4) interactive and adaptive linkages to management.

Specific recommended actions include:

1. **Use key management needs to inform the development of a comprehensive coordination and implementation plan for collecting, analyzing, modeling, and applying food web information.**

   A meaningful application and continuous evolution of a food web perspective – and the resulting modeling applications - requires focused interdisciplinary collaboration among agencies, universities, the public and Tribes. This process spans the mandates of multiple agencies and areas of expertise. With respect to coordination, many workshop participants felt that a *Collaboratory* focused on such a universal, but bounded need, would be beneficial for the Delta. Developing an implementation plan for a food web perspective within a Delta Collaboratory would be an effective test of whether this integrative multi-partner approach can be effective for addressing management goals.

   The Delta ISB believes it is essential that agencies and the community prioritize and support data sharing and collaboration with a focus on the food web to fully establish a more effective science enterprise. This includes the development of improved *mechanisms* for effectively sharing data, ideas and insights. Food web-relevant data need to be regularly updated, quality controlled, and made accessible in usable formats. For example, sampling locations should all be consistently geo-referenced and include standardized metadata. These tasks provide the foundation for meaningful syntheses of information and the generation of new knowledge.

2. **Adapt Delta research and monitoring programs to explore key aspects of food webs, relying on collaboration and best-available tools/methods.**

   The Delta ISB sees multiple opportunities for an improved understanding of species outcomes and assessment of ecosystem health through targeted research and monitoring activities that enhance our current food web knowledge base, including:

- Further examining the role of detritus and its associated organisms in underpinning system productivity.
- Evaluating additional linkages between primary producers, their availability to zooplankton, and the subsequent coupling to upper trophic levels.
- Better characterizing processes underpinning the carrying capacity and productivity (i.e., vitality) of benthic communities and early life stages of ecologically key species (e.g., Lucas et al. 2016, Mussen et al. 2024).
- Quantifying (beyond the available conceptual models) the distributions, life histories, bioenergetics, and responses to environmental drivers of the 5-10 most common/abundant species that play major ecological roles in the Delta's food webs.
- Executing special studies that would be responsive to data gaps identified by the collaborative team working on model development.
- Understanding the flow and ecological consequences of contaminants, the roles of predatory birds and mammals in maintaining aquatic productivity, and the nutritional/energetic quality of food moving through food webs.

3. **Develop appropriately scaled and spatially explicit food web models as determined by management questions and environmental drivers**.

Food web models incorporating relevant species and processes at appropriate scales enable predictions of how environmental conditions and management actions affect fish species of importance to agencies, institutions, Tribes, and the public. Identifying clear questions and hypotheses, and constructing food web-centric conceptual models, can guide modelers to the simplest model that will adequately address concerns. It will be helpful to examine and consider adopting the *processes* of model development linking science and management that have proved successful in other large ecosystems.

Food web models designed to address management questions can vary in complexity from questions involving a few key species to questions that require representing all species at each trophic level, and from fine temporal and spatial resolution (hourly or daily, using a hydrodynamic grid) to coarse resolution (annual, using one or a few spatial boxes).

4. **Link food web models to management questions and actions, monitoring, and empirical studies using an adaptive framework.**

   Adaptive management is widely used for Delta science and decision support and can be enhanced by incorporation of food web model development and application. Use of an adaptive management framework underpins ongoing and effective decision-making protocols and processes by facilitating the transfer of new insights and quantitative information derived about food webs into timely assessments of the impacts and expected responses to management actions. Food web modeling is an iterative process with advances occurring as new information becomes available and management questions evolve. The iterative aspect of model development meshes well with the adaptive management framework when both are coordinated and done synchronously. The adaptive framework provides a mechanism for the continual improvement of the science and expanding the relevance of Delta-wide monitoring and modeling activities. The previously recommended food web focused Collaboratory may be an ideal setting for ongoing adaptive management evaluations because of its ability to engage diverse data sources, partners, and perspectives.

Integral to all four of the recommendations, the Delta ISB strongly encourages:

- Evaluating the usefulness of adopting a food web perspective within a defined timeframe (~decade). Proof of concept and meaningful management applications will be necessary criteria for determining success.
- Creating teams that include students, technicians, scientists, and managers that address specific issues and who regularly exchange information and formulate potential solutions.
- Implementing proven team building and science communication strategies to establish the efficient transfer of newly generated knowledge to natural resource managers.

Concluding Remarks

The Delta ISB appreciates that the recommendations are ambitious. In the short term, additional workshops and other team building activities will be required to act on them. At a minimum, most recommendations will require several years to a decade to be fully functional – and this is only if the Delta's scientific and management community and the public deem them to be sufficiently important.

The Delta ISB believes these recommendations will advance food web science to better inform a broad range of management decisions. Collaboration and adaptive management will make implementation of the recommendations efficient and effective. The benefits include a vastly improved capacity to forecast effects on fish and other aquatic organisms from management actions and from interactions with an ever-changing climate and ecosystem. **A great majority of the interviewees and workshop participants affirmed the necessity for food web knowledge by stressing that almost every management question is a food web question, and that we need to understand *how* to represent the food web interactions in management, not whether we need to or not.**

Background and Purpose

California's Sacramento-San Joaquin Delta (the Delta) is expected to experience significant environmental modifications in the coming decades. The modifications will be largely driven by climate change, sea level rise, major flooding and storms, non-native species, water supply operations and 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 listed and other fish species and ecosystem sustainability are at the core of Delta policy and management, as they 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 improves the Delta as a place (Delta Stewardship Council and Delta Science Program 2022).

The Delta Independent Science Board (Delta ISB) undertook this review to improve the scientific understanding of upper trophic level food webs. The intention was to identify investments in data, models, and research capacity to improve understanding of fish species responses to management actions and to inform ecosystem-level goals and performance measures in Delta lands and waters. This review is consistent with the Delta ISB's charge to provide "oversight of the scientific research, monitoring, and assessment programs that support adaptive management of the Delta through periodic reviews…," as required by the Delta Reform Act. The findings and recommendations from Delta ISB reviews are designed to increase scientific credibility, improve research clarity, advance the debate about Delta issues, and seek better connectivity among science, management, and policy.

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). The current review aims to evaluate existing information on Delta food webs in the context of advancing food web modeling of upper trophic levels, to identify information gaps to advance progress, and to link the resulting knowledge to inform and improve management actions. The Delta ISB contends that a better understanding of trophic processes, from lower trophic levels to apex predators, will not only improve management actions and the assessments of management impacts on individual species, but is also essential for full consideration of multispecies responses and for implementation of ecosystem management.

The Delta ISB recognizes that food web concepts are pervasive in many past and ongoing Delta activities. This review explores the benefits of moving away from the current reliance on a mix of conceptual and species-centric models of aquatic food webs and toward greater reliance on a quantitative framework that explicitly incorporates food webs with upper trophic level representation into analyses and modeling[1].

Approach

For this report, the Delta ISB reviewed the contemporary and emerging science underpinning the current management and understanding of food webs in the Delta (see Brandt et al. 2023, L. McCormick, unpublished data). This review was focused on food web interactions at upper trophic levels (primarily fishes) to elucidate connections that can benefit individual-species and ecosystem-based management. The overall review was based on a review of the literature, public comments on a prospectus and during Delta ISB meetings, community engagement through a series of conference call interviews, and a focused two-day workshop. The workshop was held in Sacramento on November 8 and 9, 2023 and convened over 100 scientists, managers, and many other members of the Delta community with extensive experience in food web dynamics, ecology, and species management (Workshop Recordings of Day 1 and Day 2). Workshop participants addressed the importance of food web interactions in the Delta and helped to identify where improved understanding and tools (e.g., food web models, laboratory techniques) might substantially improve predictions of an individual species' responses to environmental drivers and to management actions while also enabling ecosystem-level assessments.

[1] In conducting this review, the Delta ISB recognized that future conditions driving food web dynamics are key areas of uncertainty. However, questions about future conditions were outside the scope of this review. This may be an important area of analysis for the recommended food web Collaboratory to explore.

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 been long recognized to affect ecosystem functions and link species abundances, ecosystem dynamics, and energy cycling across time and space (e.g., Lindeman 1942; Morin and Lawler 1995). Contemporary analyses of endangered fish species in the Delta are generally focused on how an individual driver or a combination of drivers (e.g., flow and temperature) directly affect abundance of the species.

The Delta ISB contends, however, that a dynamic understanding of food web interactions is critical to predicting how environmental drivers or management actions might affect an individual species (Figure 1). This is because these drivers might also affect abundances of other species and thus food web dynamics overall (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 individual species because predation causes direct mortality of prey species, and the availability of prey resources affects the growth, reproductive capacity and, ultimately, production of the predator population. Food webs are also important components of ecosystem-based management (Geary et al. 2020; Korpinen et al. 2022). For instance, understanding food web dynamics in the Chesapeake Bay and mid-Atlantic illuminated how the harvest of menhaden (*Brevoortia tyrannus*) affected populations of key predators, such as seabirds and whales, and enabled the switch from largely single-species management of menhaden to a more comprehensive ecosystem-based fishery management approach (Box 1).

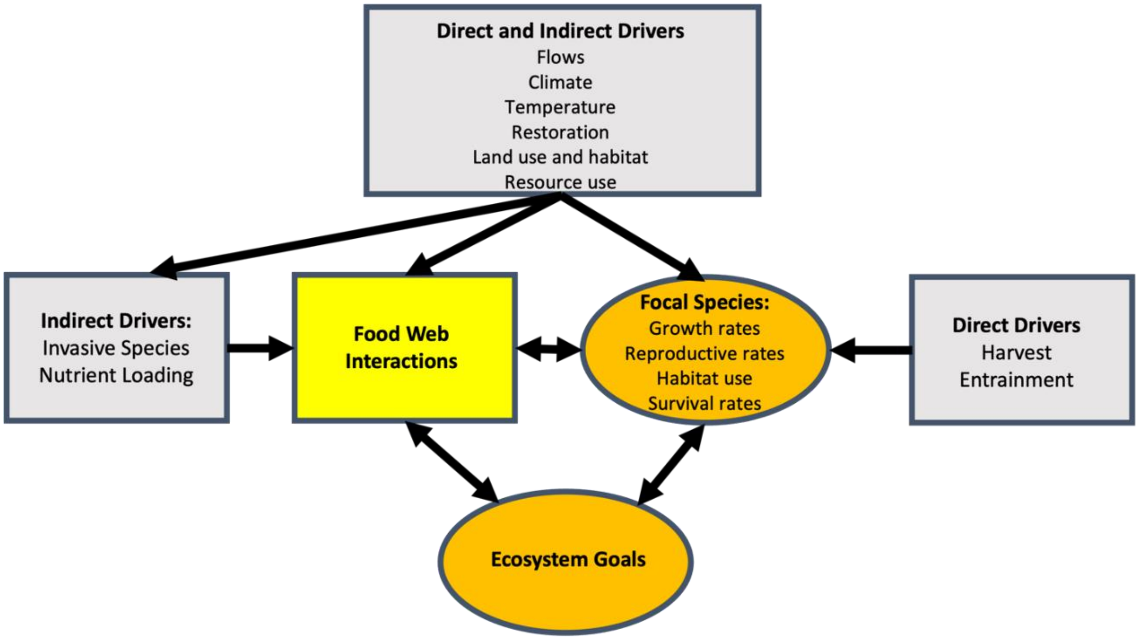

Figure 1: Conceptual diagram illustrating the importance of food web interactions (yellow box) to the abundance, function, and biological functions of focal species (orange ovals). Traditional Delta management normally considers both direct and indirect drivers (gray boxes) to focal species' populations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

Box 1. Food web science facilitates multi-species management in the Chesapeake Bay and mid-Atlantic

The Chesapeake Bay is the largest estuary in the United States connecting about 150 rivers to the Atlantic Ocean. The Chesapeake Bay watershed is home to over 18 million people and the estuarine Bay supports commercially and recreationally-important fisheries (Chesapeake Bay Program 2023). Like the Delta, managers in the Chesapeake Bay contend with non-native species introductions, watershed runoff and water contamination, population growth, land-use conflicts, and declining native species populations.

A key management challenge in the Chesapeake Bay is how to effectively reduce nutrient loading to improve water quality and maintain healthy fish and shellfish populations. Historical fisheries management in Chesapeake Bay relied on single-species assessments (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 incorporate food webs include detailed studies of the diets of the major predators, bioenergetics growth models of the key predators and dominant pelagic prey such as anchovies (*Anchoa mitchilli*) and menhaden (*Brevoortia tyrannus*), and linking the spatio-temporal growth of menhaden to a three-dimensional hydrodynamic model based on 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 goals of filling data gaps and supporting stock assessment modeling activities for both single- and multi-species modeling approaches (VIMS 2023). Data from this fisheries-independent survey are used to estimate population sizes and geographic and temporal distributions for priority species, determine major links of the food web through stomach content analysis, and determine 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 modeling efforts have continued, including the development of Atlantis (Ihde 206) and several Ecopath with Ecosim models for menhaden (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 a step-wise, iterative 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.

Predicting the impacts of habitat restoration, fisheries harvests, contaminants, and changes in environmental and biological drivers (e.g., climate, changes in nutrient loading, invasive species) on species and 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 section “Food Web Applications in other Large Ecosystems”). Food web interactions can be quantified and visualized in a variety of ways (see review by Naman et al. 2022 and section "General Food Web Modeling Approaches" below). 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 key species within a food web (dynamic or functional food webs; Embke et al. 2022).

Information on food webs can be collected through direct sampling of diets, such as stomach (gut) contents, using tracers (e.g., stable isotope analysis), and through behavioral observations. The specific method employed depends on the scientific or management questions of interest (Box 2; Zale et al. 2013). Many food web studies begin with a conceptual diagram to identify the presumed trophic connections among individual species or taxa groups. The Delta is rich with well-vetted conceptual models of many species and selected food webs, a significant jump-start to quantitative modeling.

Box 2. Two of many methods available for describing and quantifying food web interactions (see Naman et al. 2022 for a comprehensive list).

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 done without specialized equipment.

Stable isotope analysis: Stable isotope analysis relies on the presence of isotopes (primarily of carbon, nitrogen and sulfur), 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.

Food Webs in the Sacramento-San Joaquin Delta

The Delta, as one of the largest estuaries on the west coast of the United States, provides water for communities and agriculture within California while supporting many biodiverse and productive 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 an extensively 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 has complex ecosystems characterized by multiple food webs that differ regionally and vary in their structure over time and space. Physical modifications, in addition to the introduction of non-native species and the changing climate, have challenged management, changed species compositions, and significantly altered many of the food webs (Brown et al. 2016).

Fortunately, the Delta is a well-studied and monitored system, and previous investigations provide an encouraging foundation for understanding food web processes. Past investigations primarily focused on the effects of bottom-up processes and lower trophic levels in sustaining individual species (Jassby et al. 2003; Cloern et al. 2016, 2021). However, emerging investigations have shown that top-down effects can also drive food web dynamics (Rogers et al. 2024).

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, total net primary productivity in the modern Delta (e.g., via photosynthetic and bacterial processes) has decreased substantially 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 and food availability is thought to inhibit the native fish populations (Jassby et al. 2003; Bardeen 2021; Slater and Baxter 2014). Some models suggest that both planktonic and detrital food webs are important for native fish (Bauer 2010; Durand 2015; Kendall et al. 2015; Hammock et al. 2019; Sommer et al. 2020).

Other environmental changes have altered Delta food webs, including the widespread decline of pelagic organisms (primarily fishes; Sommer et al. 2007; Baxter et al. 2008). The pelagic organism decline (POD) was considered 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 non-native clams (e.g., *Potamocorbula amurensis*) on water clarity and food availability (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, contaminants, and climate change.

Uncertainty around the mechanisms underlying the POD, the role of invasive clams, and the need to improve management and understanding of protected species spurred research that contributed to a better 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 highlighted several gaps, including the need for long-term monitoring, understanding the effects of harmful algal blooms, conducting interdisciplinary analysis and synthesis, and a need for a better understanding of the causes for the POD (Kimmerer et al. 2008; Brown et al. 2016). A key suggestion from these reviews was to continue development of conceptual food web models and frameworks, ones that could be used to guide large-scale restoration and to address the spatiotemporal complexity.

Various interactions among species have been previously examined in the Delta. For example, striped bass is considered a generalist predator (Grossman et al. 2013; Grossman 2016), and their degree of focus on certain prey may increase during specific seasons and environmental conditions (Brandl et al. 2021, Colombano 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 are known to increase habitat for juvenile largemouth bass but larger, adult fish are found at all densities of vegetation (Conrad et al. 2016), indicating the importance of including life-history and stage-based life cycles in examining food web interactions.

There are, however, important gaps in food web knowledge for the Delta. While several studies identified aspects of upper trophic species interactions (e.g., Grossman 2016), absolute and spatially resolved abundances of the higher trophic levels are hard to quantify. The challenge is due, in part, to a lack of long-term and sufficiently fine-scaled data on large piscivorous fishes and the under-examined potential impacts of water operations and exports on non-listed species that dominate the biomass (Mac Nally et al. 2010; Rogers et al. 2024). 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, tidal marsh restoration 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 and quantified if they are to be effectively used in models guiding management actions (Brown et al. 2016; Sturrock et al. 2022). The fish modeling and management focus has been primarily focused on single species’ responses to environmental and ecological drivers and species restoration actions related to water management. Food web effects have only been implicitly represented (e.g., single term for natural mortality) in single species models of upper trophic levels.

General Food Web Modeling Approaches

Modeling food web processes encompasses a broad range of approaches, from simple linear models to complex, spatially and temporally explicit assemblages of data to describe species and environmental conditions (Naman et al. 2022). Improving the understanding of food webs and applying that to the development of realistic and accurate models, can help identify features that promote stability and biodiversity within an ecosystem (Kortsch et al. 2021).

In the review that follows, we describe types of food web models that have included upper trophic levels in a mechanistic or quantitative manner, using examples from waterbodies throughout North America. At the most basic level, the primary goals of food web models are to show what species are eating, what their preferred foods are, and how much of each food type they are eating (Naman et al. 2022). Each model type differs in the level of complexity, the spatiotemporal scales covered, the limitations of the model type, and the utility of the model (summarized in Table 1).

Linkage or connectedness food web models. These show generally “who is eating whom” by displaying the presence/absence of species interactions. These models are relatively easy to construct, require only a very basic level of understanding of connections between species, and allow for a general understanding of the effects of changes to network structure on the food web (Dunne et al. 2002). Depending on the temporal and spatial scales of interest, these models determine species connections through diet analyses (the identification of gut content through species identification or genetic information) or stable isotope analysis (Box 1). In this model type, linkages between species are evenly weighted, and the importance of connections between species is not displayed.

Table 1. A summary of data requirements, model advantages, analytical issues, and potential applications for the Delta of modeling approaches commonly used to understand food webs.

Model Type	Data Requirements	Model advantages	Analytical Issues	Applications for Delta, selected examples
Linkage/ connectedness food webs *Who is eating whom/presence or absence of interactions*	• Stable isotopes *(lower taxonomic resolution, but longer time scale)* • Diet analyses through identification or genetics of stomach contents *(higher taxonomic resolution, but short time scale)*	• Relatively easy to construct • Can use network analysis to understand food web connections	• Linkages are evenly weighted; cannot determine importance of each link • Can be labor-intensive (e.g., diet analyses)	Allows for a base understanding of species connections Examples: Dunne et al. 2002
Diet composition food webs *Weights linkages by the importance of each resource to consumers*	• Calculate the % contribution (by biomass) of prey to diet of each consumer • Tools: Stable isotopes and/or diet analyses	• Shows the importance of each resource to consumers	• Does not account for quantity or quality of consumption • Does not allow examination of competition, top-down control, and other important processes	Adds useful complexity to understand and rank prey items by importance for consumers Examples: Vander Zanden et al. 1999 Muro-Torres et al. 2019
Energy flow/flux food webs *Linkages are weighted by the amount of energy flow over*	• Consumer production estimates (biomass over a certain amount of time) • Consumer diet information (from diet analyses, isotopes)	• Map consumptive pathways that support species of interest • Can identify food web metrics that promote stability	• Define data requirements • May need to rely on assumptions to create	Applicable for many common management questions/issues, such as food limitation, competition, carrying capacity, and others. Examples: Cross et al. 2011

Model Type	Data Requirements	Model advantages	Analytical Issues	Applications for Delta, selected examples
a defined amount of time	• Bioenergetic information (quantity consumed)	• Management-relevant outcomes		Bellmore et al. 2013, 2015 Walters et al. 2020
Bioenergetics models *Understanding the flow of energy within individuals as they progress through their life cycle*	• Thermal experience • Temporal or ontogenetic diet composition • Consumer growth • Predator energy density • Prey energy density (These can be empirical inputs, literature values, or be used to explore different scenarios)	• Easily developed and applied to life stages of multiple species • Often used as the growth sub-model for many other model types • Provides a basis for linking across life stages for a species, and across species for a food web • Adaptable for application on different spatiotemporal scales • Consumption estimate output can be used to determine population consumption	• Define data requirements • May need to rely on assumptions • Requires additional sub-models (assumptions) on mortality to scale to the population level • Challenging to match spatiotemporal scales of lower- and upper trophic level organisms	Can use to determine how climate change, contaminant bioaccumulation, species introductions, seasonal carrying capacity, different life history strategies, energetic growth potential, and thermal changes may affect species and food webs Examples: Loboschefsky et al. 2012 Rose et al. 2013 Hansen et al. 2021
Multi-species models or Models of Intermediate	• Detailed data on the focal species in terms of growth, diet, feeding, mortality,	• Reduces uncertainties by scaling the model to the specific questions	• No general rules for determining what species and processes to include	Intermediate complexity models may provide more direct information about key questions of interest, while still

Model Type	Data Requirements	Model advantages	Analytical Issues	Applications for Delta, selected examples
Complexity for Ecosystem assessments (MICE) models *Points to 3-D models that focus on a relatively small portion of the food web to assess specific questions in sufficient process detail without the complexity of including the entire food web in detail*	predation, reproduction, movement, and distribution	• Avoids having to represent poorly understood species in detail • Can be run thousands of times to allow for propagation of uncertainty and presentation of results as probability distributions rather than point or mean values only	for the focal species and in how much detail • Challenges in how to represent the other aspects of the food web to ensure realistic predictions of the focal species • Calibration and validation are never straightforward because the model and field data may include different variables that affect the focal species	reflecting aspects of ecosystem complexity Examples: Punt et al. 2016 Angelini et al. 2016 Buchheister et al. 2017 Kaplan et al. 2019 Howell et al. 2021
Large-scale ecosystem (end-to-end) models *3-D models that usually integrate various aspects of biology, physics, geochemistry,*	Depends on the model, but likely comes from a synthesis of data: • Production to biomass ratio • Consumption to biomass ratio • Biomasses of all members of the food	• Represents all major species so that community and ecosystem-level predictions are possible • Some modeling programs can be open source and able	• Define data requirements, which may increase uncertainty in the model • Usually complex, results can be challenging to interpret	Not designed to predict the future, but can be very useful to compare scenarios for different management actions Examples: Hyder et al., 2015 de Mutsert et al. 2021 Zhang et al. 2023

Model Type	Data Requirements	Model advantages	Analytical Issues	Applications for Delta, selected examples
upper trophic levels, management, and economics. Often modular by design.	web in time and space • Diets • Spatial distributions and movement behaviors • Data requirements of the models coupled with the upper trophic levels (e.g., hydrodynamics/physics models, lower-trophic models if developed separately)	to modify source code • Tailor models to objectives and useable data, add modules • Can add fisheries mortality • Can be part of an ensemble of models can provide confidence for projections	• Coupling of models that operate on different spatiotemporal scales can be challenging	

Diet composition food webs. These weight each linkage by the importance to the consumer. This is achieved by calculating the percent contribution (usually a biomass measurement) of each prey type to the diet of a consumer and adds useful complexity to linkage or connectedness food web models by enabling understanding and ranking of prey items by importance. However, this type of model does not account for the *quantity* or *quality* (nutritional input) of the prey item, and therefore does not answer management questions that involve competition, top-down control, or other drivers to food web structure.

Energy flow or flux food web models. Each linkage is weighted by the amount of energy or nutrient flow from prey to consumer over a specific amount of time. This type of approach is applicable to many food web processes important for management, including carrying capacity, food limitation and competition. Data needs for flow models consist of three components: 1) consumer production estimates (biomass over a certain period), 2) consumer diet information (from stable isotopes or diet analysis), and 3) bioenergetics information (quantity of prey type consumed). Flow models are frequently constructed using a “Trophic Basis of Production” approach (Benke and Wallace 1997). Using flow models, managers can map consumptive pathways supporting species of interest, such as energy from phytoplankton or detritus, and can identify food web processes promoting ecosystem stability (e.g., multi-habitat feeding, predator-prey interactions) which may be crucial information for restoration projects. For instance, in the Colorado River, scientists used a flow food web to understand how altered flows from management actions changed the magnitude of energy flows from insects to rainbow trout (Walters et al. 2020). Under high flow conditions, an increase in midges (Chironomids) became a crucial food source that supported increased populations of rainbow trout, despite a decrease in their normal insect prey items (Walters et al. 2020). While food web models emphasizing the flow or flux of energy or nutrients are relatively data-intensive, they can provide information highly relevant for ecosystem management.

Bioenergetics models. These account for each organism’s ability to process energy (metabolism) related to growth and reproduction. There are several commonly used formulations, including the Wisconsin version and dynamic budget models. These models have a wide variety of benefits and capabilities, including understanding growth at different life stages, across species, and under different spatiotemporal scales. They can also be used to determine how climate change, changing temperatures, contrasting life history strategies, and energetic growth potential may affect food webs and individual species of interest. Relatively simple scaling of growth can be done with readily available data to estimate predatory demand (i.e., total mortality of a forage species due to predation). Bioenergetics models can be integrated into other food web model types (multi-species and large-scale models) and used as the basis representing growth of individuals or age/stage classes. Bioenergetics models often have relatively high data requirements, including temperature sensitivity curves for species, temporal or ontogenetic diet composition data, information on consumer growth rates, and energy densities for both prey and consumers. Data inputs can be empirical inputs or values from the literature, which may rely on assumptions of similarity between species.

Multi-species or Models of Intermediate Complexity Ecosystem assessments (MICE) models. These focus on a subset of the food web that is most relevant to addressing specific questions and do not include the entire food web in detail. These models require detailed data on the growth, diet, mortality, predation, reproduction, movement, and distribution of the focal species. Advantages of MICE models are not needing to represent poorly understood species in detail and a reduction in uncertainty by scaling the model to the guiding questions. They can be run thousands of times, thereby enabling the use of Monte Carlo methods to propagate uncertainty and express results as changes in risks. However, these models can be challenging to calibrate and validate and there are no general rules for which supporting species and processes to include. Several examples exist including the Northwest Atlantic Continental Shelf model of intermediate complexity (NWACS-MICE) (Buchheister et al. 2017), a Pacific Sardine MICE model (Punt et al. 2016), and a MICE model for Pacific sardine in the California Current (Kaplan et al. 2019).

Large-scale ecosystem (or end-to-end) models. These are usually 2-D (horizontal) or 3-D models that integrate biology, physics, geochemistry, and both upper and lower trophic levels. Some include highly detailed management and socio-economic modules; taken together with the biology and physics, these models strive to obtain a holistic understanding of ecosystem function (Kaplan and Marshall 2016). These models are often not designed for precise forecasting but can be very helpful in understanding longer-term outcomes of different species management actions, stressors, or climate conditions. Place-based examples of models used to inform species and ecosystem management include the Great Lakes Earth System Model (GLESM) (Zhang et al. 2023) and an ecosystem model for the Louisiana Coastal Master Plan (de Mutsert et al. 2021). Specific data inputs depend on the base modeling framework, such as Atlantis or Ecopath with Ecosim (EwE), but the biological data inputs for modeling food webs often include biomass values, production to biomass ratios, consumption to biomass ratios, a measure of the efficiency of the system (e.g., proportion of production used), and others. Data can come from empirical methods, the literature, fisheries stock assessments, surveys, and estimates from experts or other systems. For example, information on contaminants or economics can be added into the model or through additional modules, or a food web model can be a part of a suite of models that may provide confidence for projections. Most importantly, effectively communicating model results (whether simple or complex) to different audiences is critical for ensuring model results are appropriately interpreted and incorporated into the management decision-making. Communication has been a topic in best practices on modeling (e.g., Rose et al. 2015; Gruss et al. 2017) and in papers devoted to the topic of communication of modeling results, including non-scientists (Cartwright et al. 2016) and managers and decision-makers (Bodner et al. 2021; Schuwirth et al. 2019; Weiskopf et al. 2022).

Food Web Modeling: Complexity, Prediction and Uncertainty

Determining the optimal level of complexity for a food web model remains a challenge and is often done by the model developers and managers on a case-by-case basis (Geary et al. 2020). There are benefits and analytical issues for both simple food web models and complex food web models (Table 1). For example, simple models may not represent site-specific conditions for food webs and can have inadequate details to inform specific management decisions, but they are often preferred by management because they can be understood and clearly validated and can facilitate understanding of ecosystems. In contrast, complex models provide the flexibility to include site-specific information and can simulate specific management alternatives in detail. However, complex models can be hard to interpret, more challenging to communicate, and/or have substantial data requirements.

There are a similar set of tradeoffs for the range of spatiotemporal scales represented in food web models. Broad spatial scales may better represent the true heterogeneity at the system or watershed scale, while models with finer spatial and temporal resolution may be more useful for answering specific, localized questions or looking at short term processes. The trophic levels and species of interest may also drive the spatiotemporal range; upper trophic levels operate over longer and broader scales than lower trophic levels. The taxonomic level of resolution also can be altered by grouping species into trophic levels or functional groups, or by examining individual species.

The general issue of identifying the optimal complexity of a food web model is often done on a case-by-case basis. Food web modeling is often iterative in practice and part of these iterations is testing simpler and more complex representations of the food web to identify a representation that balances data availability and the ability to answer the management questions at needed taxonomic, spatial and temporal resolutions. The issue of what complexity is optimal is therefore often solved by testing different versions of the model on a site-specific and question-specific basis. Ultimately, the food web model type and level of complexity should be driven by the management question(s), trophic level(s), and species of interest. A combination of food web models, or ensemble models, may be helpful to address different questions or habitat types in the Delta. Multiple workshop participants stressed that models of intermediate complexity (MICE models) were very useful, and that the "best model" was often the *simplest* model that could address the primary management questions (i.e., the "sweet spot" in Collie et al. 2016).

Food web modeling done to date in many systems has been used to evaluate and predict the effects of environmental drivers (such as salinity, contaminants, nutrients, and temperature) on species abundance and interactions (such as predation risk) within the context of future climate change (e.g., Osakpolor et al. 2021; Naman et al. 2022). Quantitative models with predictive capabilities are especially useful for management because they enable an evaluation of environmental and management changes on multiple future scenarios (e.g., Trifonova et al. 2017).

Most management questions in other ecosystems, discussed as part of the workshop, expect some level of prediction from the food web models. The current state of food web modeling makes such efforts well-suited for strategic analyses in many cases, but they are limited in their ability to predict short-term (e.g., next year) and spatially specific outcomes on a fine scale (i.e., 10's to 100's of meters' resolution). In general, food web models, if properly selected, configured and tested, can make credible predictions of averaged outcomes on decadal or regime scales and for ecologically distinct regions.

Many questions require projecting the effects of actions into the future; therefore, using these models requires dealing with the direct and synergistic effects of climate change (e.g., temperature, hydroperiod). A major challenge everywhere is to formulate the food web models in a manner that enables them to be realistic under the novel (never previously observed) environmental conditions (e.g., Norgaard et al. 2021) that occur under plausible futures (Albouy et al. 2014; Zhang et al. 2017). Rose et al. (2024) recently reported on the challenges and possible solutions for equipping bioenergetics models, which often form the growth and reproduction sub-models of many food web models, for effectively incorporating environmental divers emanating from climate change.

These issues also apply more broadly to mechanistic (although less so to statistical) food web modeling. Simulation techniques such as Monte Carlo and other error propagation techniques (Santelli et al. 2008; Razavi et al. 2021), ensemble modeling that uses multiple alternative food web models (Gardmark et al.2013; Reum et al. 2020), and management strategy evaluation (e.g., Perryman et al. 2021), alone or in combination, are all candidate approaches for addressing the uncertainties of food web model predictions under climate change. These approaches will be especially useful when results are used along with other models to inform management about specific plans or actions.

Previous Food Web Modeling in the Delta

Fortunately, a massive amount of science has been conducted in the Delta, and there is good amount of ongoing, site-specific research relating to food webs that includes water quality impacts on species, diet compositions, isotopic analyses, quantifying phytoplankton and zooplankton communities, energy and nutrient flows, and the effects of environmental drivers (see the Delta Science Tracker).

Several food web models have been developed for the Bay-Delta using some of these data and analyses (e.g., Durand 2008, 2015; Bauer 2010; Rogers et al. 2024). Each model examines different temporal and spatial aspects of the Delta food web, as well as using distinct modeling methods (e.g., conceptual models, biomass-based multiple predator and prey models, multivariate statistical and structural equation models). These efforts have focused primarily on the role of bottom-up processes structuring food webs and rely heavily on long-term monitoring in the Bay-Delta conducted by state and federal agencies and by academic institutions. A collective examination of these efforts suggests, however, that it may be beneficial for new quantitative food web models to initially focus on a small number of species that comprise the highest proportion of biomass in Delta. Therefore, the newer food web models may include many non-native species, such as small-sized fishes, large predatory fishes, freshwater clams, and macrophytes, which have received less research attention in previous studies. Many workshop participants felt that once trends in the dominant aquatic species were determined, the emerging food web models could be revised to focus on specific regions of the Delta and expanded to include lower abundance species and species with high management importance.

Many of the existing Delta models that attempt to represent the entire food web are notably 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 the Bay-Delta food webs (circa 1980's) showed that mid-upper trophic levels (comprised primarily of fishes) contributed 37% of food web biomass. Phytoplankton and detritus contributed 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 as opposed to detritus and separate the roles of pelagic and littoral food webs to more clearly inform management choices.

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 estimate 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. Importantly, 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 recent food web model differentiated the role of bottom-up, top-down, and environmental drivers in shaping pelagic food webs (Rogers et al. 2024). Using structural equation modeling, this approach showed that for zooplankton and estuarine fishes, bottom-up effects were stronger in upstream, freshwater regions, and top-down effects were stronger in downstream, brackish water regions. However, the authors note that there were no long-term data on the biomass of large-bodied piscivorous fishes to add into the model. As a result, upper trophic level food web interactions may not have been accurately represented (Rogers et al. 2024). Additionally, they identified several novel relationships that were not identified in another statistically based food web model (Mac Nally et al. 2010). Specifically, the direct impact of chlorophyll on zooplankton biomass since the *Potamocorbula* clam introduction, the unique trophic relationships among zooplankton groups, and the effects of flow, salinity, and temperature on different regions of food webs across the Delta.

Previous efforts to model food webs were hampered by the ever evolving and highly altered environmental conditions within the Delta. These conditions 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. Understanding food web dynamics can offer insights into species interactions, trophic relationships, and the flow of energy throughout the system that collectively impact survival, growth, and reproduction of key species (Naman et al. 2022).

The Delta's aquatic food webs experience many stressors like those in other complex and highly altered ecosystems. Following the classic research and management actions of altering food webs by changing consumer populations to control algal growth in Lake Mendota, Wisconsin (Carpenter et al. 1985), management actions incorporating food web processes have been considered 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 (Boxes 1, 3, 4, and 5) throughout the text.

While there are differences among ecosystems, such as the non-native species or local regulations, the need to understand species interactions and the effectiveness of different management actions is 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 providing quantitative food web knowledge to inform 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; Kortsch et al. 2021; Lewis et al. 2022).

Food Web Modeling: How to Proceed in the Delta

Going forward with any food web modeling involves a major technical decision on what food web model to use. Should one select an existing food web model that is well-vetted and easy-to-apply and hopefully useful, but likely not optimal, for answering the specific questions or should one expend significant effort, engage model developers in addition to model end-users, and develop a new model? There is not a standard model building process for developing food web models as there is in building statistical models. However, there are collections of best practices for developing ecological simulation models, which includes food web modeling (Gruss et al. 2017; Swannack et al. 2012; Heymans et al. 2016; Rose et al. 2015a). All ecological modeling is driven by the questions to be answered; this is relatively straightforward for the Delta. Therefore, after defining the questions guiding food web modeling, one needs to incorporate locally accepted best practices into the development of the ecological simulation models . Below, we begin the dialogue on the initial step of model selection, as this follows the identification of guiding questions and incorporating best practices.

The step of model selection is critical because the model will be part of the rest of the entire effort, and success depends on selecting a model sufficiently suitable to answer the questions. While models are often modified as part of their updating based on performance (e.g., calibration), new information, and even the questions themselves evolving, major shifts and restarts can be labor intensive and delay having results ready to inform management. Thus, the initial decision on what model to use is very important. A thorough evaluation of the questions, what is needed in a model to answer the questions, and how well the model would be supported by empirical information must be performed. EwE and other widely used models offer a well-tested food web model and a user-friendly software package. When such models match what is needed, they are an excellent solution; however, compromises are involved with using an “off-the-shelf” model because it is not developed specifically to answer the questions, and these compromises must be weighed against the benefits of using a new or heavily modified existing model.

An important consideration for selecting a food web model of the Delta ecosystem is how to represent the spatial details and the important role of hydrodynamics that governs transport of organisms, salinity, temperature, and the lower trophic level dynamics. Adding upper trophic level species to the modelled food web also raises the new challenge of representing species movements based on behavior rather than transport.

One strategy is to continue the approach being used for the lower tropic levels, which is representing the food web in the same grid as the hydrodynamics. One could extend those lower trophic food webs to upper trophic level species (including movement) and thereby simulate the full food web on the hydrodynamics grid. Lower trophic levels and fish movement (for limited durations of weeks to months) generally have been added separately to hydrodynamics models in the Delta (MacWilliams et al. 2016; Korman et al. 2021; Gross et al. 2021). There are also examples of adding a few upper trophic level species to a hydrodynamics grid that includes a lower trophic level food web (e.g., Rose et al. 2015b; Rose et al. 2013). However, representing the full community of upper trophic level species important in the food web is challenging with this approach, and aggregating into functional groups makes it more tractable but disconnects the results from fisheries and regulatory management needs. Predictions then become about general groups and are not species-specific where most management actions operate.

At the other extreme, implicitly representing the hydrodynamics and transport on a coarser grid specific to the food web model (e.g., Delta divided into subregions) is achievable (e.g., Ecospace as part of EwE is an off-the-shelf example, see Walters et al. 2010; Rogers et al. 2023) but raises some significant conceptual and technical issues. How to realistically represent the hydrodynamics and behavioral movement that occur on fine temporal and spatial scales to fluxes of biomass among large spatial cells, and updated with weekly or monthly time steps, remains challenging.

To date, this has been mostly solved by calibration rather than by mechanistic representations within the model. The physics is then implicitly represented in the model rather than explicitly (Rose et al. 2015a). This limits the predictive capabilities of the model, especially under new conditions such as plausible futures under climate change.

A key aspect of selecting a food web model is considering how the model will be used, including the concepts of nested and multi-scale models (Wu and David 2002; Getz et al. 2018) and multiple alternative models (Lewis et al. 2021). While some questions can be examined using point or coarse-resolution food web models and their associated implicit representation of the effects of hydrodynamics, many management-relevant questions for the Delta require explicit treatment of hydrodynamics along with the food web. Food web modeling in the Delta offers an opportunity to integrate physics, movement ecology, and predator-prey dynamics to enable short and long-term predictions of food web structure and energetics on spatial scales relevant to many management actions. For example, the question of how localized pulses of food subsidies affect the food web and key upper tropic level species is prime for a food web modeling analysis.

Potential Applications of An Improved Understanding of Upper Trophic Level Food Webs

The Delta ISB recognizes that some management questions can be best answered with a species-level analysis, which equates to a population-level assessment. However, other management questions are better answered, or even can only be answered, with a food web approach. Food web modeling would enable higher confidence answers to certain questions, especially those that are heavily influenced by indirect ecological effects mediated through inter-species interactions involving predation and competition. Indirect effects can arise in a variety of situations, such as when a stressor differentially affects species in the food web, under some conditions of multiple stressors when prey or predator species are a mix of more sensitive and less sensitive species than the species of interest, and to explicitly accommodate changes in productivity or spatial distributions of prey and predators (Dill et al. 2003; Beauchesne et al. 2021; Glibert et al. 2022). Food web responses are often a mix of bottom-up and top-down controls that require explicit treatment of all the key species within a food web (Lynam et al. 2017). It is possible to include indirect effects with a species-level model (e.g., Kimmerer and Rose 2018;

Rose 2023) but it requires many assumptions and simplifications. A complementary food web level analysis, perhaps in combination with a species-level analysis, would provide a more complete quantitative evaluation of management questions that are influenced by indirect ecological effects. Further, there is a subset of management-related questions that simply require models that can generate multi-species, community, or higher-level responses.

Several direct applications of food-web models to management questions in the Delta are underway and can be further advanced or, in some cases would involve new initiatives (Rose et al. 2024). Below, we briefly illustrate five applications that have been largely informed by case studies from outside the Delta and from recent research in the Delta. Additional details, including the associated management questions, specific benefits of using a food web approach, next steps to implement a food web process, and references for each application are provided in Table 2.

Table 2. Applications for employing a food web approach to improve natural resource management in the Delta. The benefits of a food web approach, suggested priorities, and key references are described for the management questions in **bold**.

Application & Example Management Questions	Benefits of Food Web Approach	Suggested Priorities	References and Examples
Single-species management 1. **How do specific management actions and environmental drivers affect key species?** 2. What food resources support the listed species?	• Species interactions affect key species directly or indirectly; cannot be fully understood or predict changes in populations without examining key aspects of the life cycle and food web • A coherent monitoring plan advances understanding of food webs, allows treatment of management actions as experiments, and enables examination of full ecosystem responses to actions over time	1. Implement long term monitoring that quantifies **all major** aspects of the food web. Examples: • Large predators • Benthic invertebrates • *Quality* of food 2. Begin with discrete, short-term management changes (e.g., flow releases, salinity gates) designed using experimental method. Adaptively adjust management action based on outcomes as currently done for summer-fall habitat for Delta Smelt and the North Delta Flow project.	A complex, Ecopath with Ecosim food web model of the Mississippi Delta showed differential responses of black drum, blue crab, eastern oyster, and spotted seatrout to a Coastal Master Plan to mitigate land loss (de Mutsert et al. 2021). An ecosystem food web model of intermediate complexity (MICE model) showed the possible effects of different harvest rates on Atlantic menhaden predators, including birds (Chagaris et al. 2020). Predator-control sportfishing of a native salmon predator from the Columbia River, the northern pikeminnow, may cause a subsequent increase in other predators (e.g., walleye

Application & Example Management Questions	Benefits of Food Web Approach	Suggested Priorities	References and Examples
			and smallmouth bass; ISRP 2023). Several coupled flow-zooplankton-fish models already assess the potential efficacy of management actions in the Delta (e.g., Sommer et al. 2020, Beakes et al. 2021, Frantzich et al. 2021, Davis et al. 2022a, Hassrick et al. 2023, Lee et al. 2023).
Ecosystem-Based Management (EBM) **1. How do changes to environmental conditions affect food web interactions and abundances of different species?** 2. How does one manage target goals to better address tradeoffs among priorities (e.g., water quality and flow)? 3. What are the roles of high biomass species in the food web?	• Understanding food web dynamics advances effective EBM • Key ecological species may not be the same as the listed/regulated species • Examining food web responses to changing conditions may reveal differential vulnerability of species to environmental changes	*1.* Develop performance metrics that represent a holistic view of ecosystem function, such as *ecological reference points* 2. Connect laboratory or field experiments to evaluate sublethal effects of stressors on species into models 3. Create a model/ series of models (of appropriate spatiotemporal scales) designed to predict changes in species interactions over time	A spatiotemporally explicit food web model of the upper Gulf of Mexico allowed managers to understand that changes to nutrient loading and hypoxia influences habitat competition between key fisheries species (Glaspie et al. 2019). Management agencies developed ecosystem reference points to understand how menhaden harvest affects the

Application & Example Management Questions	Benefits of Food Web Approach	Suggested Priorities	References and Examples
			larger mid-Atlantic ecosystem (Chagaris et al. 2020).
Invasion of non-native species 1. **How will the Delta's ecosystem respond to new species introductions?** 2. How does aquatic weed control affect upper trophic level food webs?	● Non-native species change food web dynamics (e.g., reducing prey, increasing competition, changing predators) ● New species replacing native vegetation and prey may change *nutritional quality* of food, potentially leading to changes in foraging behavior, food web dynamics ● Eradication/reduction of non-native species may affect native species that feed on non-native species	1. Monitor non-native species in habitats outside the pelagic zone (i.e., in locations generally not included in monitoring efforts or thought to be marginal habitat) 2. Add monitoring that considers the *quality* of food resources available 3. Add modules into existing food web models to forecast the impacts of non-native species introductions or eradication	A linked, earth system model determined that non-native *Dreissena* mussels reduced the benefits of vertical mixing for most species in Lake Michigan (Zhang et al. 2023). A food web perspective showed impacts of non-native shad on salmon and other native species in the Columbia River basin, especially through habitat overlap and competition for food (ISAB 2021).
Ecosystem restoration 1. **Does restoration affect food type and availability for upper trophic levels?** 2. How does the type and location of restoration impact fish abundances?	● Evaluate to what degree habitat restoration will increase food availability for native fish ● Understanding the flow of energy and nutrients through the Delta's ecological system is essential for determining	1. Measure the biomass of fish at restoration sites, determine diet selectivity, and quantify food production. 2. Accurately monitor biomass of primary producers in the system (not just chlorophyll, which can overestimate accessible prey), noting that	The composition and nutritional quality of food resources for salmon, a representation of carrying capacity, in the lower Columbia River Basin differed across habitat types (including restored areas) (Roegner & Johnson 2023).

Application & Example Management Questions	Benefits of Food Web Approach	Suggested Priorities	References and Examples
3. What are the food web processes that influence "winners" and "losers" in response to restoration activities?	the impact on upper trophic levels • Restoration performance metrics often jump from primary production to abundance of fish, which is typically not a direct pathway An exception is the Fish Restoration Program sites, which include secondary production (zooplankton and wetland-associated invertebrates) as well as primary production (Sherman et al. 2023). • Examining effects of restoration using a food webs approach would reveal how restoration impacts individual species • Evaluate the relative response of native vs non-native competitors or apparent competitors	not all sources of primary production are equally available for consumption 3. Understand detrital processes and their roles in Delta food webs 4. Create food web models to understand how energy and nutrients reach upper trophic levels 5. Expand on the use of *in-situ* experiments with restoration that include key food web processes over time in the monitoring of restored areas	Forecasted ecosystem responses to three types of restoration in the Methow River, WA, showed that restoration effects on food web dynamics impacted the ecosystem's capacity to support native fish (Bellmore et al. 2017).

Application & Example Management Questions	Benefits of Food Web Approach	Suggested Priorities	References and Examples
Contaminant exposure and cycling **1. What are the sub-lethal effects – as delivered through the food web – of contaminants to upper trophic levels?** 2. How do contaminants affect the relative abundances of key species? 3. What are the main contaminants of concern, as related to food web processes?	● A food webs perspective enables understanding of the vulnerability of different species to contaminants and allows for quantifying bioaccumulation and bioconcentration ● Understanding *sublethal effects* can better represent the impact of contaminants; food web interactions and processes may be affected at concentrations other than the lethal dose	1. Monitor the general use (including urban use) and the concentrations in organisms for contaminants of concern, and adaptively manage 2. Conduct experiments measuring the effects of contaminants, with a focus on predator-prey interactions, movement, and behavior 3. Acquire samples for measuring contaminant concentrations during routine sampling 4. Develop a model of contaminant pathways through the Delta's ecological system	Coho salmon exposed to copper contamination displayed reduced anti-predator behaviors due to sensory impairment and were more vulnerable to predation from cutthroat trout (McIntyre et al. 2012). Field experiments and regular Delta monitoring show that selenium accumulation, in part from bioaccumulation, in native Sacramento splittail causes spinal deformities (Johnson et al. 2020; Stewart et al. 2020).

Individual species management and effects of environmental drivers

Interviewees and workshop participants noted that much of the fish-related science, management, and regulations in the Delta is focused on protection of state or federally listed species. Full life-history models are available for key species such as Chinook salmon and Delta smelt. Habitat modifications are often focused on the direct impact on these listed species as guided by regulations and legal requirements. It is well recognized among Delta scientists that food webs can play an important role in affecting 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 since nearly all these environmental drivers and management actions affect other species as well (Figure 1).

Ecosystem-based management

While ecosystem-based management (EBM) is not currently utilized in the Delta, it has great potential to improve environmental and social conditions. It recognizes the full array of interactions within an ecosystem, including humans, rather than considering single issues, one or only a few key species, or ecosystem services in isolation (Geary et al. 2020). The concept of EBM 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, has 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; Geary et al. 2020).

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, migratory birds, and other species managed for harvest. A poor understanding of food webs can impact the outcome of management actions, yet quantitative food-web science is often insufficiently included in natural resource management (Naiman et al. 2012; Naman et al. 2022).

Currently the regulatory drivers of the Delta ecosystem are single-species management, not ecosystem-based management (Mount et al. 2019). If policy decisionmakers opt for moving toward an ecosystem-based management approach, then a clear understanding of the food web dynamics, ideally with predictive capacity for comparison of management scenarios, would be needed. It is well accepted that knowledge of food web dynamics would contribute to a comprehensive understanding of the Delta ecosystem by quantifying the flows of carbon, energy, nutrients, and contaminants into and through organisms and by quantifying how the resulting flows influence population and community structures and interactions. It would allow the implementation of experimental management actions and the monitoring of management results to determine long-term success or failure (Brussard et al. 1998). For instance, modification of wetland and riparian vegetation, the arrival of an invasive species, or a change in nutrient inputs to the system (Box 3) directly influence fishes and their food supplies with the effects extending throughout the entire ecological system as individuals adjust behavior and feeding to the novel environment. These individual decisions—collectively—are ecologically manifested on larger spatial and temporal scales as enduring modifications to population dynamics and community structures. Management decisions about wetland and riparian vegetation, as well as water regimes and other components of the environment, can be adaptively used to forecast possible outcomes from the ever-evolving predator-prey dynamics.

EBM would integrate biological, social, and economic factors into a comprehensive strategy for the protection and enhancement of sustainability, diversity, and productivity of natural resources. As a *management* approach, it addresses cumulative impacts, balances multiple, often conflicting, objectives, and is guided by an adaptive management approach (O'Higgins et al. 2020). Employing a food-web perspective that extends beyond narratives and combines both upper and lower trophic levels is an integral component of an effective EBM strategy for the Delta.

Box 3. Understanding the impacts of nutrient inputs in the Gulf of Mexico

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 is required for a greater understanding of the effects of different drivers on ecosystem processes. An ecosystem (end-to-end) 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 coequal goals in the Delta (Integrated Ecosystem Assessment 2023). Several projects in the Gulf of Mexico include food web interactions as key pieces 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 directly or indirectly informed NOAA in managing the natural and socio-economic benefits that the Gulf of Mexico provides.

Invasion of non-native species

The invasion and establishment of non-native species are key drivers of ecosystem change. The San Francisco Estuary is one of the most invaded aquatic ecosystems in the United States. 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).

For instance, food web models have aided the management of non-native species in the Great Lakes both to understand the impacts of non-native species and to control non-native species through predator introduction (Box 4). In the Delta, many non-native species are clearly established, and elimination from the Delta would be expensive, if even possible. Food web models could be used to help a key management challenge—to predict the impacts of new species introductions on key species and ecosystems—by developing scenarios to evaluate the potential effects of new introduced species and manage risks accordingly.

Box 4. Using food web dynamics to balance predator-prey populations and non-native species in the Great Lakes

The Great Lakes, a series of interconnected freshwater lakes (Superior, Michigan, Huron, Erie, and Ontario), contain 84% of North America's surface freshwater and about 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 has 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).

Researchers in the Great Lakes region 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 suppress their populations. 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 population and growth were 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 habitats, and coupling across different habitats can improve fish management (Ives et al. 2019), and also serve to evaluate the adaptive capacity of the system (i.e., the ability of the system to sustain itself during disturbances such as non-native species introductions or climatic events) (McMeans et al. 2016).

Ecosystem restoration

Ecosystem restoration is the process of assisting the recovery of an ecosystem—one that has been degraded, damaged, or destroyed—by manipulating conditions sufficiently so that natural processes are reestablished (UNEP 2021). Ecosystem (habitat) restoration is a key strategy used by managers to support species. Regulatory requirements in the Delta mandate the restoration of tidal wetland and floodplain habitat. A present focus of this type of restoration is to promote lower trophic level food production (i.e., plankton and organisms that eat plankton), to then support at-risk species (e.g., Delta smelt and Chinook salmon, e.g., Hammock et al. 2019). It is vitally important to be able to assess which species benefit directly from ecosystem restoration and understand the impacts of restoration efforts (both direct and indirect) throughout the food webs.

This is especially important in the Delta where many native fish are in significant decline, as is native biodiversity. With the signing of State Bill 37 into law by Governor Gavin Newsom, California is committed to conserving 30% of state land and coastal waters by 2030 and ecosystem restoration is expected to play a central role. Further, the Delta Plan Chapter 4 Ecosystem Amendment, approved in 2023, sets a goal of 60,000-80,000 additional acres of restoration by 2050.

How can incorporating food web processes into planning and analysis contribute to the successful restoration of native fishes and species biodiversity? The expectation is that such restoration will significantly improve the carrying capacity for native fishes and improve overall biotic diversity (Box 5; Hammock et al. 2019). These improvements can be quantified by monitoring integrative food-web processes, which not only identify species benefiting from restoration actions, but also illustrate interactions between populations and communities and show possible tradeoffs among species or food web functions. Understanding food web processes with respect to restoration allows managers to gauge the success—or not—of restoration actions. For instance, restoration of the physical habitat for juvenile salmonids, and simultaneously for their preferred food supplies, can be challenging. A focus on feeding relationships provides evidence of the level of success achieved as is being done by the Delta's Fish Restoration Program (Sherman et al. 2017). Restoration actions that achieve both objectives will be successful whereas those not providing adequate feeding opportunities—or resulting in a fundamentally changed species assemblage—will be immediately apparent.

A better understanding of the impacts of restoration on Delta food webs depends upon the specific details associated with the different types of restoration. For instance, tidal wetland restoration has been shown to benefit upper trophic level food web through production of prey items and the creation of foraging habitat, especially for juvenile fishes (Colombano 2019, Colombano et al. 2021). However, due to land subsidence, many areas in the Delta are well below tidal elevation but may be restored to managed wetlands. Studies have suggested managed wetlands may provide food web support for upper trophic levels (Aha et al. 2021), but further investigation is needed to understand how broadly applicable these findings may be in the Delta. In both cases of wetland restoration, the timescales over which these benefits develop, and magnitude of their impacts are currently being investigated. Floodplain restoration and riparian habitat restoration are also likely to have their own unique impacts on the Delta food web.

In addition to the differential effects of restoration on food webs, it is also important to consider the impacts of land use changes. For instance, there is a current focus in the Delta on the potential conversion from row crops to flooded rice cultivation. The connection between rice cultivation and the Delta food web has been explicitly investigated studied as part of the Nigiri project (https://www.nigiriproject.com/), which found young fish foraging on the flooded rice field surface exited the floodplain with larger body sizes than those that did not spend time on fields (Katz et al. 2017, Jeffres et al. 2020). There are also the potential impacts of birds on Delta food webs. Rice fields provide increased bird habitat after harvest or during fallowing (Golet 2018). Programs funded by California Department of Fish and Wildlife and implemented by The Nature Conservancy are looking to pay farmers to shallowly flood additional fields for bird habitat across the Delta (https://birdreturns.org/program/farmlands/).

Box 5. Columbia River Basin: Food web impacts to habitat restoration

Dam construction, water storage infrastructure, and water withdrawals have fundamentally altered the hydrology and 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 efforts have been 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 and help determine the key components of productive and resilient food webs, those with the capacity to withstand unanticipated changes (Naiman et al. 2012).

Contaminant exposure and cycling

The quality of the water in aquatic habitats affects the health of fish and other organisms living there. Many California waters—especially in the Delta—have high levels of pesticides, bacteria, metals, and other contaminants (California Water Quality Monitoring Council 2023). These contaminants are discharged or washed into streams from land uses such as agriculture, industry, urban and residential development, and mining operations. The pollutants contaminate drinking water and harm plants and wildlife, thereby disrupting population structure and community processes. Not only do fish assimilate mercury and other toxic chemicals from the environment, when in low concentrations they can bioaccumulate many of them through the food chain eventually passing them onto higher level consumers (e.g., birds, humans; see MyWaterQuality website: https://mywaterquality.ca.gov/safe_to_eat/index.html). Other contaminants, such as copper and insecticides (e.g., pyrethroids), can be toxic and thereby alter the vitality of specific populations or life stages (depending on their sensitivity), change animal behavior, and alter community processes (Hammock et al. 2015; Mauduit et al. 2023).

Contaminants and their role within Delta food webs were mentioned across multiple discussion groups by workshop participants. Contaminants are a concern at all trophic levels but especially so at upper trophic levels due to bioaccumulation and potential impact to human health via consumption. Some members of the community who participated in this report (via public comments, interviews, workshop) articulated that there has been sufficient research on the physiological effects and lethal limits of some contaminants (e.g., heavy metals) but the effects at the population to community levels, and the sublethal effects, of contaminants are largely unknown. Sublethal effects mediated through behavior that can structure food webs include altered feeding behavior (affects growth) and predator avoidance; these were identified as important information gaps.

A holistic knowledge of food web dynamics is essential for understanding the ecosystem-scale effects of aquatic contaminants and risks to people who eat fish. Food webs are major pathways by which contaminants flow from species-to-species as well as how contaminants affect specific life stages and population and community dynamics of fish. For example, if insecticides decrease a population of crustaceans, their predators could also be reduced through a “trophic cascade”. While food web processes are a known determinant of contaminant flows, little is known about the major biotic pathways and how they differentially affect the vitality of populations or different life stages and the sustainability of communities.

Science Gaps and Additional Considerations for Incorporating a Food Web Perspective into Delta Management

To begin incorporating knowledge of food web dynamics into quantitative applications, as presented in the previous section and in Table 2, workshop and community discussion participants and the Delta ISB identified several science gaps and other aspects to consider. These considerations are designed to aid the development of best practices for incorporating food web science into management and are further reflected in the recommendations that follow.

Science gaps

The role of behavior in food web interactions

Understanding the impact of species' behavior in shaping the dominant pathways of energy flow through the system was viewed as a significant science gap in the Delta's knowledge base. Behaviors include changes in migration patterns and habitat use, predator avoidance tactics and prey switching. Behavior is challenging to quantify and incorporate into models, but having increased awareness and understanding of the role of behavior in food web interactions will prove to be useful for effective system management.

Understanding lightly investigated components of Delta food webs

The importance of detritus and benthic invertebrates for supporting Delta food webs is not empirically well-established nor widely appreciated, despite targeted advances in understanding the importance of benthic organisms (e.g., Lucas et al. 2016, Mussen et al. 2024). The role of detritus, such as dissolved organic matter, has been long recognized as a crucial food web pathway elsewhere (Sibert et al. 1977; Naiman and Sibert 1979). Initial Delta food web models that included upper trophic levels combined the pelagic and detrital aspects of food webs but suggested that detrital pathways be considered separately in future studies (Bauer 2010). While detrital components can be challenging to quantify, they are essential for understanding the movement of carbon and nutrients through the system. Importantly, the role of detritus as a component in Delta food webs is gaining recognition (Jeffres et al. 2020). Coupling the pelagic and detrital pathways, especially the role of benthic invertebrates (clams) in interrupting the transfer of detrital energy, may be paramount in understanding carrying capacity (Durand 2015). Much concern has been placed on food availability for listed fish species, such as Delta smelt in tidal wetlands and Chinook salmon in floodplains, and additional research could clarify the role of the detrital pathway as an energy source throughout ontogeny in these species.

Benthic invertebrate communities have changed substantially over time in the Delta, primarily due to introductions of non-native species. For instance, the non-native clam, *Potamocorbula amurensis*, changed the availability of phytoplankton and altered turbidity patterns (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 (*Procambarus clarkii)* 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 are not well represented in the contemporary understanding of Delta food webs. These data gaps potentially create significant misunderstandings of the relative reliance of fish on distinct food sources and other food web relationships.

A paucity of information on large fishes and predatory birds and mammals

An ecosystem perspective and food web modeling greatly expand the species of interest and the purpose of monitoring. It is known that most natural mortality of intermediate and low trophic level species is due to predation (Whipple et al. 2000). How the spatial distribution of large predators varies over time (e.g., monthly, seasonally) becomes critical knowledge for realistically imposing predation mortality on other species (their prey) in the food web. However, top level predators (piscivorous fish) occur in relatively low densities and thus their estimation of abundance or biomass distributed in space can be difficult due to low detections in contemporary monitoring and sampling, possible avoidance of gear used that target other species, and their ability to move extensively throughout the system.

Expanding the food web represented in models to include upper trophic level species will put additional demands on long-term monitoring (Fortuna et al. 2024). The Delta is an exceptionally well-sampled ecosystem with multiple stations and multiple fish surveys occurring across seasons within each year (Bashevkin et al. 2022). Current monitoring coordinated by the Interagency Ecological Program (IEP) focuses on smaller fishes or the smaller early life stages of larger fishes (e.g., striped bass) rather than the abundance and distribution of larger individuals. Nevertheless, strategically designed monitoring, including expansion of existing surveys to areas of large predators and using new technologies (e.g., acoustics, cameras), would provide sufficient data to determine the spatial distributions of high-level predators and should be accompanied with data collection (e.g., diets) that identifies their prey. How to also include non-fish predators, such as birds, remains an outstanding issue (Goedegebuure et al. 2017). In general, bioenergetics modeling can be applied to the predator species and, using rough biomasses and diet-related information, generate predatory demands on their prey for use with food web modeling (Naiman et al. 2012: Barnett et al. 2017; Brownscombe et al. 2022).

Other predators, such as birds and marine mammals, are either not regularly monitored or are not coordinated or integrated with the IEP – creating additional impediments to a full understanding of the scientific and management implications of modifications to food webs.

Data management, data and information sharing, and synthesis

The science and management community identified several gaps in data collection and availability. These include information on trophic linkages, community-level species interactions, sub-lethal effects of drivers, and behavior. Some identified issues associated with the use of many, diverse sources of data needed to support food web modeling. For instance, data collection from multiple sources often is converted to presence/absence or relative density to maintain consistency, making validation of food web model predictions of biomasses and abundances challenging. More intentional, standardized data collection (i.e., not just opportunity-based), establishing the spatiotemporal scales of monitoring, and determining Delta-wide data priorities will be essential.

Nearly all users of food web information—through interviews, formal comments on the prospectus, and the workshop—shared that continuing to improve accessibility, meta-data documentation, and digitizing older data records would make the Delta's data more user-friendly. It was recognized that data sharing and accessibility can be a challenge as data streams generate large volumes of data and are handled differently across agencies, yet most users mentioned it contributed to a significant challenge in understanding the full breadth of information that already exists. Another frequent comment was that while the Delta's scientific community possesses an incredible amount of empirical information and experts, the community lags in producing useful syntheses of knowledge that center on a full food web perspective. This gap is especially true for upper trophic levels when viewed as a dynamic part of the entire food web. The synthesis of data and the evaluation of existing knowledge are crucial to evaluate the state of the science, and to the ability to adapt management, monitoring, and science moving forward. Basically, synthesis is a key step toward open data and science communication.

It is equally important to note that there are several ongoing improvements in data quality assurance and publication. The IEP Data Utilization Work Group is working to improve data publication and standardization, and many quality-controlled datasets from Delta monitoring programs have been published on platforms such as the Environmental Data Initiative (EDI), CNRA portal, CDFW FTP site, and USGS Science Base databases for public access. Also, several integrated datasets have been produced with the help of the IEP synthesis team, including zooplankton, fish, water quality, and aquatic vegetation. Ongoing initiatives are working to coordinate data management plans for the Sacramento River watershed that will make food web data compatible among programs. The Spring-run Chinook Juvenile Production Estimate data management system, for example, has posted interagency, inter-compatible salmon data sets on EDI and is establishing shared interagency data entry applications and cloud computing resources that ensure future data streams are immediately compatible . In addition, the IEP has numerous mechanisms for effectively sharing data and insights. Examples include formal workshops and conferences (e.g., IEP annual workshop), to less formal project work teams, technical teams, and newsletters.

Additional considerations for using food web science in management

Adaptive management

Adaptive management is a science-based, structured approach to decision making that has been built into regulations for several state and federal agencies, including those 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. 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 vary regionally and by habitat and their structures are both spatially and temporally dynamic, and likely require regular updates to monitoring programs and any associated management strategies.

Temporal and spatial scales

Delta heterogeneity was frequently mentioned as a challenge in the workshop 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 who participated with this report stressed that an appropriate food-web model (or set of models) would incorporate the spatiotemporal variability in the system and better define 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 where in the life cycle habitat is a bottleneck limiting population-level productivity. 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.

Conclusions

Improved mechanistic and quantitative understanding of food webs in the California Delta, especially those that include upper trophic-levels, are essential for predicting the impacts of biophysical drivers (e.g., climate, flow, nutrients, contaminants) and management actions on individual fish species as well as on ecosystem-level processes. Changes in environmental drivers are unlikely to affect only one species in the ecosystem. Likewise, changes in the abundance of one species is likely to affect abundances of other species. The importance of predator-prey interactions is well-recognized, given the large amount of effort to assess/reduce predation on threatened species and to increase food resources through habitat restoration targeted for threatened species (e.g., Michel et al. 2020; Young et al. 2021, 2022; Davis et al. 2022). The same drivers and processes that affect listed species also affect the more abundant species in the ecosystem and they can act to shift community and food web dynamics, sometimes in unexpected ways. Despite the current level of scientific data and understanding, it remains challenging to quantify the contribution of food web interactions to species and ecosystem changes that result from natural variation and management actions.

At first glance, the development of 'operational' and quantitative food web processes and models may seem daunting given the spatial and temporal complexities in the Delta. Yet, advancements in data collection and modeling techniques have resulted in perspectives and insights into food web processes, and models are being actively applied to broad (complex) ecosystem management and socioeconomic issues in large ecosystems elsewhere (Boxes 1, 3-5; Table 2). These applications demonstrate significant advancements in food web modeling, that the modeling is feasible, and that it will generate pragmatic outcomes for improved decision-making and for natural resource management.

The Delta is a well-studied and monitored ecosystem, providing a strong foundation for understanding food web processes. Indeed, progress can be swift given the level of understanding on hydrodynamics, environmental drivers, lower trophic-level food webs, and conceptualization of upper trophic level species dynamics. The examples and literature provided in this review demonstrate that an understanding of processes and the modeling of food webs has greatly advanced in recent years, providing a strong scientific foundation for establishing a pragmatic science strategy for the Delta.

Recommendations

Given the potential demonstrated elsewhere for providing management relevant insights into ecosystem management, the Delta ISB recommends that a focused and funded, scientific collaboration among agencies, academia, Tribes, and the public be established to design and implement a food web analysis strategy. While there are existing collaborations in the Delta they are, for the most part, relatively narrow (specific) scientific activities (e.g., Nelson et al. 2022, Hartman et al. 2024). The challenge will be linking them where appropriate and expanding their perspectives. The scientific strategy—guided by agreed upon priorities that lead the development quantitative food web model(s) —should include: 1) formal coordination mechanisms, 2) flexible monitoring methods, 3) knowledge-based food web models, and 4) interactive and adaptive linkages to management. Specific initial actions include:

1. **Use key management needs to inform the development of a comprehensive coordination and implementation plan for collecting, analyzing, modeling and applying food web information.**

   A continuous evolution of knowledge about food web processes, and the resulting modeling applications, requires a focused interdisciplinary collaboration among agencies, universities, the public, and Tribes. This process spans the mandates of multiple agencies and areas of expertise. Coordination can be achieved in various ways. For instance, many workshop participants suggested establishing a *Collaboratory* focused on food web science, which is a universal but bounded need, across agencies, researchers, and stakeholders. The need for a Collaboratory was highlighted at the Science Needs Assessment workshop (2020) and identified in the Science Action Agenda and Delta Science Plan. The Delta Science Program is working on an Integrated Modeling Framework Strategy for the Delta based off a 2023 workshop, and should consider recommendations in this review.

   An example of a newly created Collaboratory is the Chesapeake Global Collaboratory (https://www.umces.edu/chesapeake-global-collaboratory). Initiating a food web implementation plan might be an effective use-case to test out the utility of a Collaboratory. A key purpose of the groups involved in collaboration would be to bring diverse perspectives to prioritize and decide on key management needs and science questions. These would drive the implementation plan and, therefore, the scope of food web research, goals for monitoring programs, and identify uses and applications for food web models.

   The Delta ISB believes that the broad Delta scientific, management, and stakeholder communities should be deeply involved—perhaps through the Collaboratory or a subsequent workshop—in establishing priorities and deciding on important actions. Admittedly, it will be challenging to advance food web science while, at the same time, achieving ambitious restoration goals and navigating new or existing regulations. This challenge could very well be the central theme of the initial workshop or an IEP or DPIIC working group.

   It is the opinion of the Delta ISB that, where possible, activities driven by the plan, especially restoration activities and management actions, should be established analogous to formal, testable experiments that will inform future food web models. It will be paramount to determine the main research questions considering a variety of perspectives and goals, and to design management and restoration as statistically valid investigations to the extent feasible. Testing hypotheses, measuring performance with set metrics, and adaptively changing strategies based on the results will advance restoration methods and improve cost-effectiveness. Use of the well-established concepts and principles of experimental science was recently employed for ecosystem restoration with success (e.g., Fish Restoration Program; Sherman et al. 2017; Hartman et al. 2019). The proposed plan should clearly identify responsibilities for each component and how the efforts will be prioritized, supported, and funded.

2. **Adapt Delta monitoring programs to explore key aspects of food webs, relying on collaboration and best available tools/methods.**

The Delta ISB believes it essential that agencies and the broader science, agency, and stakeholder communities further prioritize data sharing and collaboration to establish a more efficient science enterprise. This includes the development of *mechanisms* for effectively sharing data, ideas, and insights. Food web-relevant data need to be regularly updated, quality controlled, and made accessible in usable, standardized formats. For example, historic sampling locations should be consistently geo-referenced and include standardized metadata. Fortunately, today every data point published by any IEP survey is accompanied by GPS coordinates, either with the sampling information or in an accompanying lookup table. Collectively, these tasks provide the foundation for meaningful syntheses of information and the generation of new knowledge.

It is recognized that much of the Delta's food web monitoring and research has been, to date, highly focused on specific processes and lower trophic levels, often employing traditional methods. Traditional analysis of upper trophic level data collection is costly and time consuming and might be replaced or supplemented with newer, cost-effective techniques. However, the ability of new techniques to fully build out food web models and advance a mechanistic understanding needs to be verified. In the future, the Delta ISB sees opportunities for an improved understanding of species outcomes through research activities that enhance our current knowledge base. These include:

- Further examining the roles of detritus and their associated organisms in underpinning system productivity supporting upper trophic levels.

This builds off recently funded work by the Delta Science Program on integrating detrital materials into the Delta food web puzzle.

- Recognizing the variety of food web pathways (e.g., detrital, algal) supporting upper trophic levels where many species are generalists.
- Further evaluating additional linkages between primary producers and their availability to zooplankton, and the subsequent coupling to upper trophic levels.
- Better characterizing the diversity of important processes maintaining the vitality of benthic communities and early life stages of fishes.
- Quantifying the distributions, life histories, bioenergetics, and response to environmental drivers of the most common/abundant species that play major ecological roles in the food webs in the Delta (see IEP MAST 2015; Johnson et al. 2016; Heublein et al. 2017).
- Executing special studies that would be responsive to data gaps identified by the collaborative team working toward model development.

Additionally, it's important to understand the flow and ecological consequences of contaminants, the ecological roles of birds and mammals in maintaining aquatic productivity, and the nutritional/energetic quality of food moving through food webs. These can be explored using many of the recent advances in monitoring strategies and emerging techniques, often at lower cost and with greater accuracy than in the past.

3. **Employ appropriately scaled and spatially explicit food web models as determined by management questions and environmental driving forces and conditions**.

Appropriately scaled food web models incorporate relevant processes and represent key members at multiple trophic levels so that relationships between environmental conditions, management actions, and upper trophic level species responses are better understood. A similar need and a recommendation were also identified in the Delta ISB Review of Non-Native Species (DISB 2021). The complexity of food web models can vary from a few key species to representing all species at each trophic level, and fine temporal and spatial resolution (hourly or daily, using a hydrodynamic grid) to coarse resolution (annual, using one or a few spatial boxes).

Food web model development should be focused on the spatiotemporal scales relevant to answering the guiding management question(s) (see examples in Table 2). The efforts should start with a hypothesis and conceptual model, using the simplest model that will address the guiding question. For this process, it will be helpful to examine the *processes* of model development that link science and management (e.g., Rose et al. 2015; Geary et al. 2020); ones that have proved successful in other large ecosystems (e.g., Boxes 1, 3-5). Models can be later integrated to address a range of spatial extents and time periods or to consider other ecosystem conditions such as hydrology, as included in different types of models, to achieve a more comprehensive view of Delta ecosystem functions. Model frameworks, organized in a community workshop or series of workshops, should build on established ecological principles and enable the ability to project how species and communities might be altered under changing environmental conditions and management actions.

4. **Link food web models to management questions and actions, monitoring, and empirical studies using an adaptive framework.**

An adaptive framework (Figure 2) underpins ongoing and effective decision-making protocols and processes in the Delta. Doing so facilitates the transfer of new insights and quantitative information derived about food webs into timely assessments of the impacts and expected responses to management actions. Food web modeling is an iterative process with advances occurring as new information becomes available and management questions evolve. The iterative aspect of model development meshes well with the adaptive management framework when both are coordinated and done synchronously. An adaptive framework provides a mechanism for the continual improvement in the science and expanding the relevance of Delta-wide monitoring and modeling activities. The previously recommended food-web focused *Collaboratory* may be an ideal setting for ongoing adaptive management evaluations, which can produce specific advice for agencies and others to consider.

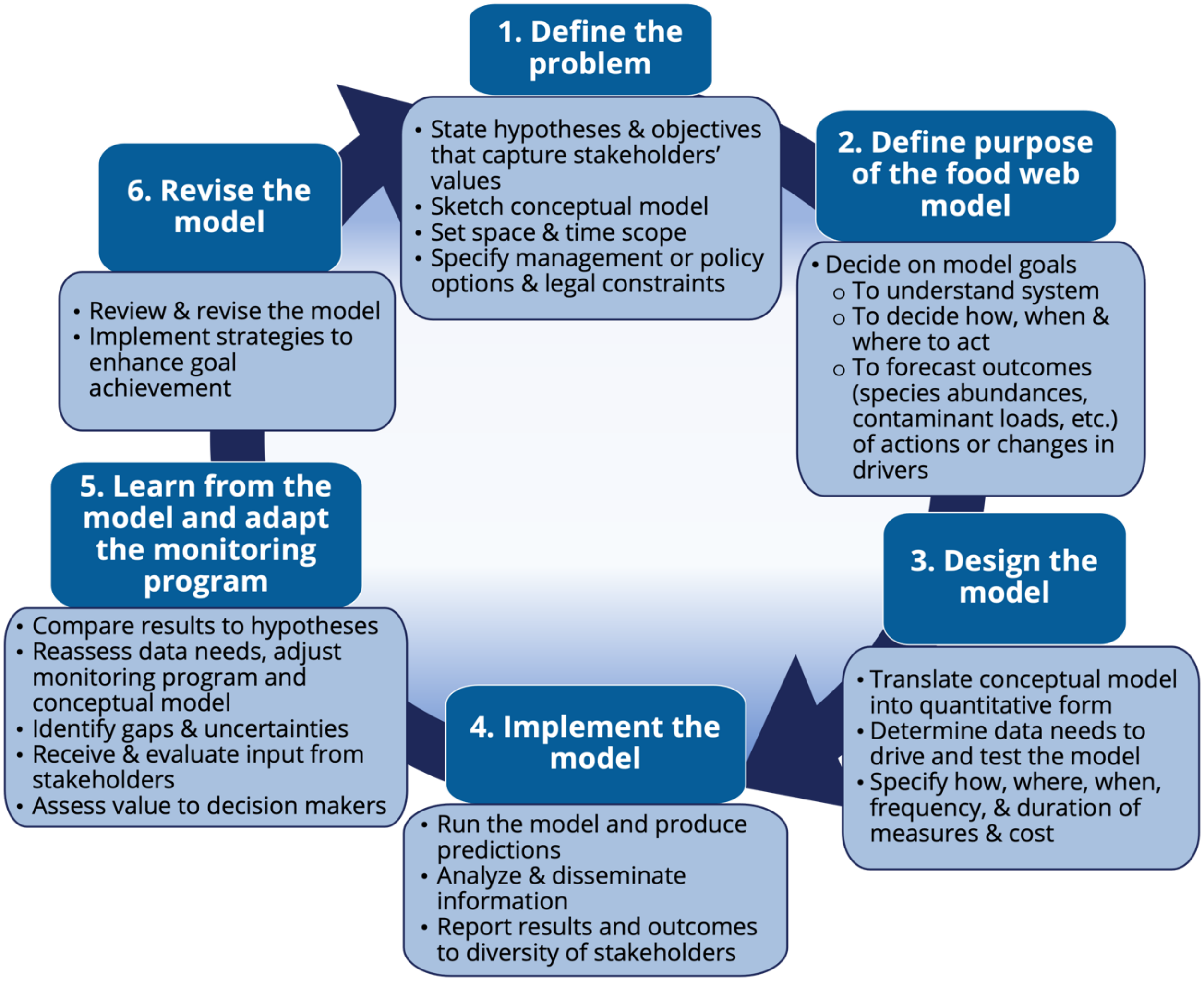

Figure 2: A detailed adaptive framework for application and continual evolution of food web models to management questions. This iterative, adaptive modeling approach should be used to connect management questions, monitoring, and empirical studies to food web models.

An iterative, team-based approach for developing food web models begins by identifying priority management questions and outcomes that would benefit from enhanced food web understanding using information and models with appropriate mechanistic detail and time and space resolution. The modeling is then coordinated with the adaptive framework (Figure 2) and applied to answer management questions (Table 2), ideally in a holistic manner. The process should help identify priority knowledge gaps, improve the model to reduce uncertainties, and adjust monitoring programs appropriately.

Integral to all four of the recommendations, the Delta ISB strongly encourages:

- Evaluating the usefulness of the activity within a defined timeframe (~decade). Proof of concept and meaningful management applications will be necessary criteria for determining success.
- Creating teams that include students, technicians, scientists, decision-makers, rights holders, and representatives from other interested parties that address specific issues and meet regularly to exchange information and formulate potential solutions (see Venter et al. 2008, for an example).
- Implementing proven team building and science communication strategies to establish the efficient transfer of newly generated knowledge to natural resource decision-makers.

The Delta ISB believes that these recommendations, collectively, will advance food web science in the Delta to better inform a broad range of management decisions. Collaboration, iterative food web modeling, and adaptive management will be needed to make implementation of the recommendations efficient and effective. The benefits will be improved capacity to project effects on fish and other aquatic organisms due to management actions and their interactions with an ever-changing climate and ecosystem. Workshop participants affirmed the necessity for food web knowledge by stressing that almost every management question is a food web question, and that the relevant scientific question is *how* to represent the food web interactions, not whether we need to do it.

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Appendix A: Community Engagement

Initial ideas for applications of improved understanding of upper food webs

A key workshop focus was to evaluate how improved science and understanding of food web interactions can inform individual species and ecosystem management in the Delta. To inform the workshop structure and content, the Delta ISB conducted 14 group interviews/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 A1).

Table A1. 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. In addition, the Delta ISB held an open forum in June 13, 2023 for the public to provide feedback to help inform the scope and purpose of the upcoming food-webs workshop. The questions informing the open forum can be found below, which were similar to the questions used to guide the group interviews.

1) What are your (top 3, or highest priority) core research, management, or other goals that you/your group have/has regarding food webs?
2) What are the important food web interactions affecting predictions of how restoration, climate change, and changes to system management (e.g., flow

rates or other environmental drivers) impact the abundances of key native species?

   a) How could a quantitative understanding of food web interactions improve the design of performance metrics used for upper trophic levels in the Delta?
   b) How will changes in food resources at lower trophic levels (e.g., phytoplankton and zooplankton) increase food resources for species of interest?
   c) Can one predict how current or future non-native species may impact native fish abundances or survival?

3) What do you think the critical inputs and outputs to a food web model are that could help improve the understanding of species interactions in the Delta?
   a) What level of complexity does a Delta food web model need to have (e.g., What temporal and spatial scales are important for understanding how the ecosystem functions)?
   b) What could food web models reveal about the indirect effects of management choices on endangered species living in the Delta?
4) Do you think food web modeling in the Delta would be useful for species management and the understanding of Delta system ecology?
   a) If so, how?
   b) Are there any barriers to using food web modeling? If so, what are those barriers?
5) What themes/products/questions in a workshop would be of most value to you and/or to the Delta?
   a) What are some suggestions for folks to invite to participate in the workshop?

In the end, we were unable to schedule discussions with all rights-holder groups and interested parties; however, the workshop and public comment sessions have provided opportunities for further and broader input on these same topics.

Appendix B: Food Web Workshop

On November 8 and 9, 2023, the Delta ISB hosted a two-day workshop as part of this review. The workshop assessed the importance of food-web interactions in the Delta and helped identify where improved understanding and tools (e.g., food-web models) might substantially improve predictions of an individual species' responses to environmental drivers and management actions. This appendix summarizes the workshop that occurred.

Key materials for the workshop include:

- Meeting Notice/Agenda
- Presenter Profiles
- Poster Abstracts
- Presentation Slides
- Posters
- Day 1 Recording
- Day 2 Recording

Session 1: Setting the Stage: Why are food webs important for management in the Delta?

Ted Sommer (Public Policy Institute of California) provided a historical overview of the development of food web science in the San Francisco Estuary, highlighting key periods and shifts in focus of the science. In the "Before Times" (1960s-1980s), the emphasis was on descriptive studies and water quality issues, with a simplistic conceptual model of nutrients leading to phytoplankton, zooplankton, and fish. The Lower Trophic Level Renaissance (1990s) marked a shift toward a more comprehensive understanding, exploring physical processes like the entrapment zone, vital rates measurement, invasive species impacts, and off-channel habitats.

The Carbon Age (2000s) saw significant tool developments, including modeling, probes, laboratory methods, and videography. Advanced, individual-based bioenergetics models were developed, continuous water quality probes became widely used, and isotopes, otoliths, genetic methods, and videography were adopted for detailed analysis. In the Modern Era (2010s), major management interventions were implemented, focusing on wastewater treatment upgrades, floodplain studies, flow pulses, and restoration programs. For the future (2030-?), Delta science needs to focus on climate change. Coupling food web science with specific management interventions will be essential. Ted also emphasized the necessity for improved tools, data integration from remote sensing, and to focus on underappreciated components of food webs (such as crayfish). Overall, there has been a lot of progress towards understanding food webs in the Delta. Steps should be taken to support ongoing research, future research, and establishing improved management actions in the face of emerging challenges.

Mike Chotkowski (United States Geological Survey) addressed the importance of food web science to inform management and forecasting. Mike noted that it’s challenging for scientists to fully understand how management decisions are made and how science fits into the process. Important changes in management typically result from discrete, major decisions at the conclusion of planning processes, rather than through ongoing management (such as adaptive management). There are pros and cons to agency science, and the characteristic focus of agencies on conducting science for regulation can lead to the science lagging behind management decisions. Surprises about “unknowns” can be avoided by using tools that allow us to develop better statistical relationships (and prevent extrapolation), focusing models on underlying processes, continuously evolving management questions, increasing the useability of research, and developing forecasting tools and spatially explicit models. For food web research specifically, the Delta should enable monitoring programs and plans that can be leveraged to inform future management decisions, and focus on science to understand mechanisms to food web processes rather than phenomena. These actions will hopefully lengthen the planning horizon for management actions and provide a clearer vision for the future Delta in the context of climate change.

The Delta ISB postdoctoral researchers, **Kristine Grace Cabugao and Lillian McCormick**, summarized the community engagement process that directed the scope of both the food webs review and the workshop. As detailed in Appendix A, the Delta ISB held a series of discussions with members of the Delta science and management community in 2023. Key themes of these Delta discussions were categorized into topics of structure and processes, human influences, tools and methods, and data and information (Figure A1).

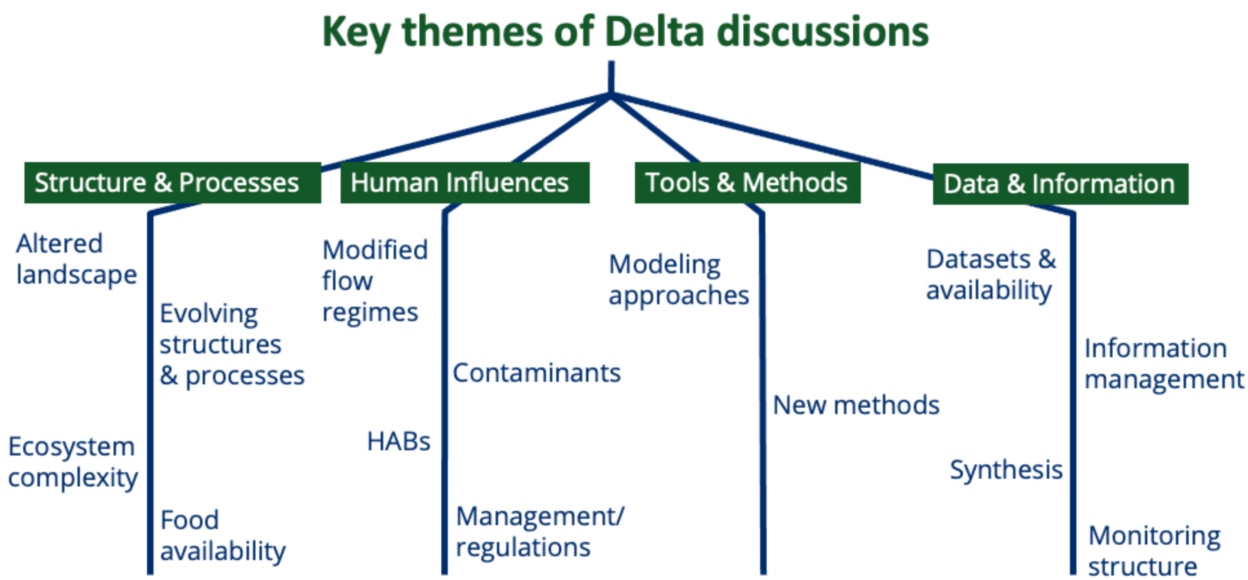

Figure A1: Key themes from the Delta discussions on food webs and their connection to management in the Delta.

For each topic, the main management questions of community members were summarized, as well as some of the aspects of science where additional information is needed to support food web science for management. Discussion participants expressed science gaps that would need to be addressed, including understanding the different components of Delta food webs, understanding the spatiotemporal complexity of habitats and species assemblages, increasing knowledge on species interactions in the Delta, connecting different habitat types, and evaluating the effects of contaminants and harmful algal blooms on species interactions. Overall, key management priorities were to 1) establish an adaptive management approach to food web science, 2) understand how to implement ecosystem-based management in the Delta, 3) use management actions and restoration as experiments to understand the effects on food webs, 4) create restoration that positively affects fish populations, and 5) develop monitoring for food web models that accurately capture system heterogeneity.

Session 2: How has a better understanding of food web interactions improved management elsewhere?

Kim de Mutsert (University of Southern Mississippi) focused on the impact of large-scale coastal restoration on ecosystems in the Louisiana Delta region. Coastal erosion has led to significant wetland and land loss, prompting Louisiana to develop a Comprehensive Master Plan (CMP) for a Sustainable Coast. Kim's team developed models that were incorporated into the master plan, aiming to evaluate the effects of plan implementation versus a future without action on the biomass and distribution of fisheries species over a 50-year period. The modeling framework included Ecopath for mass balance snapshots, Ecosim for temporal modeling, and a spatially explicit temporal-dynamic food web model coupled with the Integrated Compartment Model. The study simulated scenarios for various species, considering the chosen restoration plan, future without action, and different sea-level rise projections. The results showed increased biomass under the CMP, with species-specific responses. Despite the plan primarily targeting land building, it demonstrated positive effects on food webs and fisheries, with unexpected benefits and increased biomass in certain areas. This work showcases the interconnectedness of restoration activities with ecological benefits, and the importance of considering food webs to assess the long-term effects on fisheries and food webs in the Louisiana Delta region.

The Gulf of Mexico (GoM), particularly the Mississippi Delta, faces significant ecological challenges, including a hypoxic zone five times larger than the Sacramento-San Joaquin Delta. **Steve Brandt (Delta ISB)** mentioned that a primary management question revolves around understanding how this seasonal dead zone impacts fish and predicting fish reactions to reduced nutrient loading and improved hypoxia conditions. Reducing nutrient load may decrease hypoxia, positively influencing fish; however, a potential tradeoff could involve decreased food availability for fish. Essential Fish Habitat, defined by NOAA, considers growth rate potential and integrative responses to survival rates. Bioenergetics studies reveal non-linear growth responses, emphasizing the need to divide habitats into smaller components and run species-specific foraging models to accurately assess fish performance and understand the impacts of nutrient loading.

Steve and colleagues developed high-resolution, spatially explicit, bioenergetics and foraging models to show how oxygen, temperature, and prey density estimates inform habitat quality assessments. This model compiles data on different species, which aids in understanding competition potential, such as between bluefish and striped bass. The effects of changing nutrient levels and hypoxia are modeled, showing species-specific responses. When nutrient levels are reduced and oxygen is increased menhaden benefit, while anchovy faces habitat restrictions due to declining zooplankton from the nutrient reduction. The research emphasizes the significance of seasonal and interannual variability in understanding how species respond and interact, underscoring the need for a mechanistic perspective when evaluating the impact on food webs for management purposes, and considering species-specific responses that may be non-linear and vary across space, time, and life stages.

Doran Mason (NOAA) explored the effects of climate on food webs and fisheries in the Great Lakes. The region is home to species such as salmon, lake trout, walleye, and yellow perch, and faces challenges from trophic gradients across the lakes and non-native species. The Great Lakes Fisheries Commission operates as a binational organization between the US and Canada to manage fisheries in one of the largest freshwater systems globally. With a focus on ecosystem-based management, a primary management goal is to anticipate changes beyond the typical 1- to 3-year planning horizon, especially considering climate change and altered nutrient levels. To address these complex issues, the Fisheries commission has adopted a scenario-based forecasting approach, employing ensemble modeling. The Great Lakes Earth System Model (GLESM) integrates climate, watershed, lake physics, chemistry, and ecology to forecast ecosystem conditions under different scenarios, including the impact of invasive species and nutrients. It is modular by design, allowing for flexibility and adaptability for multiple conditions. For example, the Lake Michigan Atlantis Ecosystem Model (LM-AEM) includes food web interactions and a fisheries system module, defined in a 3D domain with depth strata. The model offers insights into the seasonality of vertical mixing in the Great Lakes and understanding its importance for the food web, especially for lower trophic levels. Ongoing developments include incorporating ice effects on the food web, improving spatiotemporal vertical mixing, and integrating socio-economic models for a comprehensive understanding of the Great Lakes ecosystem. Overall, the Atlantis model proves valuable for assessing the impact of multiple factors and providing confidence in projections through its ensemble modeling approach.

Atlantic menhaden is a schooling forage fish on the East coast that is crucial for linking lower trophic levels to upper trophic levels and supporting various species and fisheries.

Andre Buchheister (Humbolt State University) discussed challenges in balancing the food supply for key species (such as birds) while sustaining a significant fishery. Atlantic ecosystem management shifted their focus from single-species management to broader ecosystem management, leading to the development of the Northwest Atlantic Continental Shelf (NWACS) ecosystem model. The complexity of the NWACS model prompted the creation of a simplified model of intermediate complexity (NWACS-MICE). This model was designed to determine ecological reference points (ERPs) by analyzing the sensitivity of predators to menhaden fishing, particularly striped bass and avian predators. Different options along a tradeoff frontier are explored, with ERPs proving more conservative than single species models but still allowing for increased fishing. Lessons learned include the importance of early engagement with managers and stakeholders, quantifying uncertainty, and embracing incremental progress. Future directions for this model involve updating models using surveys and assessments, addressing uncertainties in the food web, and exploring the linearity of model projections with future considerations.

Using the Columbia River Basin system as an example, **Stan Gregory (Oregon State University)** presented food web relationships, including the impact of piscivorous birds and the presence of non-native species like American shad on salmon, emphasizing the need to consider the entire ecosystem rather than focusing on a single species. Examples from the Methow River Floodplain and the Columbia River estuary illustrate the importance of understanding diverse food web resources and the influence of restoration activities on fish assemblages. An additional example was the use of bioenergetics models to assess salmon movement through a dam, emphasizing the oversight of salmon's food requirements in management considerations. Stan identified challenges in ecosystem restoration such as contaminants, bioaccumulation, and connectivity issues, stressing the need for comprehensive information about the entire food web, as it is challenging to separate upper and lower trophic levels. Similarly, it is important to consider not just biomass, but also the energy contribution of phytoplankton to the ecosystem to understand food web dynamics in restoration.

Session 3: What are the important fisheries and management issues for the Delta and what do we know about food web drivers?

Panel 1: Food webs and fisheries management

Panelists: Zachary Emerson, Matthew Nobriga, Carson Jeffres, Jim Hobbs, Steve Lindley, Fred Feyrer

Zachary Emerson (United Auburn) highlighted the integration of traditional ecological knowledge (TEK) and cultural fire practices into modern approaches for fisheries management and restoration. Zachary emphasized the importance of engaging with Indigenous communities, and stressed the need for long-term planning, understanding ecosystems, and establishing partnerships to incorporate TEK effectively.

Matthew Nobriga (USFWS) explained that smelt entrainment has been effectively regulated since 2004 for larvae and 2009 for adults, and the proportion of total mortality of Delta smelt has generally remained below the threshold of concern. Despite the focus on listed species in Delta management, there's a shift in the ecosystem's faunal composition, with less of an emphasis on striped bass and cyprinids, and an increased presence of water weeds, challenging food web models that may lack comprehensive information on key species.

Carson Jeffres (UC Davis) focused on landscape-scale subsidies from floodplains, particularly in wet years, and showing how this impacts the seasonal dynamics of the food web and influences the abundance and fullness of salmon. The timing of salmon outmigration is shrinking over time, posing challenges for fish growth and migration opportunity, and emphasizing the urgency of understanding changing hydrological processes before addressing management strategies.

California Department of Fish and Wildlife (CDFW) and the Interagency Ecological Program (IEP) jointly conduct fish, invertebrate, and water quality monitoring in the Bay Delta since 1959 to fulfill obligations under the California Endangered Species Act (CESA) and for water rights to DWR and USBR. **Jim Hobbs** presented on the IEP's various monitoring surveys, including the summer tow-net survey and San Francisco Bay study, that provide valuable data on larval Delta smelt entrainment, understanding of large-bodied fish in the Delta, and other aspects of Delta ecology. These studies have the potential to address key management questions related to food webs, including the influence of harvest slot limits for striped bass, new harvest management actions for white sturgeon, sea lion predation on salmon, striped bass, and sturgeon, as well as the impact of predation on entrainment estimates and various management actions in the Delta.

Steve Lindley (NMFS Southwest Fisheries Science Center) explained that resource management in the Delta primarily focus on salmon, with food web interactions implicit, but not explicitly modeled. The challenge lies in understanding how changes in water management actions, shifting predator hotspots, and habitat modifications might influence food webs, considering the non-linear nature of these processes and the uncertainties associated with species introductions and historical variations in food webs.

The Sacramento splittail, an endemic minnow, is a wetland and marsh-dependent species that used to be listed as endangered but was delisted. **Fred Feyrer (USGS)** presented research showing that floodplain inundation is crucial to their life history, and that recent findings reveal spinal deformities in juveniles caused by exposure to selenium through food web interactions in multiple habitats. Understanding such complexities requires field studies and goes beyond broad, generalized food web models, highlighting the importance of empirical studies and considering space-time elements in ecosystem research.

The panel discussion illuminated the importance of understanding both rare "needle in the haystack" species and abundant ones that may influence prey resources and predators. Participants expressed a need to focus on the nutritional quality of food, considering caloric content, and unexpected nutrition-related issues (such as disease) affecting fish. Understanding how to efficiently identify and prioritize research questions (in the face of unknowns), will be important, and several participants suggested that starting with habitat restoration, examining different habitat types, and also respecting and engaging with Indigenous knowledge will be helpful.

Panel 2: Food webs and ecosystem management

Panelists: Shawn Acuña, Brian Mahardja, Rachel Wiggington, John Durand, Zachary Emerson, Louise Conrad

Shawn Acuña (Metropolitan Water District of California) presented a collaborative report on decision support tools for Delta smelt management (Reed et al. 2021). This report was developed by engaging with managers and technical staff to identify gaps in science and suggest conceptual models that would address various science objectives, including biomass, predation, and distribution of species. The emphasis for these decision support tools is to align food web models closely with management needs, consider the sensitivity of decisions, define spatial and temporal requirements, and integrate multiple decision support tools with different levels of specificity to ensure effective validation and understanding of direct and indirect effects of management actions.

Brian Mahardja (**USBR)** explained why a food webs perspective would be beneficial for management. A goal is to understand the state of the ecosystem and the interactions of key species with existing water management actions, which emphasizes the need for quantitative food web modeling using existing data for forecasting and modeling the effects of management actions. The level of complexity in modeling is context-dependent and should consider regions, seasons, years, and equipment improvements, with identified gaps and opportunities including the need to connect different habitat types in a single food model, explore top-down effects of large-bodied fishes, and understand the impact of climate change and water management on food webs and species populations.

Rachel Wigginton (Delta Conservancy) highlighted the importance of considering complex food web interactions, especially with emergent (non-native) plants invading streamside and floodplain habitats, affecting vertebrates' foraging behavior and nutritional dynamics. The need for adaptive management, early detection, and rapid response to limit the integration of invaders into food webs is emphasized, along with the recognition that restoration projects can inadvertently spread non-native species. Scientific and management needs include establishing density relationships for adaptive management and understanding how restoration site food webs shift with increasing invader density and diversity.

John Durand (UC Davis) expressed that most work in the Delta (a relatively well-funded ecosystem) primarily follows a top-down approach focused on three key species. John emphasized the importance of understanding zooplankton productivity dynamics, expressing concerns about overly complex models that can lack conceptual clarity, and proposed research ideas exploring the mechanisms of primary and secondary production, trophic relay, and fish mobility in marshes. John highlighted the significance of considering the benefits of *disconnectivity* in invaded systems and suggested tips for experimentation, including involving morphologically variable sites, gradients, and manipulative structures, in addition to advocating for the integration of adaptive management and human interactions in landscape management for a comprehensive ecological understanding.

Zachary Emerson (United Auburn) emphasized the historical role of Tribes as the foremost apex predators, managing the ecosystem since time immemorial, contrasting it with the current view of sport fishers as apex predators in Western science. The need to acknowledge and treat these different apex predators distinctly in food web and ecosystem management is highlighted, with a focus on re-establishing access and considering the disproportionate impacts on Indigenous communities.

Louise Conrad (DWR) emphasized key management needs, including understanding the impacts of tidal restoration on the food web, managing invasive species, and addressing the effects of climate change. The urgency of broadening the scope of food web science, investing in long-term monitoring, and diversifying funding sources is highlighted, with a call for an open and participatory process to develop comprehensive ecosystem models that consider broader knowledge and stewardship actions. The potential outcomes include the formation of a group to direct funding and drive these initiatives, and a shift towards a more collaborative and exploratory approach in modeling processes.

The panel discussion involved recognizing the importance of incremental progress in using food web models to guide management decisions. Participants highlighted small milestones, including building models for the North Delta Food Web subsidy and studying the effects of Suisun marsh salinity control gates. Participants discussed the challenge of conveying information from complex ecosystem models to the public, and emphasized the importance of communication and community engagement, such as the iterative discussions and trust building employed in the

Franks Tract scenario-building process. The difficulty and feasibility of predator removals was discussed, and new opportunities for complete removal of a juvenile salmon predator (black bass) from the North Delta were suggested.

Breakout Session 1:

What are the key management questions in the Delta where an upper trophic level food web modeling approach is critical to predicting responses to management actions or changes in environmental drivers?

What are the important food web interactions affecting predictions of how restoration, climate change, and changes to system management (e.g., flow rates or other environmental drivers) impact the abundances of key native species?

How can we use knowledge from management choices in other large ecosystems to improve management in the Delta?

Main comments:

- **Need to identify *what* we are *managing for* before deciding on the important questions.** Is there a way to simplify the models (e.g., aggregate fish behaviors/groups)? How do we reconcile visions of what we want the landscape to look at? Important to identify the non-linearities to get the complexity of the system correctly. Perhaps do comparative studies across ecosystems? Can control many things in the Delta (flows, restoration, temperature to some degree, etc.).
- Physical process/human impacts/climate change/restoration. Chlorophyll measurements (customary monitoring), may not be accurate, need to monitor in ways that doesn't bias (overestimate, underestimate) what is available to the system. Contaminants are an issue; don't know which contaminants to measure, don't understand their effects, don't have a good understanding of contaminants from urban systems. Contaminants studies need to be done at a whole food web scale to understand differential impacts to individual species. **Important to consider *processes* that worked for other ecosystems, rather than specific tools or models (e.g., scenario development, community engagement).**
- Understanding which species are being impacted from increased food availability or restoration activities is very important. Learning how to conduct experiments with flow changes (e.g., voluntary agreements) and how species respond. Look to the future, and invest in long-term predictive capacity. Climate change impacts include temperature increases, salinity

intrusion, etc., these should be focused on. Connect senior agencies to share info on management; cross-ecosystem collaboration.

- Apparent competition; what is feeding the rare species predators? Top-down effects of management actions. How much of the changes we observe from management actions are from the management actions themselves vs. top-down ecosystem changes? **Almost any question you can think of is a food web question; need to understand HOW to represent the food web interactions in management, not whether you need to or not.** Classic questions, of how do specific management actions (e.g., water diversions) affect key species. All interactions are important, the key is to understand their sensitivity to different conditions (e.g., when is the response of the key species sensitive to change in predation, etc.) and how that may impact vulnerability (examine system drivers). Classic bioenergetics, need to understand the high biomass species and their role in the food web, because that's what is currently in the system (*key ecological species may not always be the regulated/listed species).* Salinity intrusion will be important to examine with respect to physiology of species. Much more is known about temperature and physiology, etc. Results from other systems may not directly transfer to the Delta (they all have different species, regulations, and issues), but lessons learned and processes are transferable between systems. Learn from both successes and less successful strategies. May be more helpful to look at rates (e.g., growth, mortality, recruitment), rather than just focusing on abundance.
- Main categories of questions were: climate change impacts, management or restoration impacts to food webs from management or restoration projects that were not designed for food webs (including conveyance projects, rice farming for subsidence reversal), management or restoration impacts that were designed to enhance food webs, basic science questions in support of food web modeling, questions about uncertainty and modeling. Key interactions include: predation, life-cycle dynamics, temporal and spatial dynamics of food webs, and non-native species disruption of trophic interactions. What are the limits of and the degree to which what we have learned from other systems is transferrable to the Delta? Also, what have we learned/developed in the Delta that could benefit other systems around the country and world?

Session 4: Food web models and approaches, emerging tools, data needs, and applicability for the Delta

The second day began with a plenary by **Ryan Bellmore (US Forest Service)** discussing the importance of studying food webs to understand productivity patterns, controls, and features promoting stability and biodiversity in ecosystems. Ryan explored the complexity of food web investigations, considering spatial and temporal scales, taxonomic resolution, and empirical approaches across different methods for quantifying linkages between trophic levels, such as linkage webs, diet composition webs, and flow or flux webs. The need for spatial and temporal explicitness in food web studies was emphasized, highlighting the existence of "foodscapes" for mobile consumers. Ryan addressed the connections between food webs and the challenges of quantifying consumer movements, along with perspectives on mathematical food web simulation modeling, ranging from simple heuristic models to complex, site-specific ones. The conclusion advocates for combining highly detailed empirical studies with mostly simple models using an adaptive modeling feedback. The limitations of complex models, including difficulties in understanding and potential errors, are acknowledged, and the role of hierarchy theory in representing different scales is considered. The importance of adjusting models to specific research questions is emphasized, along with the need for collaboration across different scientific disciplines.

Zachary Emerson's (United Auburn) talk focused on the eco-cultural revitalization of the Delta, particularly within Indigenous communities. Zachary is a leader in the Coyote Crew Revitalization Program, which utilizes both traditional knowledge and modern tools to reintroduce fire for management, recognizing the intertwined nature of culture and ecology. The importance of fire in restoring and revitalizing native lands is underscored, including in objectives such as disease reduction, maintaining species diversity, and promoting habitat heterogeneity, while offering cost-effective and sustainable alternatives to traditional ecosystem restoration methods. The benefits of cultural fire extend beyond ecological impacts to physical, spiritual, social, economic, and cultural realms, emphasizing the need for collaboration and engagement with cultural practitioners in the broader ecosystem revitalization efforts.

Andre Buchheister (Humbolt State University) provided an overview of ecosystem modeling using the Ecopath with Ecosim (EwE) approach, widely used for fisheries applications worldwide. Comprising of Ecopath, Ecosim, and Ecospace, this modeling system incorporates various components, with Ecopath serving as a biomass accounting tool based on mass balance equations. Ecosim is a time-dynamic version that relies on time-series data, particularly fishing mortality/fishing effort, to simulate changes. Ecospace allows for spatial modeling of Ecopath and Ecosim within model grid cells. The presentation emphasizes tailoring models to specific goals and available data, necessitating varying levels of taxonomic resolution and addressing trophic and fishing fleet structures. Core data needs and forcing functions are highlighted, enabling the exploration of scenarios, and addressing uncertainty. Andre discussed the pros and cons of EwE models, emphasizing their role in identifying knowledge gaps, developing indicators, making and evaluating hypotheses, and evaluating tradeoffs in ecosystem management. Andre underscored the importance of finding a balance between simplicity and realism in model construction to minimize uncertainty and provide greater relevance for management.

Kim de Mutsert (University of Southern Mississippi) presented the utilization of EwE, specifically focusing on the Ecospace component for incorporating spatiotemporal dynamics, and additional modules within the Ecopath with Ecosim framework. Kim shows that many systems use modeling to understand and try out different management ideas in a "digital twin" of the system (e.g., Hyder et al. (2015). The EcoTracer module is introduced as a tool for tracing contaminants in ecosystems, with a focus on its applications in understanding the spread of contaminants through different species. EwE and its modules are valuable tools for assessing marine protected areas, suitability of habitats for different species, and issues like restoration. As with other speakers, Kim states the importance of tailoring models to specific goals and questions. EwE is a valuable tool for informing ecosystem management decisions, and has an increasing role in answering management questions globally.

Dave Beauchamp (USGS) explored the applications of bioenergetic modeling in addressing various management goals, emphasizing its role in understanding the limits to survival and growth of different species and in quantifying food web interactions. Bioenergetics are crucial for understanding the impacts of changing temperature on the distribution of organisms and the effects on growth. This type of modeling can be used to address common research and management questions, including to determine the limits to survival and growth for species, and the impact of trophic interactions. Specific examples, such as the effects of water operations and climate change on reproduction in fish, demonstrate the versatility of bioenergetic modeling in informing ecosystem management decisions. Dave also stressed the importance of considering access to prey, detection, and capture for food webs. For example, many salmon predators are visual, and the visual capability of predators to detect their prey changes with depth, turbidity, time of day, and with artificial lighting sources. Understanding these aspects of species interactions would contribute to knowledge on predator hot spots and spatiotemporal heterogeneity of predation.

Lightning Talks:

Fish eye lenses, due to their highly proteinaceous and sequentially deposited nature, serve as an ideal archival tissue to recreate fish ontogeny and gather diet information. **Matthew Young (USGS)** showed that eye lenses can be analyzed for isotopes such as carbon, nitrogen, and sulfur, across cross-sections to investigate habitat use, contaminants, and lifetime diet. Applications include understanding habitat use in native hitch from Clear Lake, assessing contaminant exposure such as diet sources of selenium and mercury, and tracing ontogenetic mercury accumulation through time to distinguish between piscivorous and non-piscivorous fish.

Levi Lewis (UC Davis) showed that by combining field studies and geochemical analysis, otoliths offer valuable insights in fisheries and ecosystem-based management. Otoliths, the ear bones in fishes, can serve various purposes, from fish identification based on specific shapes to providing taxon-specific information. Strontium isotope analysis can enable tracing migration, determining provenance, and understanding salinity exposure gradients. These applications help elucidate complex species interactions and contribute to biomass energy flow studies, informing management strategies for diverse fish species such as smelt, salmon, and sturgeon, and informing the diets of avian predators such as the Least Tern.

Lance Takata (NOAA) explained that Predation Event Recorders (PERs) are an instrument for estimating relative predation risk that integrates GPS tracking and a camera to record predation events by employing live, tethered prey activated by a timer. It comes in various forms, including stationary, free-floating, shore-mounted, and castable versions, allowing deployment in diverse environments such as rivers, channels, lakes, estuaries, and marine settings. The data interpretation involves assessing relative predation amounts with controls and treatments, considering environmental conditions (e.g., temperature, depth), and utilizing GPS tracking for spatial mapping. This instrument enables the identification of predation hotspots and predator species through video recordings and has been field-tested in various settings, including predation around submerged aquatic vegetation and diversion structures.

Vamsi Sridharan (Tetra Tech) presented a particle tracking model with relevance to examining Delta food webs. The model can simulate fish travel in both space and time, and has been used to explore the coupling of salmon migration with other trophic levels (Sridharan et al. 2023). This model is built on a hydrodynamical model, and can incorporate components like day/night cycles, swimming behaviors, predation, and more. Model outputs of simulated survival through the Delta has been validated with mark-recapture data, which demonstrates the model's capability to capture complex behaviors. The tool has various applications as a test bed for studying fish and food web dynamics in the Delta, such as mapping eDNA movement and simulating the spread of viruses like sea shasta.

Shruti Khanna (CDFW) explained the data available to map the presence of macrophytes in the Delta, including data from 1978 to the present available online. While the use of Landsat is currently restricted, the Department of Water Resources (DWR) has expanded its capacity through drone imagery. Hyperspectral data, satellite data, and drone imagery provide varying resolutions and extents based on spatial, spectral, and temporal characteristics of data. Ongoing projects, like NASA's funding for operationalizing Sentinel 2 data in the Delta, aim to utilize remote sensing for building species distribution models and understanding the relationship between depth, velocity, and submerged aquatic vegetation (SAV) species in different habitats.

In the Delta, there is a wealth of publicly accessible data, particularly water data mandated by law to be accessible. However, **Rosemary Hartman (DWR)** showed that the challenge lies in integrating diverse datasets with different formats. The Interagency Ecological Program (IEP) addresses this using GitHub to compile and collaborate on making databases, such as for zooplankton, phytoplankton, and fish, available in a cohesive format. While data integration remains challenging, the community has made strides in increasing data literacy, coding skills, and collaboration, with interactive tools like Bay Delta Live and CalFish Track that aid in data visualization and analysis. Despite progress, there are still gaps in comprehensive diet data, particularly for large fish, and predation rates for birds and mammals that can be used in food web models.

Breakout Session 2:

- *What models and tools might be most effective in the Delta?*
- *What level of complexity does a Delta food web model need to have (e.g., what temporal and spatial scales are important for understanding how the ecosystem functions)?*
- *What data are needed to develop the identified models? Are there existing datasets that can be used, or do we need to alter monitoring?*
- *Are there any barriers to using food web modeling? If so, what are those barriers?*

Main comments:

- A useful model depends on the question(s) being asked. Best approach is an ensemble model approach, e.g., a hierarchical model. A set of small-scale models can be more adaptable and used to feed into a larger scale model. Not just food "web", but food "webs"; multiple models are encouraged. Need a type of strategic plan, shared idea of why it's important to do food web modeling, and why food web modeling addresses the strategic plan. Need funding, science, governance to support. A backlog of synthesis and information in the Delta
- Different types of models; difference between strategic and tactical models. There may already be enough data to use multiple smaller models (e.g., MICE models) that can then be combined for the full region. Multiple scales and functionally different ecosystems; different time horizons exist and it's important to specify what scales your model covers. Models that can test the same location regularly, or can compare across models the areas. Monitoring fish passages through open areas or restricted areas like junctions. Important to be careful about sticking within the limits of the model, understanding the uncertainties of the inputs and how that will be magnified in the model outputs. Reminder to also pay attention to funding and how that defines what is feasible for monitoring and modeling
- Management questions that we are currently facing are not "crisp" enough; need to hone these questions and make more specific to drive actual implementation/modeling. Variation in spatial/temporal scales, but need both simple and complex models. Can start simple and build up, or start

complex and shave off details as you define the questions. Many data types are needed, but currently the main issue is not having a comprehensive place for all diet data. Not sure what is out there, so it's hard to know what is needed. A lot of barriers, including resources, time, reluctance to change, effects of flow changes, etc.

- Complexity should be as simple as possible, only develop a model where you really have the data to build it out. Managing for a lot of listed species, but may lose opportunities to manage non-listed species. Think about uncertainty in models, how it can be used to determine major future changes. How can they be used to capture tipping points? To what degree have these models been used in ways that go beyond "expert knowledge"? How do we know whether a model is the best tool for the job? Models are designed to support decision making, but perhaps they aren't answering the right questions. These can be determined with sustained engagement and sustained communication.

In between breakout sessions, **Peter Goodwin** discussed how to accelerate knowledge and synthesis under uncertainty in the Delta, while facing complex challenges with billions of dollars at stake that makes decision-making difficult. Despite the uncertainty, bold decisions are needed for problem-solving. Initiatives like the Laurel Larson-led Collaboratory aim to organize science efficiently. The data-rich but wisdom-poor environment of the Delta requires synthesizing knowledge, with tools like Bay Delta Live aiding visualization. Harnessing "big data" and AI's potential, particularly in federal planning, is underway. Despite the complexity of Delta's species interactions, there is the tendency for agencies to focus on a few key species due to regulations. The Collaboratory's urgency aligns with climate change challenges, emphasizing co-equal goals and the need for an innovative hub, workforce enhancement, and a pursuit group to drive collaborative efforts. The Collaboratory seeks to bring together diverse perspectives and big thinkers to address the Delta's urgent and unprecedented funding needs, as well as provide the resources and time for creative thinking.

Breakout Session 3:

In the Delta, what are the top 3 things that we can do to make progress on food web science/modeling in the Delta?

Group 1

(1) Engage with diverse interests to identify the questions in the Delta that could benefit from added or enhanced food web modeling, based on available data. [Both existing questions and engagement to encourage new questions]
(2) Evaluate the types of modeling that could support those questions [compare modeling goals and data availability, evaluate feasibility of filling data gaps]
(3) Compare lessons learned with other estuarine systems considering the contextual similarities and differences. [To what extent were tools used in decision making? Are there generalizable and transferable conclusions to understudied areas and species?]

Group 2

(1) Create a strategic plan that makes the case that food web models are essential. You need to define what you want the model to do.
(2) Synthesize the existing data we have into an empirical model and then apply scenario analysis to identify where the gaps are
(3) Predatory fishes are an important knowledge gap to food web modeling

Group 3

(1) A strategic prospectus and implementation plan covering a discrete time horizon that accounts for a diversity of priorities and relies on a proof of concept, interdisciplinary approaches, clear goals, and implementation of co-management opportunities.
(2) Collaboratory that serves as a place and a process that can facilitate broad community engagement, learning, experimentation, and observation.
(3) Have enough support (resources) to implement the plan.
(1) Increasing resources (i.e. funding a dedicated modeling team, computational/human resources, synthesis effort)
(2) Building a conceptual model or models (maybe via a workshop) which can help us clarify our management objectives
(3) Data collection/sharing

Additional notes:

- Including the private sector will be important (need modelers, external facilitators)
- Broad, early engagement is key
- Co-management is important: a seat at the table AND a seat during implementation (specifically referring to Tribes)

- United Auburn Indian Community is trying to find funding/develop a collaborative laboratory where people can come out in person and take classes, show the outcomes of TEK, etc.
- Need a comprehensive diet database
- Establish a well-funded food web modeling team
- Still a need to convince managers that food webs method has value- most are still focused on zooplankton (i.e. food availability)
- Need a separate workshop to develop a full conceptual model