DRAFT (DO NOT CITE)

Exploring scientific and management implications of upper trophic level food webs in the Delta

An assessment of the scientific needs to inform management actions in the Delta

Delta Independent Science Board

Draft- Do Not cite (February 15, 2024)

If you have comments, please submit them to disb@deltacouncil.ca.gov

Table of Contents

Executive Summary

This review examines the scientific requirements and management implications of achieving a better understanding of upper trophic level food webs in the Delta. The intention is to provide critical information that would help agencies determine if a “food web” perspective is warranted and, if so, how it might be attained. The Delta Independent Science Board (Delta ISB) undertook this activity with the related goals of assisting natural resource managers to improve the vitality of individual fish species/populations while concurrently supporting agencies as they implement and experiment with new management actions, explore ecosystem-based management, and adopt allied performance measures in Delta lands and waters.

The call for a food web perspective in natural resource management, and the related goals of this activity, are not new but they are essential for evaluating and sustaining a healthy Delta ecosystem. 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 ISB’s Non-Native Species Review (Delta ISB 2021). A quantitative understanding of food-web interactions allows managers to evaluate the impact of their actions aimed at supporting fish populations under climate and other system-wide changes. The

Delta ISB food web review evaluates existing information on Delta food webs, identifies informational gaps impeding progress, and links the resulting knowledge to inform management actions. The Delta ISB contends that a better understanding of trophic processes will improve management actions and the assessments of management impacts on individual species, as well as be essential for multispecies and ecosystem management.

The Delta ISB reviewed the contemporary and emerging science underpinning the current management and understanding of food webs in the Delta. 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 of the Delta. The overall effort was based on a review of the literature, on open public comments on a prospectus and public suggestions during Delta ISB board meetings, on community engagement through a series of conference calls, and on a focused two-day workshop. The workshop was held in Sacramento, California, on November 8 and 9, 2023, and brought together over 100 scientists, managers and other members of the Delta community, most with extensive experience in food-web dynamics, ecology, and species management.

The workshop and community conversations helped inform how a contemporary understanding of upper trophic level structure and dynamics could add new scientific capabilities to anticipate fish population changes in response to management and environmental drivers. Specifically, the overall review evaluated the degree to which the inclusion of food-web interactions across trophic levels might benefit and/or facilitate ecosystem management in the Delta, and whether available data and science can support the development of such tools.

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

Fortunately, the Delta is a well-studied and monitored system, and previous investigations provide a solid foundation for understanding food-web processes. The Delta ISB re-affirmed during the review that past investigations primarily focused on the effects of bottom-up processes and lower trophic levels in sustaining populations of individual species. However, we found an emerging perspective in some recent investigations demonstrating that top-down effects can also drive food web dynamics. These investigations show that knowledge of food web species interactions, such as prey preferences and anti-predator behavior, are important for supplementing long-term studies on diet and prey availability to fully represent the roles of upper-trophic level interactions in ecosystem dynamics.

The workshop, interviews with Delta scientists and managers, and comments received on the prospectus, highlighted the diversity of approaches employed for understanding food webs. At the most basic level, food web models show what species are eating, what their preferred foods are, and how much of each food type they are eating. Food web models can also be used to evaluate the effects of environmental drivers (e.g., salinity, contaminants, nutrients, and temperature) on species' abundance and interactions (e.g., predation risk) within the context of future climate change. There are several widely used modeling approaches that, depending on the type, on the level of complexity, on the spatiotemporal scales covered, on the limitations of the model type, and on the utility of the model. The review illustrates examples of commonly used food web model types, ranging from simple to complex, and these are summarized in Table 1.

Specific to the Bay-Delta, there have been several food web models already developed. Each represents an examination of different temporal and spatial aspects of the Delta food web, as well as employing a distinct modeling method (e.g., conceptual models, Ecopath with Ecosim, structural equation models). Overall, these efforts have focused primarily on the role of bottom-up processes structuring food webs and have relied heavily on long-term monitoring in the Bay-Delta conducted by state and federal agencies and by academic institutions. It is important to note, however, that many of the more comprehensive Delta models are limited in spatial/temporal coverage, are conceptual in nature, or are data-limited with respect to upper trophic levels.

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

With these examples in mind, the review identifies several direct applications of food-web models to the Delta's most pressing natural resource management issues. Five of these applications are addressed in detail: 1) Individual species management and effects of environmental drivers, 2) Ecosystem-based management, 3) Invasion of non-native species, 4) Ecosystem restoration, and 5) Contaminant exposure and cycling. For each application, the fundamental management questions, benefits of using a food web strategy, a brief exploration of steps to establish this strategy, and key examples for each approach are explored in Table 2. Additionally, considerations related to establishing an effective adaptive management process, to identifying appropriate spatial and temporal scales, to the role of behavior in food web interactions, and to the importance of exploring additional components of food webs (e.g., detritus, benthic invertebrates) are briefly addressed.

Data management, data and information sharing, and synthesis are the pillars of a well-functioning system using a food web perspective. The science and management community identified several gaps in data collection and availability, including information on trophic linkages, on community-level species interactions, on sub-lethal effects of environmental drivers, and on species' behavior. Other community members identified issues associated with the quality and consistency of data. For instance, data collection centered around presence/absence and timing cannot always be translated into species abundance. In general, *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 the understanding of food web processes as an aid to improving management.

Nearly all data users shared that continuing to improve data accessibility, transparency, and digitizing older records would make the Delta's data more user-friendly. It was recognized that data sharing and accessibility are not always the highest priorities for agencies, yet most data users mentioned it contributed to a significant challenge in understanding the full breadth of information that already exists. Importantly, it was generally recognized that the Delta's scientific community possesses an unimaginable amount of information and experienced people, yet the community is lagging in producing syntheses of both the information and the existing knowledge.

Recommendations

An improved mechanistic understanding of upper trophic-level food webs in California's Delta is essential to 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 that are 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 funded, scientific collaboration among agencies, academia, Tribes, and the public be developed to design and implement a **food web science strategy.** The food web science strategy should include 1) formal coordination and funding mechanisms, 2) flexible monitoring using emerging methods, 3) knowledge-based food web models, and 4) interactive and adaptive linkages to management. Specific initial actions include,

1. **Develop a comprehensive coordination and implementation plan for food web information, with an assignment of responsibilities.**

   A meaningful application and continuous evolution of an understanding of food web processes and the resulting modeling applications for the Delta require a focused interdisciplinary collaboration among agencies, universities, the public and Indigenous Tribes (Tribes), as this process spans the mandates of multiple agencies and areas of expertise. With respect to coordination, the workshop participants suggested that a *Collaboratory* focused on such a universal, but bounded need, would be beneficial for the Delta. Initiating a food web implementation plan might be an effective way to test out the utility of a collaboratory. A key purpose of the groups involved in implementation would be to use diverse perspectives to prioritize and **decide on key management needs and science questions** that will drive the implementation plan and therefore the **scope of food web research,**

goals for monitoring programs, and drivers for the development of food web models.

Where possible, activities driven by the plan, especially restoration activities and management actions, should be established as formal experiments. It will be paramount to explore the main research questions considering a variety of perspectives and goals, as well as to design management and restoration as statistically valid investigations – with hypotheses and set performance metrics to measure progress – and to adaptively manage/change strategies based on the results and feedback from the collaborators/community.

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

The Delta ISB sees opportunities for an improved understanding of species outcomes through research activities that include:

- Examining the roles of detritus in underpinning system productivity
- Accurately evaluating the linkage between primary producers and their availability to zooplankton
- Better characterizing the important processes maintaining the vitality of benthic communities and early life stages
- Quantifying the distributions, life histories, bioenergetics, and response to environmental drivers of the 5-10 most common/abundant species in the Delta.

Additionally, it's important to understand the flow and ecological consequences of contaminants, the predatory 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 in emerging techniques, often at lower cost and possessing greater accuracy than in the past.

With respect to monitoring, the Delta ISB believes it is essential that agencies and the community prioritize and normalize data sharing and collaboration to fully 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 formats. These tasks provide the foundation for meaningful syntheses of information and the generation of new knowledge.

3. **Develop comprehensive, spatially explicit, food-web models that are driven by management questions and tied to environmental driving forces and conditions**.

   Comprehensive food web models incorporate relevant processes and trophic levels so that relationships between environmental conditions and upper trophic level species of importance to agencies, institutions, Tribes, and the public, are better understood. A similar need and a recommendation were also identified in the Delta ISB Review of Non-native Species (DISB 2021).

   Food web model development should be focused on the spatiotemporal scales relevant to the guiding management question(s). The efforts should start with a hypothesis and conceptual model, using the simplest model that will address the guiding question. **It will be helpful to examine the *processes* of model development that have proved successful in other large ecosystems**. Models can be later combined over space and time, or with additional model types (e.g., hydrology, and others), to achieve a more comprehensive view of Delta ecosystem functions. Food web models can also be used to evaluate ecosystem-level goals and explore ecosystem-based management.

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

   An adaptive framework underpins ongoing and effective decision-making protocols and/or processes. Doing so facilitates the transfer of new insights and quantitative information derived about food webs into timely management actions and continual improvements in the science, relevance of monitoring activities, model applicability, and management focus.

   Adaptive management in this context begins by identifying priority management questions and outcomes that would benefit from enhanced food web understanding using models with appropriate time, space, and parameter scales. The adaptive framework (see details in Figure 3) can be applied to each management question (Table 2). The process is intended to help identify priority knowledge gaps, improve the model to reduce uncertainties, adjust monitoring programs appropriately, and help crystalize the management needs.

Integral to all four components of this process, the Delta ISB also recommends:

- Implementing proven team-building strategies to encourage the efficient transfer of newly generated knowledge to natural resource decision-makers.
- Establish teams (to include students, technicians, scientists, and decision-makers), that address specific issues and will regularly exchange information and formulate solutions.
- Evaluate the usefulness of the activity within a defined timeframe (~decade). Proof of concept and meaningful management applications will be necessary criteria for determining success.

The Delta ISB believes that these recommendations will advance food web science to serve a broad range of management decisions. Collaboration and adaptive management will be needed to make it efficient and effective. We anticipate that this effort will require some change to the current communication, monitoring, and management approaches. However, the benefits will be improved capacity to forecast effects on fish and other aquatic organisms due to management actions and their interactions with an ever-changing climate and ecosystem. One workshop participant summed up the necessity for food web knowledge simply, "**Almost any [management] question you can think of is a food web question; we need to understand *how* to represent the food web interactions in management, not whether you 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 are largely driven by climate change, sea level rise, major flooding and storms, non-native species, water supply diversions, shifts in land use, restoration actions, and a host of other influences originating from a growing human population (Norgaard et al. 2021). Understanding and predicting how those drivers affect the abundances of fish species and ecosystem sustainability are at the core of Delta policy and management, and are critical to achieving the Delta Plan's coequal goals of providing a more reliable water supply and protecting, restoring and enhancing the Delta ecosystem in a manner that protects and 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 provide critical information that would help agencies manage individual fish species and adopt ecosystem-level goals and performance measures in Delta lands and waters. The Delta ISB is charged with the “oversight of the scientific research, monitoring, and assessment programs that support adaptive management of the Delta through periodic reviews…” 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). A quantitative understanding of food-web interactions is needed to evaluate the impact of management actions aimed at supporting fish populations under climate and other system-wide changes. The Delta ISB food web review aims to evaluate existing information on Delta food webs, to identify informational gaps impeding progress, and to link the resulting knowledge to inform management actions. The Delta ISB contends that a better understanding of trophic processes will not only improve management actions and the assessments of management impacts on individual species, it is essential for multispecies and ecosystem management in the Delta.

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. 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 of the Delta. The overall review was based on a review of the literature, open public comments on a prospectus and during Board Meetings, community engagement through a series of conference calls, and, primarily on a focused two-day workshop. The workshop was held in Sacramento on November 8 and 9, 2023 and brought together 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) might substantially improve predictions of an individual species' responses to environmental drivers and to management actions.

The workshop helped to inform how a contemporary understanding of upper trophic level dynamics could add new scientific capabilities to anticipate fish population changes in response to management and environmental drivers. Specifically, the overall review evaluated the degree to which the inclusion of food-web interactions across trophic levels might benefit and facilitate ecosystem management in the Delta, and whether available data and science can support the development of such tools.

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

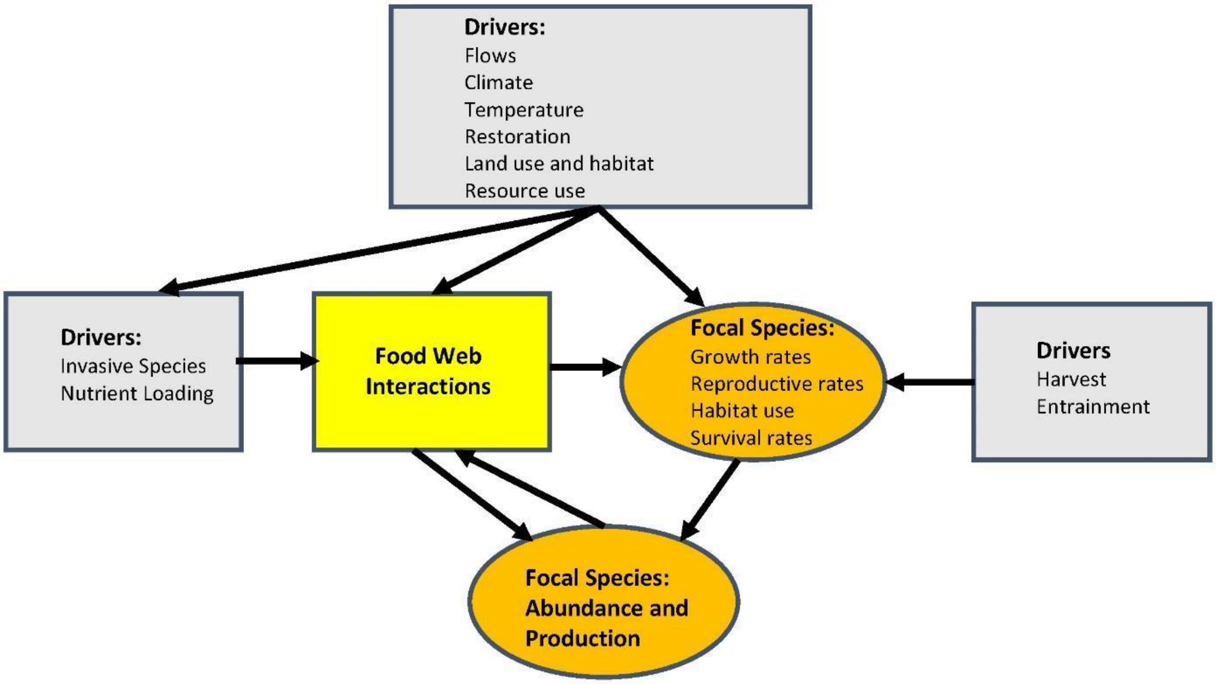

Figure 1: Conceptual diagram illustrating the importance of food web interactions (yellow box) to the abundance, function, and biological functions of focal species (orange ovals). Traditional Delta management normally considers both direct and indirect drivers (gray boxes) to a species' population but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

Predicting the impacts of habitat restoration, fisheries, changes in environmental drivers (e.g., climate, changes in nutrient loading, invasive species) and the bioaccumulation of contaminants on species or the ecosystem requires an understanding of food web processes. The degree that food webs need to be understood or quantified depends on the management applications (e.g., see section "Food-web Applications in other Large Ecosystems"). Food web interactions can be quantified and visualized in a variety of different 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 species within an ecosystem (dynamic or functional food webs; Embke et al. 2022).

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

Box 1. Methods to describe food web interactions

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

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

Food Webs in the Sacramento-San Joaquin Delta

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

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

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

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

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

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

There are still additional, and important, gaps in food web knowledge for the Delta. While several studies identified aspects of upper trophic species interactions (e.g., Grossman 2016; Appendix 2), the higher trophic levels are hard to quantify, in part, due to a lack of long-term data on large piscivorous fishes and the impacts of water exports on population abundances (Mac Nally et al. 2010; Rogers et al. 2022). **Knowledge of prey preferences and anti-predator behavior are important to**

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

General Food Web Modeling Approaches

Food web modeling has been used to evaluate 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). 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 accurate models can help identify features that promote stability and biodiversity within an ecosystem. Furthermore, quantitative models with predictive capabilities are especially useful for management because they enable an evaluation of the influence of environmental and management changes on multiple future scenarios (e.g., Trifonova et al. 2017).

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 ranges in the level of complexity, the spatiotemporal scales covered, the limitations of the model type, and the utility of the model (Table 1). Here we cover some examples of food web model types, ranging from simple to complex (summarized in Table 1).

Linkage or connectedness food web models show generally “who is eating who” by displaying the presence/absence of species interactions. These models are relatively easy to construct and show a base understanding of connections between species, 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, benefits, analytical issues, and potential applications for the Delta of modeling approaches commonly used to understand food webs and their internal processes.

Model Type	Data Requirements	Benefits	Analytical Issues	Applications for Delta, examples
Linkage/ connectedness food webs *Who is eating who/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, can’t tell how important each link is • 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*	• Calculate the % contribution (by biomass) of prey to diet of each consumer	• Shows the importance of each resource to consumers	• Does not account for quantity or quality of consumption • Does not allow examination of competition, top-	Adds useful complexity to understand and rank prey items by importance for consumers Examples: Vander Zanden et al. 1999

Model Type	Data Requirements	Benefits	Analytical Issues	Applications for Delta, examples
each resource to consumers	• Tools: Stable isotopes and/ordiet analyses		down control, and other important processes	[Muro-Torres et al. 2019](#)
Flow/flux food webs *Linkages are weighted by the amount of energy flow over a defined amount of time*	• Consumer production estimates (biomass over a certain amount of time) • Consumer diet information (from diet analyses, isotopes) • Bioenergetic information (quantity consumed)	• Map consumptive pathways that support species of interest • Can identify food web metrics that promote stability • Management-relevant outcomes	• High 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](#) [Bellmore et al. 2013](#), [2015](#) [Walters et al. 2020](#)
Bioenergetics models *Understanding the flow of energy and incorporating how energy is processed*	• Thermal experience • Temporal/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)	• Understand food web processes at different spatiotemporal scales, life stages, and species • Consumption estimate output can be used to get population consumption • Can add into other models (like	• High data requirements • May need to rely on assumptions	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](#)

Model Type	Data Requirements	Benefits	Analytical Issues	Applications for Delta, examples
		hydrodynamic or foraging models)		Hansen et al. 2021
Large-scale ecosystem models *3-D models that usually integrate various aspects of biology, physics, geochemistry, fisheries management, and economics. Often modular by design.*	Depends on the model, but likely comes from a synthesis of data: • Production to biomass ratio • Consumption to biomass ratio • Biomass • Proportion of production used in the system (e.g., ecotrophic efficiency) • Data requirements of extra model (e.g., EcoSpace, EcoTrace, hydrodynamics/physics models)	• Some modeling programs can be open source and able 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	• High data requirements, which increases 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 Buchheister et al. 2017 Chagaris et al. 2020 de Mutsert et al. 2021 Zhang et al. 2023

Diet composition food webs 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 understand and rank 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.

In 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 not only useful but 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 time period), 2) consumer diet information (from stable isotopes or diet analysis), and 3) bioenergetic 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 in 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 data-intensive, they can provide information highly relevant for ecosystem management.

Bioenergetics models account for both the amount of energy moving through the system (as in flow food web models) and each organism’s ability to process the energy (metabolism). These models have a wide variety of benefits and capabilities, including understanding food web processes at different life stages, for different 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. Bioenergetics models can be added into other food web models such as flow models or large-scale ecosystem models. Bioenergetics models have 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.

Large-scale ecosystem models are usually 3-D models that integrate biology, physics, geochemistry, fisheries management, and economics to obtain a holistic understanding of ecosystem function. These models are often not designed for precise forecasting, but can be very helpful in understanding scenario outcomes of different species management actions, stressors, or climate conditions. Place-based examples of models used to inform species and ecosystem management include the Northwest Atlantic Continental Shelf (NWACS) full ecosystem model, the Northwest Atlantic Continental Shelf model of intermediate complexity (NWACS-MICE) (Buchheister et al. 2017, Chagris et al. 2020), 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 likely 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, stock assessments, surveys, or estimates from experts or other systems. In addition to substantial data requirements, these complex models can create results that are challenging to interpret with high model uncertainty. However, modeling frameworks can often be open source (e.g., EwE) and be customized to the management questions or purpose of the model. 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.

While the assumption is often that more complex models are always superior, there are benefits and obstacles 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 management decisions, but they can be extremely useful to facilitate understanding of ecosystems and often rely on clear assumptions. In contrast, complex models include site-specific context and can simulate management alternatives in detail. However, complex models can be hard to interpret, have unclear assumptions, and/or have substantial data requirements.

There are a similar set of tradeoffs for the range of spatiotemporal complexity in food web models. Broad spatial scales may better represent the true heterogeneity of the landscape, while models with finer spatial and temporal resolution may be more useful for answering specific questions or looking at short term processes. The trophic levels and species of interest may also drive the spatiotemporal range; upper trophic levels generally 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.

Ultimately, the food web model type and level of complexity should be driven by, and linked to, 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 were very useful, and that the “best model” was often the *simplest* model that would address the primary management questions.

Previous Food-web Modeling in the Delta

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

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

Many of the more comprehensive Delta models are limited in spatial/temporal coverage or are conceptual in nature (e.g., Durand 2015; Brown et al. 2016); however, a quantitative evaluation of the effects of management or species population changes requires quantitative modeling. For example, an Ecopath with Ecosim model of 1982 Bay-Delta food webs showed that mid-upper trophic levels (comprised primarily of fishes) contributed 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 and energy obtained by detritus, as well as separate the roles of the pelagic and littoral food webs. A second example is from the Delta Regional Ecosystem Restoration Implementation Plan (DRERIP). DRERIP developed a series of conceptual food web models for each trophic level to determine the impacts of restoration activities (Durand 2008, 2015). These qualitative models focused on a variety of drivers (e.g., temperature, hydrology, habitat, depth, contaminants, water diversions, and more) and their effects on food web dynamics. 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 more recent food-web model differentiates the role of bottom-up, top-down, and environmental drivers in shaping pelagic food webs. Using structural equation models, this model showed that for zooplankton and estuarine fishes, bottom-up effects were stronger in upstream, freshwater regions, but top-down effects were stronger in downstream, brackish water regions (Rogers et al. 2022). However, the authors mention that there were no long-term data on large-bodied piscivorous fishes to add into the model and, as a result, upper-trophic level food web interactions may not have been accurately represented (Rogers et al. 2022). Additionally, they showed several novel relationships that were not identified in another multivariate food web model (Mac Nally et al. 2010), including the direct impact of chlorophyll on zooplankton biomass since the *Potamocorbula* clam introduction, unique trophic relationships among zooplankton groups, and the effects of flow, salinity, and temperature on different regions of food webs across the Delta (Rogers et al. 2022).

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

Food-web applications in other large ecosystems

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

Box 2. Great Lakes: Non-native species and the balance of predator-prey populations

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

Like the Delta, the Great Lakes struggle with the impacts of non-native species on the ecosystem (Delta ISB 2021). The invasion of non-native dreissenid (zebra and quagga) mussels 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 keep their populations down. The program was so successful that stocking was expanded to support an economically important sports fishery valued at $7 billion (Great Lakes Fishery Commission 2023). Ultimately, overstocking of salmon reduced population levels of prey to such an extent that salmon populations and growth was reduced, which impacted the sports fishery. As a result of the improved understanding of food-web processes, fisheries management in the Great Lakes evolved toward an ecosystem-level focus in order to capture natural and human modifiers to fish production (Ives et al. 2019) and to protect the Great Lakes fisheries.

Box 3. Columbia River Basin: Food web impacts to habitat restoration

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

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

Box 4. Gulf of Mexico: Managing nutrient inputs

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

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

Box 5. Chesapeake Bay: Multi-species management

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

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

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

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

Applications of Improved Understanding of Upper Food Webs in the Delta

There are a number of direct applications of food-web models to management questions in the Delta. Below, we briefly illustrate 5 of these applications. 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 discussed in Table 2.

Table 2. Applications for employing a food web approach to improve natural resource management in the Delta.

Application & Associated Management Questions	Benefits of Food Web Approach	Next Steps for the Delta	References and Examples
Single-species management 1. **How do specific management actions affect key species?** 2. What are the food resources that support the rare species?	● Species interactions affect key species directly or indirectly; cannot fully understand or predict changes in populations without examining key aspects of the life cycle and ecosystem ● 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 (e.g., -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 .	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 showed the possible effects of different harvest rates on Atlantic menhaden predators, including birds (Buchheister et al. 2017). 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 and smallmouth bass; ISRP 2023)

Application & Associated Management Questions	**Benefits of Food Web Approach**	**Next Steps for the Delta**	**References and Examples**
Ecosystem-Based Management (EBM) **1. How do changes to environmental conditions affect food web interactions?** 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. Conduct laboratory or field experiments to evaluate sublethal effects of stressors on species 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 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 levels 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	1. Evaluate whether species reduction/eradication is feasible and cost-effective; otherwise manage system for the current residents 2. Monitor non-native species in habitats outside the pelagic zone (i.e., in locations not currently included in food webs models) 3. Add monitoring that considers the *quality* of food resources available	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).

Application & Associated Management Questions	Benefits of Food Web Approach	Next Steps for the Delta	References and Examples
	native species that feed on non-native species	4. Add modules into existing food web models to forecast the impacts of non-native species introductions or eradication	
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? 3. What are the food web processes that influence "winners" and "losers" in response to restoration activities?	- Current premise of biological opinions is that 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 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 - Examining effects of restoration using a food webs approach would reveal how restoration impacts individual species	1. Accurately monitor biomass of primary producers in the system (not just chlorophyll, which can overestimate accessible prey) 2. Understand detrital processes and their roles in Delta food webs 3. Create flow food web models to understand how energy and nutrients reach upper trophic levels 4. Conduct experiments with restoration by including key food web processes over time in the monitoring of restored areas, and not just terrestrial flora or acreage measurements	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). 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).
Contaminant exposure and cycling	- A food webs perspective enables understanding of the vulnerability of different	1. Monitor for contaminants of concern (including urban	Coho salmon exposed to copper contamination displayed reduced anti-predator

Application & Associated Management Questions	Benefits of Food Web Approach	Next Steps for the Delta	References and Examples
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?	species to contaminants and allows for quantifying bioaccumulation - 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	use), and adaptively manage based on current science 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 flow model of contaminants through the Delta's ecological system (e.g., EcoTracer)	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

Workshop participants re-iterated that much of the fisheries science and management and regulations effort in the Delta is focused on protection of threatened 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 threatened species as guided by regulations and requirements. It is well recognized that food webs can play an important role in the abundances of individual species. Key ecosystem drivers such as climate change, restoration efforts, and water flows can affect a species directly and indirectly through the food web since nearly all of these environmental drivers and management actions will affect other species as well (Figure 1).

Ecosystem-based management

Ecosystem-based management (EBM) is an environmental management approach that recognizes the full array of interactions within an ecosystem, including humans, rather than considering single issues, species, or ecosystem services in isolation. 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 have emerged as crucial for spatially diverse and evolving landscapes and contributes toward a more holistic view of ecosystem health, within the limits of existing regulations (e.g., Rieman et al. 2015; Delta Stewardship Council and Delta Science Program 2019; Mount et al. 2019). An important component of both ecosystem-based and multispecies management is an understanding of food web interactions. For instance, the carrying capacity (abundance or biomass of species a particular habitat can support) largely depends on food availability and food web interactions, in combination with other biotic and abiotic conditions. Improving carrying capacity is essential for successful restoration of fish, migratory birds, or species managed for harvest. A poor understanding of food webs can impact the outcome of management actions, yet food-web science is not often included in natural resource management (Naiman et al. 2012; Naman et al. 2022).

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

A food-web perspective contributes 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 allows 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 – or the arrival of an invasive species – directly influence fishes and their food supplies with the effects communicated throughout the entire aquatic ecosystem 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.

Invasion of non-native species

The invasion and establishment of a non-native species are considered to be key drivers of ecosystem change. The San Francisco Estuary is one of the most invaded aquatic ecosystems in the USA. A key management challenge is to predict the impacts of new species introductions. In a review by the Delta ISB of the science of non-native species in the Delta, a key recommendation was to

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

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

Ecosystem Restoration

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

Ecosystem restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed by manipulating conditions sufficiently so that natural processes are established (UNEP 2021). This is especially important in the Delta where most native fish are in significant decline, as is native biodiversity. With the signing of State Bill 37 into law by Govenor Gavin Newsom, California is committed to conserving 30% of state land and coastal waters by 2030 – and ecological 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 a food-web perspective contribute to the successful restoration of native fishes and aquatic biodiversity? The expectation is that ecological restoration will significantly improve the carrying capacity for native fishes and improve overall biotic diversity. These can be quantified by examining aquatic food-web processes, which not only identify species benefiting from restoration actions but also illustrate interactions between populations and communities. The food-web perspective allows managers to gauge the success – or not – of restoration actions. For instance, restoration of the physical habitat both 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. Restoration actions doing both will be successful whereas those not providing adequate feeding opportunities – or results in a fundamentally changed species assemblage – will be immediately apparent.

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, and other contaminants (California Water Quality Monitoring Council 2023). These contaminants are discharged or wash 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 take in mercury and other toxic chemicals from the environment, when in low concentrations they can bioaccumulate many of them through the food chain to higher level consumers (e.g., birds, humans; see 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 (depending on their sensitivity) and community processes.

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 to impact human health. Some community members articulated that there has been sufficient research on the physiological effects and lethal limits of some contaminants (e.g., heavy metals) but that the ecosystem effects and sublethal effects of contaminants are largely unknown. In addition, it was noted that sublethal impacts from contaminants on species and how they may impact feeding behavior or predator avoidance are important informational gaps.

A food-web perspective is essential for understand the ecosystem-scale effects of aquatic contaminants. Food webs are a major pathway by which contaminants flow from species-to-species as well as how contaminants affect the population and community dynamics of fish. Management decisions to reduce contaminant inputs to the Delta should understand the main pathways before actions are taken, if they are to be fully effective. For instance, food-web processes are an important determinant of the flows of contaminants in the Delta. Yet, little is known about the major biotic pathways and how they differentially affect the vitality of populations and the sustainability of communities.

Science Gaps and Additional Considerations for Incorporating Food Webs into Delta Management

To begin implementing a food webs approach for the applications presented in the previous section and in Table 2, workshop and community discussions participants and the Delta ISB identified several science gaps and aspects to consider while taking this approach. These considerations are designed to aid the development of best practices in implementing food web science into management.

Adaptive management

Establishing an adaptive management approach in the creation and use of food web models for upper-trophic level management is essential. 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 in the Delta. Adaptive management is an iterative process, which requires periodic re-evaluation of the key management problem or goals, knowledge acquisition, and monitoring (Wiens et al. 2017). Food webs in the Delta are both spatially and temporally dynamic, and likely require regular updates to monitoring programs and any associated management strategies. An understanding of the dynamics of food webs will be vital for creation of adaptively managed ecosystem-based management strategies in the Delta.

Temporal and spatial scales

Delta heterogeneity was frequently mentioned as a topic of concern in the discussions with Delta scientists and managers. The spatial diversity of habitats and the prevalence of seasonal and short-term changes in the system underpin many food web interactions (e.g., Nobriga and Feyrer 2007; Young et al. 2021). Additionally, a wide variety of spatiotemporal scales of environmental and anthropogenic drivers impact Delta species. Understanding how these drivers affect resource availability, predation, competition, and other food-web interactions is critical. The science and management communities stressed that an appropriate food-web model (or set of models) would help incorporate the spatiotemporal variability in the system and 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 bottlenecks in habitat use. Similarly, a model with predictive capabilities that could forecast the effects of management decisions on species would be especially useful for managing State and Federally listed species.

The role of behavior in food web interactions

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

Understanding lightly investigated components of Delta food webs

The importance of detritus and benthic invertebrates for supporting Delta food webs is not empirically well-established. The role of detritus, such as dissolved organic carbon, has been long-recognized as a crucial food web pathway elsewhere (Sibert et al. 1977; Naiman and Sibert 1979). Initial Delta food web models combined the pelagic and detrital aspects of food webs but suggested that detrital pathways be considered separately in future studies (Bauer 2010). While detrital components can be challenging to quantify, they are essential for understanding the movement of carbon through the system. The importance 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, and additional research could clarify the role of the detrital pathway throughout ontogeny in these species.

Benthic invertebrate communities in the Delta have changed over time, primarily due to the introduction of non-native species. For example, the non-native clam, *Potamocorbula amurensis*, changed the availability of phytoplankton and altered turbidity patterns in the Delta (Kimmerer et al. 1994; Kimmerer and Orsi 1996; Kimmerer and Thompson 2014; Durand 2015). The food web effects of other benthic invertebrates have been explored less, such as the role of the non-native red-swamp crayfish (*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.

Data management, data and information sharing, and synthesis

Science and management community members identified several gaps in data collection and availability, including information on trophic linkages, community-level species interactions, sub-lethal effects of drivers, and behavior. Some identified issues associated with the quality and consistency of data. For example, data collection is often centered around presence/absence and timing, which cannot always be translated into species abundance. More intentional data collection (i.e., not just opportunity-based), establishing the spatiotemporal scales of monitoring, and determining Delta-wide data priorities are essential for improving understanding as well as management.

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

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

Conclusions

Improved mechanistic understanding of upper trophic-level food webs in the California Delta is essential to 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 (See Figure 1). A workshop participant summed up the necessity for food web knowledge simply, “**Almost any [management] question you can think of is a food web question; we need to understand *how* to represent the food web interactions in management, not whether you need to or not.**”

Essentially, 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 and vitalities of other species. The importance of bilateral predator-prey interactions is well- recognized in the Delta, 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. The same drivers and processes also affect the more abundant species in the ecosystem and likely shift community dynamics. Nevertheless, it remains challenging to estimate the level of changes that food web interactions can have because these processes have not been well quantified or modeled in the Delta, as they have in some other large ecosystems.

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 techniques, perspectives and insights in food web processes and models are being actively applied to broad (complex) ecosystem management and socioeconomic issues in large ecosystems elsewhere (Boxes 2-5; Table 2), with 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, we argue that progress can be swift given the level of understanding on hydrodynamics, environmental drivers, and lower trophic-level food webs. The workshop and examples/citations provided in this review demonstrate that an understanding of processes and the modeling of aquatic food webs has greatly advanced in recent years, providing a strong scientific foundation for establishing a pragmatic food web science strategy for the Delta.

Recommendations

An improved mechanistic understanding of upper trophic-level food webs in California's Delta is essential to 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 that are 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 funded, scientific collaboration among agencies, academia, Tribes, and the public be developed to design and implement a **food web science strategy.** The food web science strategy should include 1) formal coordination mechanisms, 2) flexible monitoring using emerging methods, 3) knowledge-based food web models, and 4) interactive and adaptive linkages to management. Specific initial actions include,

> **1. Develop a comprehensive coordination and implementation plan for food web information, with an assignment of responsibilities.**
>
> A meaningful application and continuous evolution of an understanding of food web processes and the resulting modeling applications for the Delta require a focused interdisciplinary collaboration among agencies, universities, the public and Tribes, as this process spans the mandates of multiple agencies and areas of expertise. Coordination can be done in various ways, but workshop participants suggested that a *Collaboratory* focused on a universal, but bounded need, would be beneficial for the Delta. 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 implementation should be to use diverse perspectives to prioritize and **decide on key management needs and science questions** that will drive the implementation plan and therefore the **scope of food webs research, goals for monitoring programs, and drivers for the development of food web models.**
>
> **Where possible, activities driven by the plan, especially restoration activities and management actions, should be established as formal experiments.** It will be paramount to explore the main research questions considering a variety of perspectives and goals, as well as to design management and restoration as statistically valid investigations – with hypotheses and set performance metrics to measure progress – and to

adaptively manage/change strategies based on the results and feedback from the collaborators/community. The plan should spell out who has responsibility for specific components and how the efforts will be prioritized, supported, and funded.

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

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 but time-consuming and costly methods. In the future, **the Delta ISB sees opportunities for an improved understanding of species outcomes through research activities that include:**

- **examining the roles of detritus in underpinning system productivity,**
- **accurately evaluating the linkage between primary producers and their availability to zooplankton,**
- **better characterizing the important processes maintaining the vitality of benthic communities and early life stages, and**
- **quantifying the distributions, life histories, bioenergetics, and response to environmental drivers of the 5-10 most common/abundant species in the Delta.**

Additionally, it's important to understanding 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 in emerging techniques, often at lower cost and with greater accuracy than in the past.

With respect to monitoring, **the Delta ISB believes it is essential that agencies and the community prioritize and normalize data sharing and collaboration to fully 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 formats. It may be helpful to develop and maintain a common database on the diets, food quality and nutrition of Delta species. These tasks provide the foundation for meaningful syntheses of information and the generation of new knowledge.

3. Develop comprehensive, spatially explicit, food-web models that are driven by management questions and tied to environmental driving forces and conditions.

By comprehensive, we mean food web models that incorporate relevant processes and trophic levels so that relationships between environmental conditions and upper trophic level species of importance to agencies, institutions, Tribes, and the public, are better understood. A similar need and a recommendation were also identified in the Delta ISB Review of Non-native Species (DISB 2021).

Food web model development should be focused on the spatiotemporal scales relevant to the guiding management question(s) identified in Table 2. The efforts should start with a hypothesis and conceptual model and begin with the simplest model that will address the guiding question. For this process, **it will be helpful to examine the *processes* of model development that have proved successful in other large ecosystems**. Models can be later combined over space and time, or with additional model types (e.g., hydrology, and others), to achieve a more comprehensive view of Delta ecosystem functions. Model frameworks, perhaps organized in a workshop or series of workshops, should establish ecological principles and enable the ability to forecast how species and communities will be altered under changing environmental conditions and management actions. Food web models can also be used to evaluate ecosystem-level goals and explore ecosystem-based management.

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

The adaptive framework (Figures 2 and 3) should be used to establish ongoing and effective decision-making protocols and/or processes. Doing so facilitates the transfer of new insights and quantitative information derived about food webs into timely management actions and continual improvements in the science, relevance of monitoring activities, model applicability, and management focus.

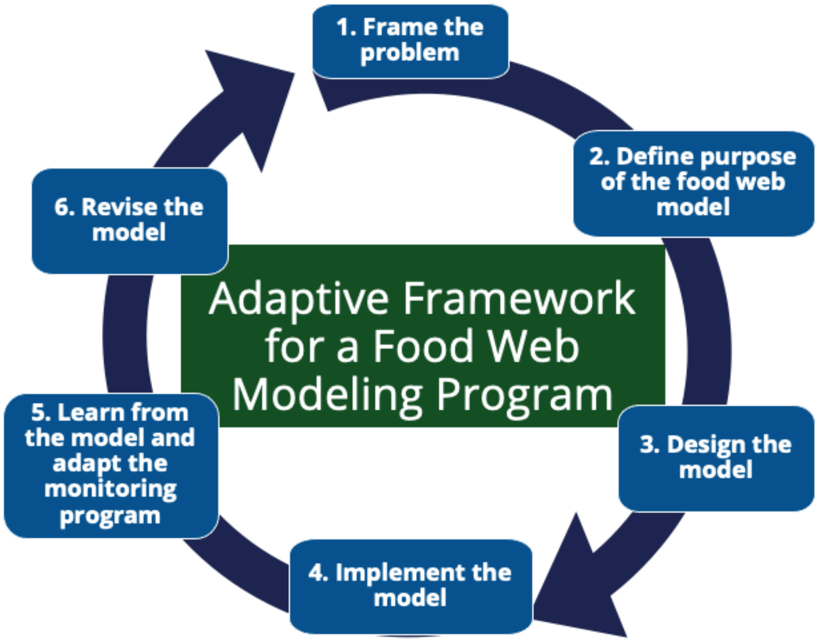

Figure 2: An adaptive framework for application and continual evolution of food web models to management questions.

Adaptive management in this context begins by identifying priority management questions and outcomes that would benefit from enhanced food web understanding using models with appropriate time, space, and parameter scales. The adaptive framework (see details in Figure 3) can be applied to each management question (Table 2). The process is intended to help identify priority gaps, improve the model to reduce uncertainties, adjust monitoring programs appropriately, and help crystalize the management needs.

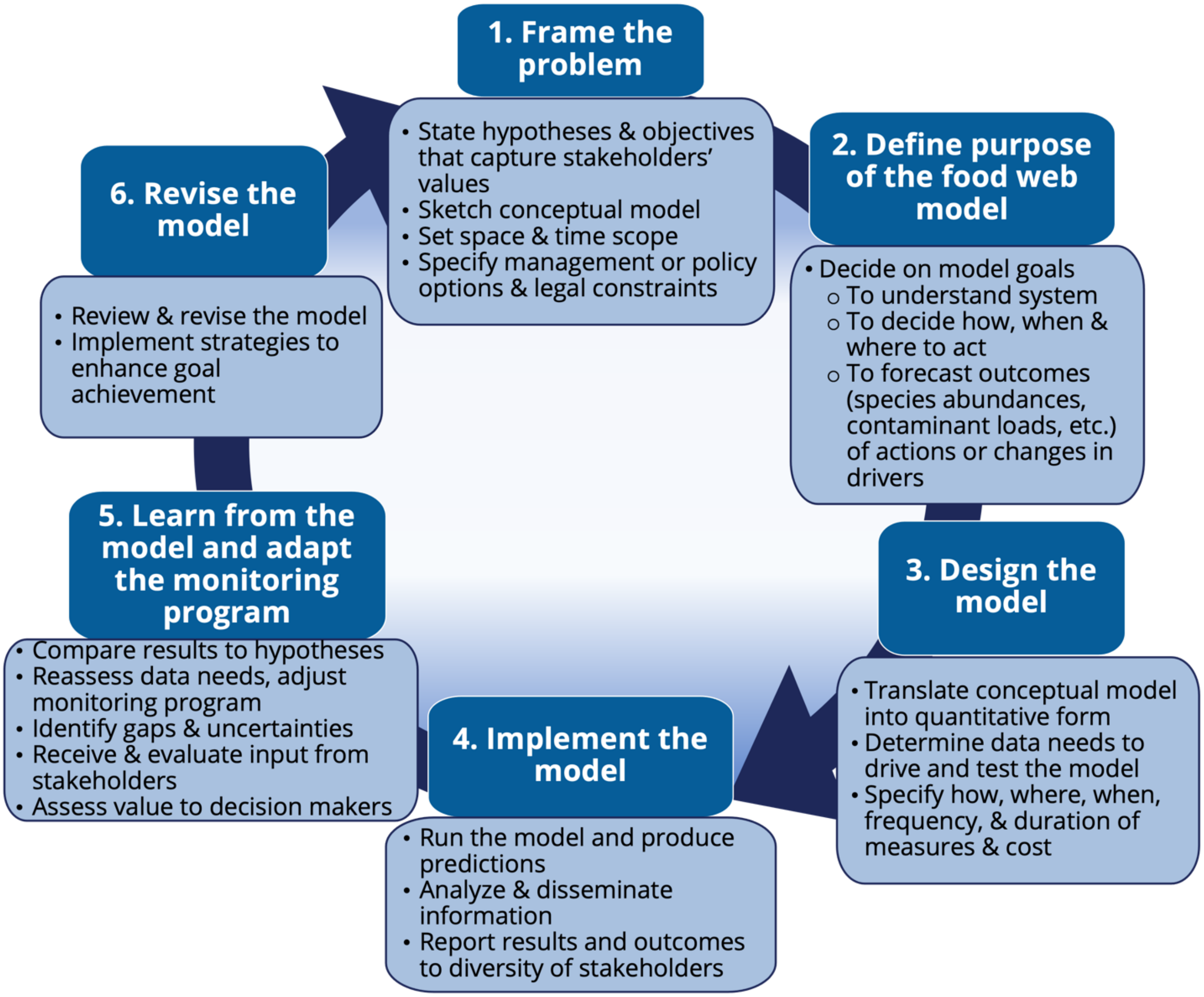

Figure 3: An example of a detailed adaptive framework for application and continual evolution of food web models to management questions.

Integral to all aspects of this process, the Delta ISB also recommends:

- Implementing proven team-building strategies to encourage the efficient transfer of newly generated knowledge to natural resource decision-makers (e.g. Venter et al. 2008).
- Establish teams (to include students, technicians, scientists, and decision-makers), that address specific issues and will regularly to exchange information and formulate solutions.
- Examine the usefulness of the activity within a defined timeframe (~decade). Proof of concept and meaningful management applications will be necessary criteria for determining success.

The Delta ISB believes that these recommendations, collectively, will advance food web science in the Delta to serve a broad range of management decisions. Collaboration and adaptive management of the effort will be needed to make it efficient and effective. And even though it will require finding new resources, 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.

References

Anstead, K. A., K. Drew, D. Chagaris, and others. 2021. The Path to an Ecosystem Approach for Forage Fish Management: A Case Study of Atlantic Menhaden. Front. Mar. Sci. **8**. doi:10.3389/fmars.2021.607657

Bardeen, S. 2021. Why Is the Delta Starving? PPIC Blog Post. https://www.ppic.org/blog/why-is-the-delta-starving/#:~:text=We%20continue%20to%20manage%20the,waves%20and%20multi%2Dyear%20droughts

Bauer, M. 2010. An ecosystem model of the Sacramento-San Joaquin Delta and Suisun Bay, California USA. California State University, Chico. https://dspace.calstate.edu/bitstream/handle/10211.3/10211.4_254/Final%20-%20Marissa%20Bauer.pdf?sequence=1

Baxter, R., R. Breuer, L. Brown, and others. 2008. Pelagic Organism Decline Progress Report: 2007 Synthesis of Results Interagency Ecological Program for the San Francisco Estuary. https://d1wqtxts1xzle7.cloudfront.net/53830267/2007_iep-pod_synthesis_report_031408-libre.pdf?1499799485=&response-content-disposition=inline%3B+filename%3DPelagic_Organism_Decline_Progress_Report.pdf&Expires=1696294118&Signature=N5WtAv5UzU-YDAEflxDMGeDmp2txXRSnsD12xRfyDXOgslaaiGL2Ei8caBOWmVHpx7n8~JZLou7KYWv08DwcYCvqFCO-Amv3RyswizO~BcV4iNwFp4R7qS0m78JYKLkdm~t9oUPPmos96cjVBksVcFdhKAxe2F2gvP7bcpqu-9y9RsBbOYD6cCqi9YMVoPFhoiIJXqchz1QcEF3h2O1FrqdhthXaY9Xr-mnfkSDimjahoLPfUKIr6Xx7CWJFSKcSTEoN2Kr8xMWu2YJHejf6zEfeZgJmas2wcJOFcyady79j23N5Jr8DOVjmaNqZXVNjl~nqOnLT7-nO3P2vZ-PyYw__&Key-Pair-Id=APKAJLOHF5GGSLRBV4ZA

Bellmore, J. R., C. V. Baxter, K. Martens, and P. J. Connolly. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecol. Appl. **23**(1): 189-207. doi:10.1890/12-0806.1

Bellmore, J. R., C. V. Baxter, and P. J. Connolly. 2015. Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. Ecology. **96**(1): 274-283. doi:10.1890/14-0733.1

Benke, A. C. and J. B. Wallace. 1997. Trophic basis of production among riverine Caddisflied: Implications for food web analysis. Ecology. **78**: 1132-1145. doi:10.1890/0012-9658(1997)078[1132:TBOPAR]2.0.CO;2

Brandl, S., B. Schreier, J. L. Conrad, B. May, and M. Baerwald. 2021. Enumerating Predation on Chinook Salmon, Delta Smelt, and Other San Francisco Estuary Fishes Using Genetics. North Am. J. Fish. Manag. 41: 1053–1065. doi:10.1002/nafm.10582

Brandt, S. B., and D. M. Mason. 2003. Effect of nutrient loading on Atlantic menhaden (*Brevoortia tyrannus*) growth rate potential in the Patuxent River. Estuaries 26: 298–309. doi:10.1007/BF02695968

Brown, L. R., W. Kimmerer, J. Louise Conrad, S. Lesmeister, and A. Mueller-Solger. 2016. Food webs of the delta, Suisun bay, and Suisun marsh: An update on current understanding and possibilities for management. San Fr. Estuary Watershed Sci. 14. doi:10.15447/sfews.2016v14iss3art4

Brussard, P.F., J.M. Reed, C.R. Tracy 1998. Ecosystem management: what is it really? Landscape and Urban Planning 40:9-20.

Buchheister, A., T. J. Miller, and E. D. Houde. 2017. Evaluating ecosystem-based reference points for Atlantic Menhaden. Mar. Coast. Fish. 9: 457–478. doi:10.1080/19425120.2017.1360420

Bunnell, D. B., R. P. Barbiero, S. A. Ludsin, and others. 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. Bioscience 64: 26–39. doi:10.1093/biosci/bit001

California Water Quality Monitoring Council. 2023. Are our streams and rivers healthy? https://mywaterquality.ca.gov/index.html

Chagaris, D., K. Drew, A. Schueller, and others. 2020. Ecological reference points for Atlantic Menhaden established using an ecosystem model of intermediate complexity. Front. Mar. Sci. **7**: 606417. doi: 10.3389/fmars.2020.606417

Chesapeake Bay Fisheries Ecosystem Advisory Panel. 2006. Fisheries Ecosystem Planning for Chesapeake Bay, American Fisheries Society. ISBN 1-888569-75-1

Chesapeake Bay Program, 2023. https://www.chesapeakebay.net/issues

Christensen, V., A. Beattie, C. Buchanan, and others. 2009. Fisheries Ecosystem Model of the Chesapeake Bay: Methodology, Parameterization, and Model Exploration. Natl. Ocean. Atmos. Adm. https://spo.nmfs.noaa.gov/sites/default/files/TM106%20FINAL.pdf

Cloern, J. E., and A. D. Jassby. 2012. Drivers of change in estuarine-coastal ecosystems: Discoveries from four decades of study in San Francisco Bay. Rev. Geophys. 50: 1–33. doi:10.1029/2012RG000397

Cloern, J. E., A. Robinson, A. Richey, and others. 2016. Primary Production in the Delta: Then and now. San Fr. Estuary Watershed Sci. 14. doi:10.15447/sfews.2016v14iss3art1

Cloern, J. E., S. M. Safran, L. Smith Vaughn, and others. 2021. On the human appropriation of wetland primary production. Sci. Total Environ. 785: 147097. doi:10.1016/j.scitotenv.2021.147097

Conrad, J. L., A. J. Bibian, K. L. Weinersmith, and others. 2016. Novel Species Interactions in a Highly Modified Estuary: Association of Largemouth Bass with Brazilian Waterweed Egeria densa. Trans. Am. Fish. Soc. 145: 249–263. doi:10.1080/00028487.2015.1114521

Craig, J. K. and J. S. Link. 2023. It is past time to use ecosystem models tactically to support ecosystem-based fisheries management: Case studies using Ecopath with Ecosim in an operational management context. Fish Fish. **24**(3): 381-406. doi:10.1111/faf.12733

Cross, W. F., C. V. Baxter, K. C. Donner, and others. 2011. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. Ecol. Appl. **21**: 2016-2033. doi:10.1890/10-1719.1

Delta Independent Science Board. 2021. The Science of Non-native Species in a Dynamic Delta. https://deltacouncil.ca.gov/pdf/isb/products/2021-05-21-isb-non-native-species-review.pdf

Delta Plan Interagency Implementation Committee and Delta Independent Science Board (Delta ISB). 2021. Strategic Science Needs Assessment.

Delta Stewardship Council, and Delta Science Program. 2019. 2019 Delta Science Plan. https://deltacouncil.ca.gov/pdf/2019-delta-science-plan.pdf

Delta Stewardship Council, and Delta Science Program. 2022. Science Action Agenda 2022-2026. https://scienceactionagenda.deltacouncil.ca.gov/pdf/2022-2026-science-action-agenda.pdf

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol. Lett. **5**: 558-567. doi:10.1046/j.1461-0248.2002.00354.x

Durand, J. 2008. DRERIP Delta Aquatic Foodweb Conceptual Model. https://h8b186.p3cdn2.secureserver.net/wp-content/uploads/2017/10/DRERIP_Fish_Habitat_Linkage_Model_23Jan08_djr.pdf

Durand, J. 2015. A conceptual model of the aquatic food web of the upper San Francisco Estuary. San Fr. Estuary Watershed Sci. 13. doi:10.15447/sfews.2015v13iss3art5

Dybala, K. E., T. Gardali, and R. E. J. Melcer. 2020. Getting Our Heads Above Water: Integrating Bird Conservation in Planning, Science, and Restoration for a More Resilient Sacramen to San Joaquin Delta. San Fr. Estuary Watershed Sci. 18: 1–25. doi:10.15447/sfews.2020v18iss4art2

Embke, H. S., E. A. Nyboer, A. M. Robertson, and others. 2022. Global dataset of species-specific inland recreational fisheries harvest for consumption. Sci. Data **9**: 1–10. doi:10.1038/s41597-022-01604-y

Environmental Protection Agency [EPA]. 2023. Facts and Figures about the Great Lakes. https://www.epa.gov/greatlakes/facts-and-figures-about-great-lakes

Fera, S. A., M. D. Rennie, and E. S. Dunlop. 2017. Broad shifts in the resource use of a commercially harvested fish following the invasion of dreissenid mussels. Ecology **98**: 1681–1692. doi:10.1002/ecy.1836

Fitzpatrick, K. B., B. C. Weidel, M. J. Connerton, and others. 2022. Balancing prey availability and predator consumption: a multispecies stock assessment for Lake Ontario. Can. J. Fish. Aquat. Sci. **79**: 1529–1545. doi:10.1139/cjfas-2021-0126

Glaspie, C. N., M. Clouse, K. Huebert, S. A. Ludsin, D. M. Mason, J. J. Pierson, M.R. Roman, and S. B. Brandt. 2019. Fish Diet Shifts Associated with the Northern Gulf of Mexico Hypoxic Zone. Estuaries and Coasts **42**: 2170–2183. doi:10.1007/s12237-019-00626-x

Great Lakes Fisheries Commission. 2023. Fisheries Management: Working to sustain the resource.

Grossman, G. 2016. Predation on fishes in the Sacramento-San Joaquin Delta: Current knowledge and future directions. San Fr. Estuary Watershed Sci. **14**. doi:http://dx.doi.org/10.15447/sfews.2016v14iss2art8

Grossman, G., T. Essington, B. Johnson, J. Miller, N. E. Monsen, and T. N. Pearsons. 2013. Effects of fish predation on salmonids in the Sacramento River–San

Joaquin Delta and associated ecosystems. doi:10.15447/sfews.2016v14iss2art8

Hansen, A. G., J. R. Gardner, K. A. Connelly, M. Polacek, and D. A. Beauchamp. 2022. Resource use among top-level piscivores in a temperate reservoir: implications for a threatened coldwater specialist. Ecol. Freshw. Fish. **31**: 469-491. doi:10.1111/eff.12644

Hartman, K. J., and S. B. Brandt. 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Trans. Am. Fish. Soc. **124**: 520–537. doi:10.1080/1548-8659(1995)124[lt]0520[co]TRPDAG[gt]2.3.CO;2

Hyder, K., A. G. Rossberg, J. I. Allen, and others. 2015. Make modelling count-increasing the contribution of shelf-seas community and ecosystem models to policy development and management. Mar. Policy. **61**: 291-302. doi:10.1016/j.marpol.2015.07.015

Independent Science Advisory Board [ISAB]. 2021. American Shad in the Columbia River: Past, Present, Future. https://www.nwcouncil.org/media/filer_public/88/b2/88b2dbc4-2bce-4ca2-9e69-d5d51306ea69/ISAB_2021-4_Shad_Report.pdf

Independent Scientific Review Panel [ISRP]. 2023. 2023 Follow-up Review of Project #1990-077-00, Development of Systemwide Predator Control (Northern Pikeminnow Management Program). https://www.nwcouncil.org/media/filer_public/7e/94/7e9493a3-904b-44b1-95e4-d8858d34c617/ISRP_2023-04_NPMP_FollowUpReview.pdf

Integrated Ecosystem Assessment. 2023. Gulf of Mexico Integrated Ecosystem Assessment. https://www.integratedecosystemassessment.noaa.gov/regions/gulf-mexico

Ives, J. T., B. C. McMeans, K. S. McCann, A. T. Fisk, T. B. Johnson, D. B. Bunnell, K. T. Frank, and A. M. Muir. 2019. Food-web structure and ecosystem function in the Laurentian Great Lakes—Toward a conceptual model. Freshw. Biol. **64**: 1–23. doi:10.1111/fwb.13203

Jaeger, W. K., and M. D. Scheuerell. 2023. Return(s) on investment: Restoration spending in the Columbia River Basin and increased abundance of salmon and steelhead. PLoS One **18**: 1–21. doi:10.1371/journal.pone.0289246

Jassby, A. D., J. E. Cloern, and A. B. Müller-Solger. 2003. Phytoplankton fuels Delta food web. Calif. Agric. **57**: 104–109. doi:10.3733/ca.v057n04p104

Jeffres, C. A., E. J. Holmes, T. R. Sommer, and J. V. E. Katz. 2020. Detrital food web contributes to aquatic ecosystem productivity and rapid salmon growth in a managed floodplain. PLoS One **15**: 1–20. doi:10.1371/journal.pone.0216019

Jordán, F., W. C. Liu, and A. J. Davis. 2006. Topological keystone species: Measures of positional importance in food webs. Oikos **112**: 535–546. doi:10.1111/j.0030-1299.2006.13724.x

Kaplan, I. C., S. K. Gaichas, C. C. Stawitz, and others. 2021. Management Strategy Evaluation: Allowing the Light on the Hill to Illuminate More Than One Species. Front. Mar. Sci. **8**: 1–22. doi:10.3389/fmars.2021.624355

Kendall, C., M. B. Young, S. R. Silva, T. E. C. Kraus, S. Peek, and M. Guerin. 2015. Tracing nutrient and organic matter sources and biogeochemical processes in the Sacramento River and Northern Delta: proof of concept using stable isotope data. doi:10.5066/F7QJ7FCM

Kimmerer, W. J., Gartside, E., and J. Orsi. 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Marine Ecology Progress Series **113**: 81-93. https://doi.org/10.3354/meps113081

Kimmerer, W. J., and J. Orsi. 1996. Changes in the zooplankton of the San Francisco Bay Estuary since the introduction of the clam *Potamocorbula amurensis*. *In* J. Hollibaugh [ed.], San Francisco Bay: The Ecosystem, Pacific Division American Association for the Advancement of Science, San Francisco, 403-424.

Kimmerer, W. J., L. Brown, S. Culberson, P. B. Moyle, M. L. Nobriga, and J. Thompson. 2008. Aquatic Ecosytems, p. 174. *In* M. Healey, M. Dettinger, and R. Norgaard [eds.], The State of Bay-Delta Science 2008. https://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/docs/cmnt081712/dfg/cdfghealey2008.pdf

Kimmerer, W. J., A. E. Parker, U. Lidström, and E. J. Carpenter. 2012. Towards an idea-centered, principle-base design to as creation approach support learning knowledge. Estuaries and Coasts **35**: 913–929. doi:10.1007/sl

Kimmerer W. J., and J. K. Thompson. 2014. Phytoplankton growth balanced by clam and zooplankton grazing and net transport into the low-salinity zone of the San Francisco Estuary. Estuaries and Coasts **37**(5): 1202-1218. doi: 10.1007/s12237-013-9753-6

Korpinen, S., L. Uusitalo, M. C. Nordström, and others. 2022. Food web assessments in the Baltic Sea: Models bridging the gap between indicators and policy needs. Ambio **51**: 1687–1697. doi:10.1007/s13280-021-01692-x

Lathrop, R. C., B. M. Johnson, T. B. Johnson, and others. 2002. Stocking piscivores to improve fishing and water clarity: A synthesis of the Lake Mendota biomanipulation project. Freshw. Biol. **47**: 2410–2424. doi:10.1046/j.1365-2427.2002.01011.x

Lewis, K. A., R. R. Christian, C. W. Martin, K. L. Allen, A. M. McDonald, V. M. Roberts, M. N. Shaffer, and J. F. Valentine. 2022. Complexities of disturbance response in a marine food web. Limnol. Oceanogr. **67**: S352–S364. doi:10.1002/lno.11790

Lewitus, A. J., D. M. Kidwell, E. B. Jewett, S. B. Brandt, and D. M. Mason. 2009. Ecological impacts of hypoxia on living resources. J. Exp. Mar. Biol. Ecol. **381**: S1-S3. doi:10.1016/j.jembe.2009.07.009

Li, J., V. Ianaiev, A. Huff, J. Zalusky, T. Ozersky, and S. Katsev. 2021. Benthic invaders control the phosphorus cycle in the world's largest freshwater ecosystem. Proc. Natl. Acad. Sci. U. S. A. **118**. doi:10.1073/pnas.2008223118

Lindeman, R. L. 1942. The Trophic-Dynamic Aspect of Ecology. Ecology **23**: 399–417. doi:10.2307/1930126

Link, J., W. Overholtz, J. O'Reilly, and others. 2008. The Northeast U.S. continental shelf Energy Modeling and Analysis exercise (EMAX): Ecological network model development and basic ecosystem metrics. J. Mar. Syst. **74**: 453–474. doi:10.1016/j.jmarsys.2008.03.007

Loboschefsky, E., G. Benigno, T. Sommer, and others. 2012. Individual-level and population-level historical prey demand of San Francisco Estuary striped bass using a bioenergetics model. San Francisco Estuary Watershed Sci. **10**(1). doi:10.15447/sfews.2012v10iss1art3

Luo, J., K. J. Hartman, S. B. Brandt, C. F. Cerco, and T. H. Rippetoe. 2001. A spatially-explicit approach for estimating carrying capacity: An application for the Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. Estuaries **24**: 545–556. doi:10.2307/1353256

Mac Nally, R., J. R. Thomson, W. J. Kimmerer, and others. 2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). Ecol. Appl. **20**: 1417–1430. doi:10.1890/09-1724.1

Madenjian, C. P., D. B. Bunnell, D. M. Warner, and others. 2015. Changes in the Lake Michigan food web following dreissenid mussel invasions: A synthesis. J. Great Lakes Res. **41**: 217–231. doi:10.1016/j.jglr.2015.08.009

Maryland Sea Grant. 1995. Multispecies Management in the Chesapeake Bay- A Far Future? Mar. Notes.

https://www.mdsg.umd.edu/sites/default/files/files/MN13_4_5.PDF

McMeans, B. C., K. S. McCann, T. D. Tunney, A. T. Fisk, A. M. Muir, N. Lester, B. Shutter, and N. Rooney. 2016. The adaptive capacity of lake food webs: from individuals to ecosystems. Ecol. Monogr. **86**: 4–19. doi:10.1890/15-0288.1

Mount, J., B. Gray, K. Bork, and others. 2019. A Path Forward for California's Freshwater Ecosystems. Public Policy Inst. Calif. https://www.ppic.org/wp-content/uploads/a-path-forward-for-californias-freshwater-ecosystems.pdf

Muro-Torres, V. M., M. F. Soto-Jiménez, L. Green, J. Quintero, and F. Amezcua. 2019. Food web structure of a subtropical coastal lagoon. Aquat. Ecol. **53**: 407-430. doi:10.1007/s10452-019-09698-0

de Mutsert, K., J. Steenbeek, K. Lewis, J. Buszowski, J. H. Cowan, and V. Christensen. 2016. Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model. Ecol. Modell. **331**: 142–150. doi:10.1016/j.ecolmodel.2015.10.013

de Mutsert, K., K. Lewis, S. Milroy, J. Buszowski, & J. Steenbeek. 2017. Using ecosystem modeling to evaluate trade-offs in coastal management: Effects of large-scale river diversions on fish and fisheries. Ecol. Model. **360**: 14-26. doi:10.1016/j.ecolmodel.2017.06.029

de Mutsert, K., K. A. Lewis, E. D. White, and J. Buszowski. 2021. End-to-end modeling reveals species-specific effects of large-scale coastal restoration on living resources facing climate change. Front. Mar. Sci. **8**: 624532. doi:10.3389/fmars.2021.624532

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, and others. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proc. Natl. Acad. Sci. U. S. A. **109**: 21201–21207. doi:10.1073/pnas.1213408109

Naiman, R. J. and J. R. Sibert. 1979. Detritus and juvenile salmon production in the Nanaimo Estuary. III. Importance of detrital carbon to the estuarine ecosystem. J. Fish. Res. Bd. Canada **36**: 504-520. doi:10.1139/f79-074

Naman, S. M., S. M. White, J. R. Bellmore, and others. 2022. Food web perspectives and methods for riverine fish conservation. Wiley Interdiscip. Rev. Water **9**: 1–21. doi:10.1002/wat2.1590

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest, The National Academies Press. doi:10.17226/4976

Nobriga, M. L., and F. V. Feyrer. 2007. Shallow-Water Piscivore-Prey Dynamics in California's Sacramento-San Joaquin Delta. San Fr. Estuary Watershed Sci. **5**.

doi:10.15447/sfews.2007v5iss2art4

Norgaard, R. B., J. A. Wiens, S. B. Brandt, and others. 2021. Preparing Scientists, Policy-Makers, and Managers for a Fast-Forward Future. San Fr. Estuary Watershed Sci. **19**: 1–22. doi:10.15447/SFEWS.2021V19ISS2ART2

O'Higgins, T.G., Lago, M., DeWitt, T.H. (editors) Ecosystem-Based Management, Ecosystem Services and Aquatic Biodiversity: Theory, Tools and Applications. Springer. 2020

Osakpolor, S. E., M. Kattwinkel, J. Schirmel, A. Feckler, A. Manfrin, and R. B. Schäfer. 2021. Mini-review of process-based food web models and their application in aquatic-terrestrial meta-ecosystems. Ecol. Modell. **458**. doi:10.1016/j.ecolmodel.2021.109710

Rieman, B. E., C. L. Smith, R. J. Naiman, and others. 2015. A Comprehensive Approach for Habitat Restoration in the Columbia Basin. Fisheries **40**: 124–135. doi:10.1080/03632415.2015.1007205

Robinson, K. F., P. J. Alsip, A. R. Drake, Y. C. Kao, M. A. Koops, D. M. Mason, E. S. Rutherford, and H. Zhang. 2021. Reviewing uncertainty in bioenergetics and food web models to project invasion impacts: Four major Chinese carps in the Great Lakes. J. Great Lakes Res. **47**: 83–95. doi:10.1016/j.jglr.2020.11.003

Roegner, G. C. and G. E. Johnson. 2023. Export of macroinvertebrate prey from tidal freshwater wetlands provides a significant energy subsidy for outmigrating juvenile salmon. PLoS ONE **18**(3): e0282655. doi:10.1371/journal.pone.0282655

Rogers, T. L., S. M. Bashevkin, C. E. Burdi, and others. 2022. Evaluating top-down, bottom-up, and environmental drivers of pelagic food web dynamics along an estuarine gradient. doi: 10.32942/X2MK5Z

Rose, K. A., W. J. Kimmerer, K. P. Edwards, and W. A. Bennett. 2013. Individual-based modeling of Delta Smelt population dynamics in the upper San Francisco Estuary: I. Model description and baseline results. Trans. Am. Fish. Soc. **142**(5): 1238-2359. doi:10.1080/00028487.2013.799518

San Francisco Estuary Institute- Aquatic Science Center [SFEI-ASC]. 2016. A Delta Renewed: A Guide to Science-Based Ecological Restoration in the Sacramento-San Joaquin Delta. https://www.sfei.org/sites/default/files/biblio_files/DeltaRenewed_v1pt3_111516_highres.pdf

Schückel, U., V. de Jonge, A. Ludovisi, D. Giebels, S. Horn, N. Niquil, H. Asmus, R. Asmus, E, Igor,, S. Georges, and U. Scharler. 2018. Use of Coastal and Estuarine

Food Web Models in Policy Making and Management: the Need for an Entire Approach. 26 pages.

Sibert, J. R., T. J. Brown, M. C. Healey, B. A. Kask, and R. J. Naiman. 1977. Detritus based food webs: Exploitation by juvenile chum salmon (*Oncorhynchus keta*). Science **196**: 649-650. doi:10.1126/science.196.4290.649

Slater, S. B., and R. D. Baxter. 2014. Diet, prey selection, and body condition of age-0 delta smelt, Hypomesus transpacificus, in the upper San Francisco Estuary. San Fr. Estuary Watershed Sci. **12**. doi:10.15447/sfews.2014v12iss3art1

Smith, M., D. Chagris, R. Paperno, and S. Markwith. 2023. Tropical estuarine ecosystem change under the interacting influences of future climate and ecosystem restoration. Glob. Chang. Biol. **29**: 5850-5865. doi: 10.1111/gcb.16868

Sommer, T. R., C. Armor, R. D. Baxter, and others. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. Fisheries **32**: 5–24. doi:10.1577/1548-8446(2007)32[270:TCOPFI]2.0.CO;2

Stouder, D. J., P. A. Bisson, and R. J. Naiman, eds. 1997. Pacific salmon and their ecosystems, Springer Link. doi:10.1007/978-1-4615-6375-4

Sturrock, A. M., M. Ogaz, K. Neal, and others. 2022. Floodplain trophic subsidies in a modified river network: managed foodscapes of the future? Landsc. Ecol. **37**: 2991–3009. doi:10.1007/s10980-022-01526-5

Townsend, H., C. J. Harvey, Y. deReynier, and others. 2019. Progress on Implementing Ecosystem-Based Fisheries Management in the United States Through the Use of Ecosystem Models and Analysis. Front. Mar. Sci. **6**: 1–17. doi:10.3389/fmars.2019.00641

Trifonova, N., D. Maxwell, J. Pinnegar, A. Kenny, and A. Tucker. 2017. Predicting ecosystem responses to changes in fisheries catch, temperature, and primary productivity with a dynamic Bayesian network model. ICES J. Mar. Sci. **74**: 1334–1343. doi:10.1093/icesjms/fsw231

Tsehaye, I., M. L. Jones, T. O. Brenden, J. R. Bence, and R. M. Claramunt. 2014. Changes in the Salmonine Community of Lake Michigan and Their Implications for Predator-Prey Balance. Trans. Am. Fish. Soc. **143**: 420–437. doi:10.1080/00028487.2013.862176

United Nations Environment Programme (UNEP). 2021. Becoming #GenerationRestoration: Ecosystem restoration for people, nature and climate.

Nairobi. https://www.unep.org/resources/ecosystem-restoration-people-nature-climate

Vander Zanden, M. J., J. D. Olden, and C. Gratton. 2006. Food- web approaches in restoration ecology. Found. Restor. Ecol. 165–189. https://jvzlab.limnology.wisc.edu/wp-content/uploads/sites/1902/2022/11/Vander-Zanden_06_Foundationsofrestorationecology_Ch8.pdf

Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature. **401**: 464-467. doi:10.1038/46762

Vasslides, J. M., K. de Mutsert, V. Christensen, & H. Townsend. 2016. Using the Ecopath with Ecosim modeling approach to understand the effects of watershed-based management actions in coastal ecosystems. Coast. Manage. **45**(1): 1-12. doi: 10.1080/08920753.2017.1237241

Venter, F. J., R. J. Naiman, H. C. Biggs, and D. J. Pienaar. 2008. The evolution of conservation management philosophy: Science, environmental change and social adjustments in Kruger National Park. Ecosystems. **11**: 173-192. doi:10.1007/s10021-007-9116-x

Virginia Institute of Marine Science [VIMS]. 2023. What is ChesMMAP? https://www.vims.edu/research/units/programs/multispecies_fisheries_research/chesmmap/index.php

Walters, D. M., W. F. Cross, T. A. Kennedy, and others. 2020. Food web controls on mercury flixes and fate in the Colorado River, Grand Canyon. Sci. Adv. **6**: eaaz4880. doi:10.1126/sciadv.aaz4880

Weinersmith, K. L., D. D. Colombano, A. J. Bibian, M. J. Young, A. Sih, and J. L. Conrad. 2019. Diets of Largemouth Bass (Micropterus salmoides) in the Sacramento-San Joaquin Delta. San Fr. Estuary Watershed Sci. **17**. doi:10.15447/sfews.2019v17iss1art3

Whipple, A., R. Grossinger, D. Rankin, B. Stanford, and R. Askevold. 2012. Sacramento-San Joaquin Delta Historical Ecology Investigation: Exploring pattern and process. https://www.sfei.org/sites/default/files/biblio_files/Delta_HistoricalEcologyStudy_SFEI_ASC_2012_medres.pdf

Whitley, S. N., and S. M. Bollens. 2014. Fish assemblages across a vegetation gradient in a restoring tidal freshwater wetland: Diets and potential for resource competition. Environ. Biol. Fishes **97**: 659–674. doi:10.1007/s10641-013-0168-9

Wiens, J. A., J. B. Zedler, V. H. Resh, and others. 2017. Facilitating adaptive management in California's Sacramento-San Joaquin Delta. San Fr. Estuary Watershed Sci. **15**: 0–15. doi:10.15447/sfews.2017v15iss2art3

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annu. Rev. Ecol. Syst. **25**: 443–466. doi:10.1146/annurev.ecolsys.25.1.443

Young, M., E. Howe, T. O'Rear, K. Berridge, and P. Moyle. 2021. Food Web Fuel Differs Across Habitats and Seasons of a Tidal Freshwater Estuary. Estuaries and Coasts **44**: 286–301. doi:10.1007/s12237-020-00762-9

Zale, A., D. L. Parrish, and T. Sutton [eds.]. 2013. Fisheries Techniques, 3rd Edition, American Fisheries Society. doi:10.47886/9781934874295

Zhang, H., S. A. Ludsin, D. M. Mason, and others. 2009. Hypoxia-driven changes in the behavior and spatial distribution of pelagic fish and mesozooplankton in the northern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. **381**: S80-S91. doi: 10.1016/j.jembe.2009.07.014

Zhang, H., D. M. Mason, N. W. Boucher, and others. 2023. Effects of vertical mixing on the Lake Michigan food web: an application of a linked end-to-end earth system model framework. Ocean Dyn. **73**: 545-556. doi: 10.1007/s10236-023-01564-w

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 1).

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. 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

For the workshop agenda, please visit: https://deltacouncil.ca.gov/pdf/isb/meeting-notice/2023-10-27-isb-meeting-notice.pdf

Workshop Section Summaries:

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).

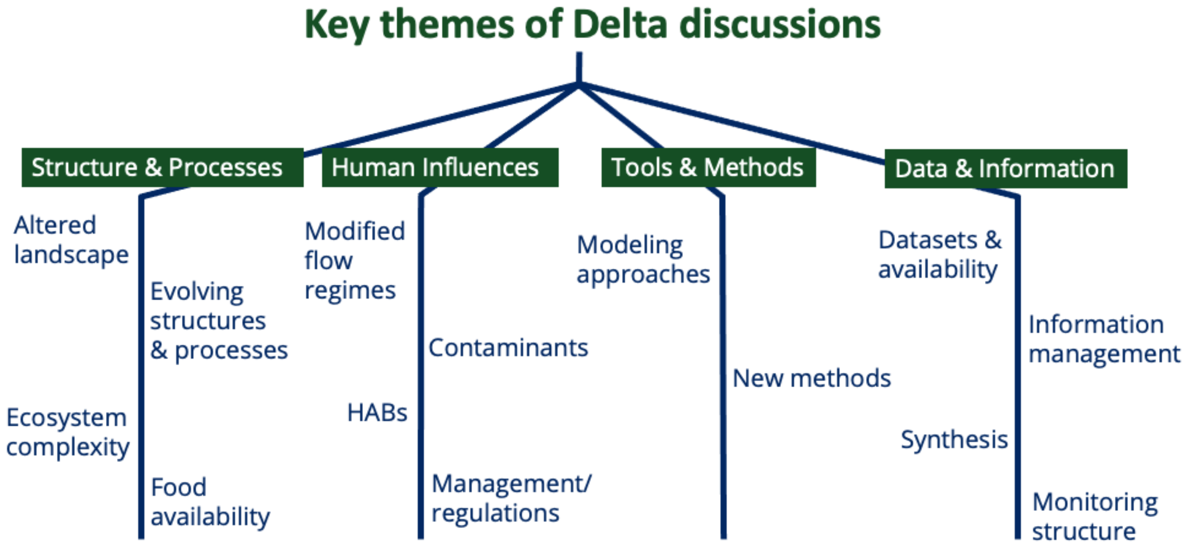

Figure A1. Key themes from the Delta discussions on food webs and their connection to management in the Delta.

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 oppotunity, 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 Integrated Ecosystem 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