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Keywords:
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Abstract:
This paper reviews and highlights recent research findings on food web processes since an earlier review by Kimmerer et al. (2008). We conduct this review within a conceptual framework of the Delta–Suisun food web, which includes both temporal and spatial components. The temporal component of our framework is based on knowledge that the landscape has changed markedly from historical conditions. The spatial component of our framework acknowledges that the food web is not spatially static; it varies regionally and across habitat types within regions. The review

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highlights the idea of a changing baseline with respect to food web function. New research also indicates that interactions between habitat-specific food webs vary across the current landscape. For example, based on early work in the south Delta, the food web associated with submerged aquatic vegetation was thought to provide little support to species of concern; however, data from other regions of the estuary suggest that this conceptual model may not apply across the entire region. Habitat restoration has been proposed as a method of re-establishing historic food web processes to support species of concern. Benefits are likely for species that directly access such restored habitats, but are less clear for pelagic species. Several topics require attention to further improve the knowledge of food webs needed to support effective management, including: (1) synthesis of factors responsible for low pelagic biomass; (2) monitoring and research on effects of harmful algal blooms; (3) broadening the scope of long-term monitoring; (4) determining benefits of tidal wetland restoration to species of concern, including evaluations of interactions of habitat-specific food webs; and (5) interdisciplinary analysis and synthesis. The only certainty is that food webs will continue to change in response to the changes in the physical environment and new species invasions.

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SPECIAL ISSUE: STATE OF BAY–DELTA SCIENCE 2016, PART 2

Food Webs of the Delta, Suisun Bay, and Suisun Marsh: An Update on Current Understanding and Possibilities for Management

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ABSTRACT

This paper reviews and highlights recent research findings on food web processes since an earlier review by Kimmerer et al. (2008). We conduct this review within a conceptual framework of the Delta–Suisun food web, which includes both temporal and spatial components. The temporal component of our framework is based on knowledge that the landscape has changed markedly from historical conditions. The spatial component of our framework acknowledges that the food web is not spatially static; it varies regionally and across habitat types within regions. The review highlights the idea of a changing baseline with respect to food web function. New research also indicates that interactions between habitat-specific food webs vary across the current landscape. For example, based on early work in the south Delta, the food web associated with submerged aquatic vegetation was thought to provide little support to species of concern; however, data from other regions of the estuary suggest that this conceptual model may not apply across the entire region. Habitat restoration has been proposed as a method of re-establishing historic food web processes to support species of concern. Benefits are likely for species that directly access such restored habitats, but are less clear for pelagic species. Several topics require attention to further improve the knowledge of food webs needed to support effective management, including: (1) synthesis of factors responsible for low pelagic biomass; (2) monitoring and research on effects of harmful algal blooms; (3) broadening the scope of long-term monitoring; (4) determining benefits of tidal wetland restoration to species of concern, including evaluations of interactions of habitat-specific food webs; and (5) interdisciplinary analysis and synthesis. The only certainty is that food webs will continue to change in response to the changes in the physical environment and new species invasions.

KEY WORDS

Food web, invasive species, production, submerged aquatic vegetation, pelagic, zooplankton, microzooplankton, phytoplankton

INTRODUCTION

The northern reaches of the San Francisco Estuary (the estuary), including the Sacramento–San Joaquin Delta, Suisun Bay, and Suisun Marsh, have undergone substantial shifts over the last 150 years in configuration, hydrology, species composition, and the dominance of humans on the landscape (Nichols et al. 1986; Whipple et al. 2012). As a result of these shifts, the upper estuary and most notably the Delta engender nearly intractable conflicts over land use, water use and ecosystem protection (NRC 2012; Luoma et al. 2015). Much of this conflict is between human water uses (e.g., agriculture and urban) and protection for the endangered Delta Smelt *Hypomesus transpacificus*, a Delta endemic, and other declining native fish species. Reasons for the declines are many, but a factor that contributes to the lack of recovery of these species is a shortage of food (Slater and Baxter 2014; Hammock et al. 2015). The consequent interest in the estuarine food web has led to new ideas and findings about why food web productivity is so low compared to that in other estuaries (Dugdale et al. 2012, 2013; Wilkerson et al. 2015; Cloern and Jassby 2012; Kimmerer et al. 2012), but also to conflicting ideas about the potential to reverse these declines.

The principal objective of this paper is to highlight recent research findings on estuary food web processes since the review by Kimmerer et al. (2008). Research during the previous three decades had led to considerable understanding of food web processes in the Delta, so recent improvements in understanding of food webs have been largely incremental. Because much of the recent work builds on previous work, we review earlier work as needed to provide appropriate background; however, it is not our intent to provide a comprehensive review of the estuary's food web literature. We also do not consider factors that could affect food webs but for which data are insufficient for assessment. Specifically, we do not discuss pesticides, which are known to have episodic effects on organisms and mesocosm food webs, but sustained food web effects in the environment have not been demonstrated (Fong et al., submitted). We review the available information from temporal, spatial, and habitat-specific perspectives, all of which are needed to inform management actions intended to re-establish food web functions for the benefit of species of concern.

Our geographic scope ranges from the legal Delta seaward to Carquinez Strait, including Suisun Bay and Suisun Marsh (Figure 1). We also consider floodplain areas that have been shown to be important to Delta ecology. We discuss nformation from more seaward areas of the San Francisco Estuary and from other estuaries as needed. Because specific studies often focus on only one or two of these regions, we use "Delta–Suisun" to refer to all three regions combined, and otherwise refer to the Delta, Suisun Bay, or Suisun Marsh, separately.

We start this review by presenting our conceptual framework of the Delta–Suisun food web, which includes both temporal and spatial components. The temporal component is based on knowledge that the landscape has changed markedly from historical conditions. The spatial component of our framework acknowledges that the food web is not spatially static; it varies regionally and across habitat types within regions. We first present a brief history of some important changes in the Delta–Suisun region over time and a description of their current condition. We then consider food web findings for different habitats and Delta–Suisun regions, using a two-part conceptual framework. Finally, we discuss the relevance of these findings for habitat management actions that have been proposed to increase food web support for species of concern (e.g., Herbold et al. 2014). We do not consider other potential benefits of such actions here.

CONCEPTUAL FRAMEWORK

Our conceptual framework highlights food web differences among historical periods, habitats and geographic areas of the Delta–Suisun region. We first describe some of the key food web changes since the Gold Rush up until the current time. Understanding the history of ecological changes is important when actions intended to restore functions and services are considered (Lotze and Muir 2009; Lotze and Worm 2009), including food web functions. Since the majority of research on estuarine food webs in the estuary has focused on pelagic habitat, our discussion of historical periods is also pelagic-focused. Given that systematic scientific data

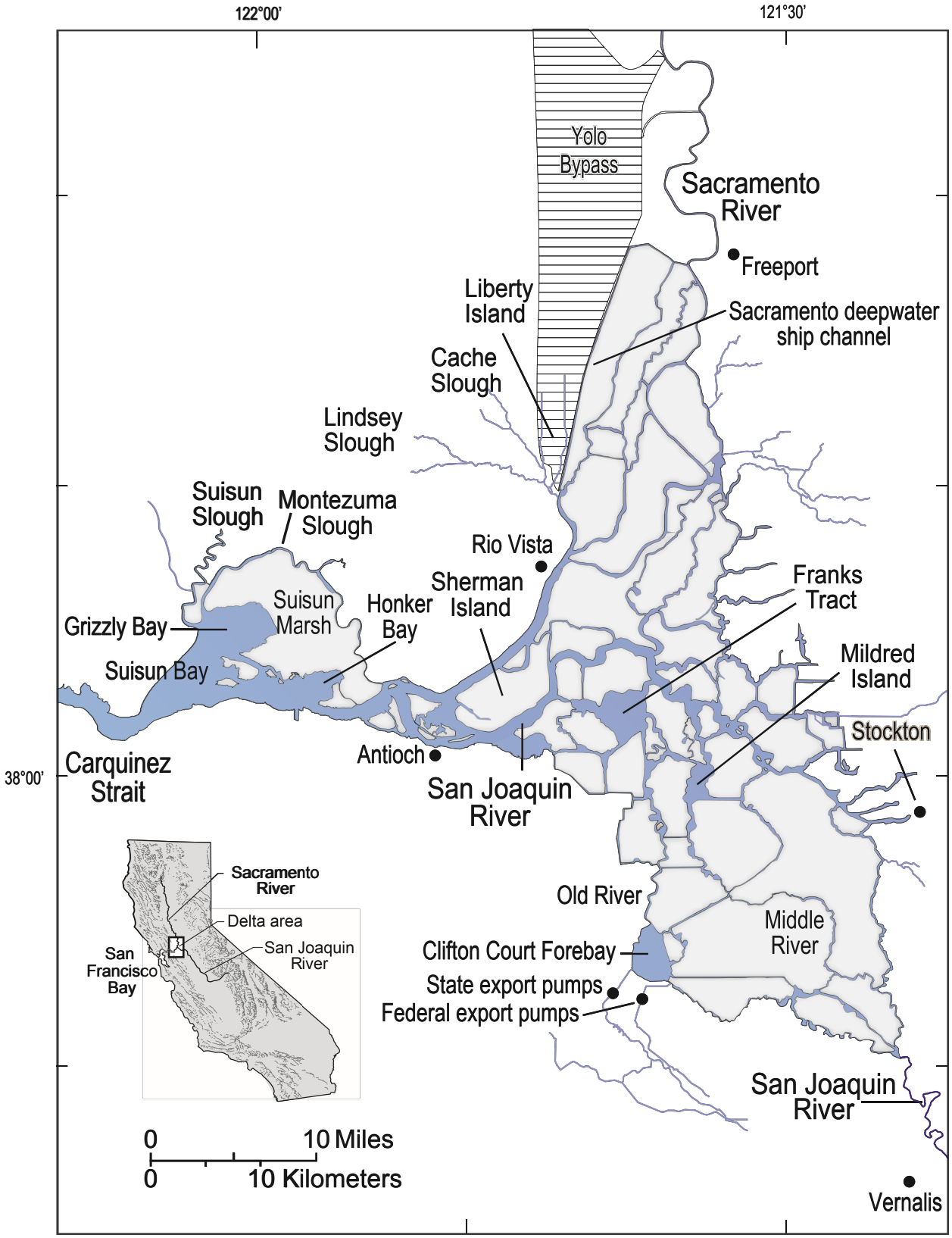

Figure 1 Map of the Sacramento–San Joaquin Delta, Suisun Bay, and associated areas discussed in this paper

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collection did not begin until the mid-20th century, our characterizations of early food web processes are limited and speculative, but new work on the historical landscapes of the Delta–Suisun region (Whipple et al. 2012; Robinson et al. 2014) provides an increasingly solid basis for such speculation, and efforts are underway to estimate historic primary production (Robinson et al. 2016; Cloern et al. 2016).

The spatial part of the conceptual framework incorporates the idea of differences in food webs associated with different geographic regions (Figure 2) and habitats (Figure 3). We discuss pelagic and benthic food webs together because they are tightly linked through the grazing effects of benthic organisms—primarily clams—on pelagic organisms. We define geographic areas where we believe food web processes are relatively similar across the region (Figure 2). Within each geographic region we discuss the habitat-associated food webs for which data are available and that are likely important. Geographic differences in food web structure and function in an estuarine system this large and complex are to be expected. Importantly, geographic boundaries between the areas defined here are not sharp; they are blurred by the high variability characteristic of estuarine environments on tidal, seasonal, and annual scales (Kimmerer 2004). In this paper, we are mainly concerned with freshwater and low-salinity water areas because they dominate the Delta–Suisun region during most years and are most thoroughly studied. The low-salinity zone (LSZ) has been variously defined by researchers, but generally ranges between 0.5 to 1.0 salinity at the low end and 5.0 to 6.0 salinity at the high end. The position of the entire salinity field fluctuates across Delta–Suisun areas in response to freshwater flow on longer time-scales, and to tides on the shortest time-scales.

DELTA–SUISUN FOOD WEBS: A CHANGING BASELINE

The concept of changing baselines has received attention in the last 2 decades (Duarte et al. 2009). It has become apparent globally that the historical trajectories of human-dominated ecosystems cannot be retraced, and that the historical condition of these systems cannot be recaptured. Thus, the past serves as a guide but not a template for future actions to restore or improve the ecosystem.

Pre-Gold Rush Era (< ca. 1850)

Until the California Gold Rush, the Delta landscape was dominated by tidal and seasonal wetlands and floodplains (Whipple et al. 2012). Recent research on historical landscapes of the Delta (Whipple et al. 2012; Robinson et al. 2014) has provided essential details on the historical distribution and diversity of habitat types. For example, the central Delta was dominated by freshwater tidal wetlands, with dead-end sloughs and tidal channels linking marsh plain to open waters. The north Delta included large flood basins behind natural levees, combined with a network of tidal channels, ponds, and perennial, tidal, and seasonal freshwater wetlands. The south Delta was dominated by a complex network of distributary river channels, oxbow lakes, and tidal sloughs embedded in extensive tidal and non-tidal freshwater wetlands and floodplains. Further to the west, the bays of the estuary were fringed by expansive tidal flats and wetlands and Suisun Marsh was the largest brackish water marsh in the western U.S.

Although no direct scientific accounts exist, the food webs in these landscapes were likely fueled by a combination of biologically available organic matter produced by native marsh and floodplain vegetation and phytoplankton produced in the channels and open waters of the system (Robinson et al. 2016). Hypotheses about primary production in the historical landscapes are currently being addressed (Robinson et al. 2016; Cloern et al. 2016). Many of the small dead-end sloughs in the tidal wetlands were likely very productive, especially if their length exceeded the tidal excursion (Geyer and Signell 1992) so that long residence time allowed for accumulation of biomass. Complexity theory (Campbell Grant et al. 2007) and historical research (Williams 2006; Whipple et al. 2012; Robinson et al. 2014, 2016) suggest that the change from a reticulate dendritic landscape, with channels of various sizes and mixed residence time, to a much less complex, channelized landscape probably had profound influences on the habitat value of the Delta; however, there are no quantitative data or estimates of the abundances of the native

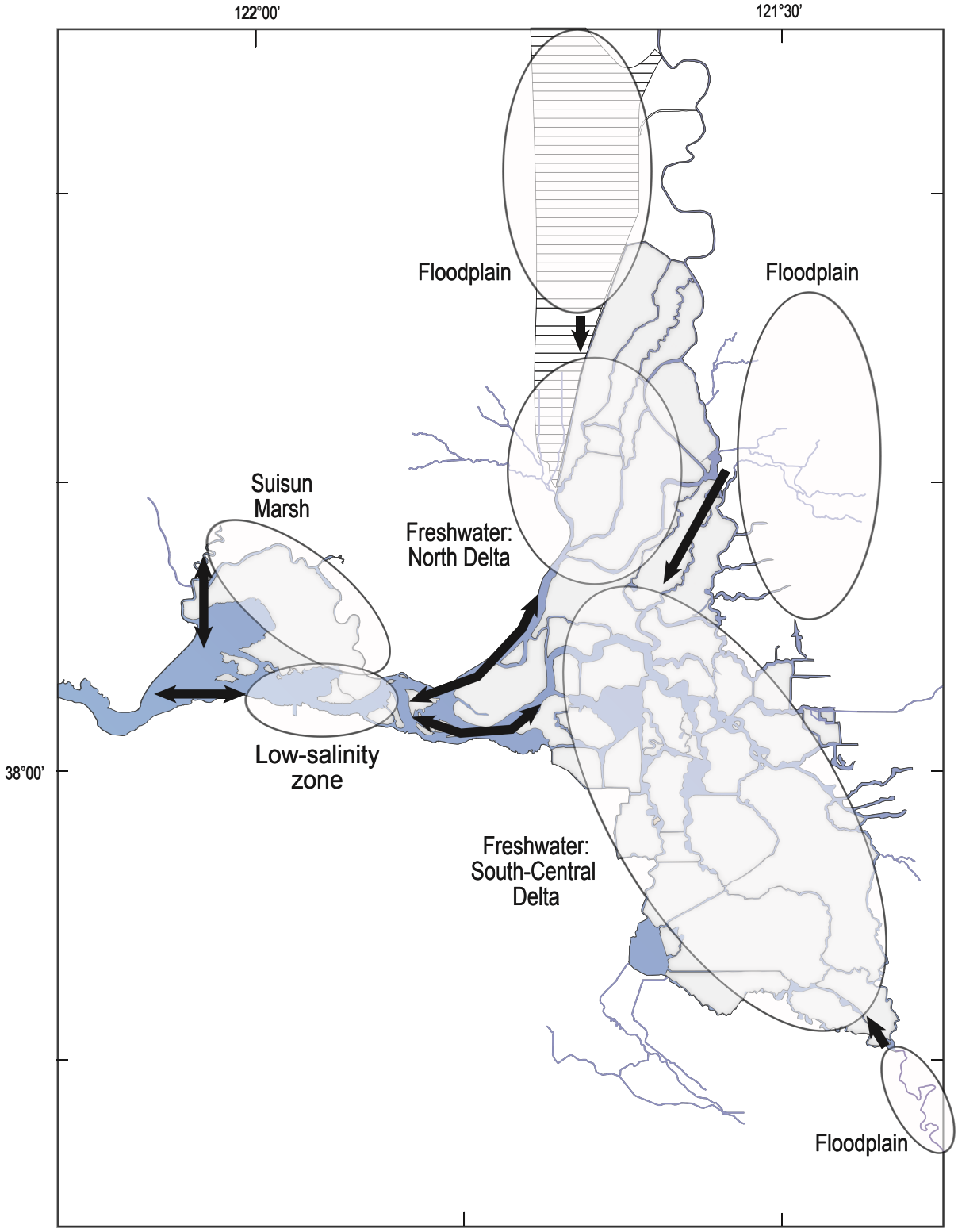

Figure 2 Conceptual framework for the discussion of food webs in selected geographic areas. The two-headed arrows indicate that the position and extant of the low-salinity zone will change seasonally and annually in response to flow conditions.

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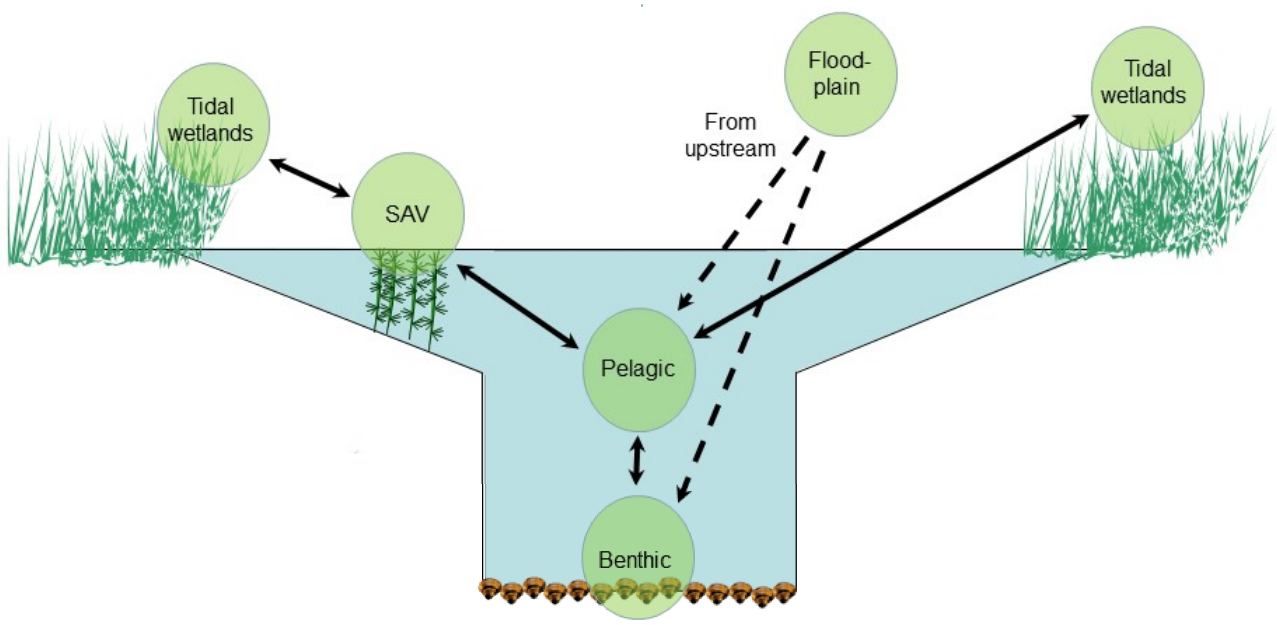

Figure 3 Conceptual framework for the discussion of habitat-specific food webs. The circles filled with green indicate habitat-specific food webs discussed in this paper. The solid black arrows represent hypothetical two-way exchanges between food webs. The dotted lines indicate one-way exchange of floodplains with downstream food webs. For simplicity, not all possible food webs or arrangements are shown.

invertebrates, fishes, and other organisms during this time-period.

Landscape Change and Development (ca. 1850–1960s)

The landscape of the estuary and watershed changed markedly with the onset of land and water development in the 19th century, and especially after the huge influx of settlers during and after the Gold Rush, with negative effects on native biota (Brown and Moyle 2005; Whipple et al. 2012; Robinson et al. 2014). Diking and draining of wetlands in the Delta for farming and other human activities, along with widening of the main channels and permanent flooding of several subsided islands, completely altered the Delta. Before development, wetland area exceeded open-water area by about 14:1; today this ratio is 1:6, an 80-fold switch in dominant habitat types (Whipple et al. 2012). Loss of wetlands in the Delta is estimated to be about 97% of the pre-Gold Rush area (Whipple et al. 2012). Losses of San Francisco Bay tidal flats and wetlands have been estimated as 70% to 93% (Callaway et al. 2011). Losses of Suisun Marsh natural habitats from conversion to managed wetlands or other human land uses have also been extensive (Manfree 2014). Large changes in a variety of landscape metrics (Table 1; Robinson 2014) suggest comparable changes in sources, extent, transport, and fate of estuarine organic matter and primary production; although, these changes have not yet been quantified. Watersheds, dam construction, diking, and water diversions in the Delta changed flow dynamics to the estuary and severed connections between flood plains and rivers, thereby reducing the supply of biologically available organic matter and primary productivity from floodplains to the Delta (Ahearn et al. 2006; Lehman et al. 2008; Opperman 2012). A pulse of sediment from hydraulic mining shoaled the estuary by ~1 meter in some places, and the shoaling lasted over a century (Schoellhamer et al. 2013).

The influx of settlers also brought a wave of species introductions, notably deliberate introductions in the 1870s of anadromous Striped Bass *Morone saxatilis* and American Shad *Alosa sapidissima* from the Atlantic Coast. Both species rapidly became established and developed large populations in the estuary (Moyle 2002). The introduction of Striped Bass was likely a large perturbation to the food webs of the estuary, but whether Striped Bass simply replaced native predators or placed increased demands on lower trophic levels is unknown.

Numerous inadvertent introductions of invertebrates to the estuary, especially into San Francisco Bay, occurred with increased shipping commerce (Cohen and Carlton 1997; Choi et al. 2005) with substantial effects on the Delta–Suisun food web (described below). Over the last 150 years numerous other fishes, invertebrates and plants have invaded the region, in most cases with undocumented effects.

By the onset of scientific study and monitoring of Delta and Suisun Bay ecology in the middle 1960s, a broad array of non-native species had been established as competitors of and predators on native fishes and other aquatic organisms, diverting resources away from native species. Such invasions have continued with additional invertebrate (Table 2) and fish (Moyle 2002) invasions since monitoring began. Native planktivorous species including Delta Smelt and Longfin Smelt *Spirinchus thaleichthys* were still fairly abundant during this period, despite the introductions of several competitors including American Shad and Threadfin Shad *Dorosoma petenense*.

Pre-*Potamocorbula*: The Pelagic Food Web is the Focus of Study (1960s – ca. 1986)

By the time consistent monitoring began in the 1960s – 1970s, pelagic sources dominated aquatic production in the Delta and Suisun Bay (Kelley 1966). Monitoring was motivated by concerns about the ecological effects of the federal and state water projects, which started diverting water from the Delta in 1950 and 1968, respectively. During this period, the species composition of the plankton and benthos was relatively stable, and was described by a classical food web conceptual model with direct links from phytoplankton to zooplankton to fish. Diatom blooms with chlorophyll-*a* concentrations >10 µg L^{-1} were common in Suisun Bay and the western and southern Delta during spring through summer in most years (Ball 1977; Ball and Arthur 1979; Peterson 1979; Merz et al. 2016). Some of the variability in phytoplankton biomass during this period, however, was linked to water exports. Notably, chlorophyll-*a* values in the LSZ declined between 1968 and 1989 (Jassby and Powell 1994). Mass balance analyses suggest that a median of 62% of chlorophyll-*a* was

Table 1 Changes in selected landscape metrics indicative of changes in the importance of different food webs. Data for Pre-Gold Rush, era of landscape modification, and pre-*Potamocurbula* were obtained from Robinson et al. (2014). For post-*Potamocurbula* and post-pelagic organism decline, metric values were assumed to not vary substantially (indicated by ≈), except for submerged aquatic vegetation. Area of submerged aquatic vegetation is unknown (indicated by ?) in the historic area but is known to have expanded in the modern era.

			Modern Delta		
	Pre-Gold Rush	Landscape modification	Pre-*Potamocorbula*	Post-*Potamocorbula*	Post-pelagic organism decline
Pelagic–benthic					
Open water (ha)	16,344	↑63%	26,554	≈	≈
Tidal wetland					
Freshwater emergent wetland (ha)	193,224	↓98%	4,296	≈	≈
Area subject to tidal inundation (ha)	≈ 150,000	↓144,000	≈ 6,000	≈	≈
Dendritic channels adjacent to marsh (km)	1,151	↓93%	84	≈	≈
Floodplain					
Wet meadow/Seasonal wetlands (ha)	37,561	↓93%	2,445	≈	≈
Seasonally flooded habitat (ha)	117,000	↓85%	19,000	≈	≈
Fluvial and detached channels (ha)	2,225	↓87%	298	≈	≈
Submerged aquatic vegetation (ha)	?	?	lowest modern	↑	4,000–8,000[a]

a Between 2004 and 2008, total submerged aquatic vegetation coverage declined from approximately 80 to 40 km^2, possibly as a result of an herbicide application program targeting *Egeria densa* initiated by the California Department of Boating and Waterways in 2001 (2015 Personal conversation between E. Hestir, UC Davis, and J. L. Conrad, unreferenced, see "Notes"). However, by fall 2014, submerged aquatic vegetation coverage had rebounded to approximately 70 km^2 (2015 Personal conversation between S. Khanna, UC Davis, and J. L. Conrad, unreferenced, see "Notes").

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exported by south Delta pumps from 1975 to 1989, though annual estimates were highly variable (Jassby and Powell 1994).

Zooplankton biomass was dominated by rotifers and cladocerans in the Delta and by rotifers and the copepod *Eurytemora affinis* in the LSZ (Orsi and Mecum 1986; Winder and Jassby 2011). The abundant mysid *Neomysis mercedis* together with *E.affinis* comprised much of the diets of young fishes (Heubach et al. 1963; Meng and Orsi 1991; Feyrer et al. 2003). However, from 1972 to 1980, the pelagic food web began changing for unknown reasons, as phytoplankton biomass and abundance of rotifers, *E. affinis*, and *N. mercedis* declined by greater than two-fold (Orsi and Mecum 1986, 1996; Kimmerer et al. 1994; Kimmerer 2005).

During this time-period, the benthic community and grazing pressure of the Delta–Suisun region responded to the differences in flow. The seasonally fluctuating salinity (a result of flow variability) in Suisun Bay suppressed benthic invertebrate numbers and grazing except during extended and severe dry or wet periods (Nichols 1985; Peterson and Vayssières 2010). The 1976–1977 drought in particular allowed marine species to invade Suisun Bay, resulting in a depression of phytoplankton biomass (Nichols 1985; Alpine and Cloern 1992). The freshwater clam *Corbicula fluminea*, introduced well before monitoring began, likely affected the food web in the freshwater Delta, given its substantial grazing effect on phytoplankton in the Delta and elsewhere (Cohen et al. 1984; Lopez et al. 2006; Lucas and Thompson 2012) but the quantitative effect is unknown.

Through the mid-1980s, the LSZ was an area of high phytoplankton biomass (Ball and Arthur 1979), as in other estuaries (Morris et al. 1978; North et al. 2005). In the estuary, the LSZ was important rearing habitat for Striped Bass and the native Delta Smelt and Longfin Smelt (Stralberg et al. 1985; Moyle et al. 1992; Hobbs et al. 2006). At this time, primary production in pelagic estuary habitats was shown to be mainly light-limited (Cole and Cloern 1984; Alpine and Cloern 1988), with production being low in comparison to many other estuaries (Cloern et al. 2014).

Post-*Potamocorbula*: The Pelagic Food Web Declines (1986–2000)

An abrupt change in the estuarine food web began in 1987, after the invasion of the "overbite" clam *Potamocorbula amurensis* (Nichols et al. 1990). Native to estuaries of mainland East Asia, *P. amurenis* thrives in brackish water and tolerates variable salinity (Paganini et al. 2010). Its spread may have been facilitated by drought after a high-flow year (1986) that swept Suisun Bay clear of other benthic grazers (Nichols et al. 1990). Phytoplankton biomass decreased about five-fold in Suisun Bay and the western Delta (Alpine and Cloern 1992), the size distribution of phytoplankton shifted toward smaller cells (Kimmerer et al. 2014a), and production by diatoms nearly ceased in this region (Kimmerer 2005). The abundance of brackish-water rotifers and *E. affinis* and other copepods declined, apparently from predation by and competition with clams (Kimmerer et al. 1994; Kimmerer and Lougee 2015). Abundance of the mysid *N. mercedis* in brackish water declined sharply, apparently because of reduced food supply (Orsi and Mecum 1996), as did abundance of Northern Anchovy *Engraulis mordax*, in an apparent behavioral response to poor feeding conditions in the LSZ (Kimmerer 2006). The taxonomic composition of the benthos changed to a more diverse assemblage dominated by recently introduced species, although the assemblage shifted with seasonal and interannual movement of the salinity field (Peterson and Vayssières 2010).

In retrospect, the series of events that began after the *P. amurensis* invasion constitute an ecological "regime shift" (see "Sidebar 1"; Scheffer et al. 2001; Carpenter 2003; Folke et al. 2004). The *P. amurensis* invasion was clearly a major driver of this regime shift, but other drivers likely contributed as well, such as a prolonged drought, ammonia loading (Dugdale et al. 2007, 2012, 2013; Wilkerson et al. 2015; Dahm et al., submitted), and changes in water inflows and exports from the estuary (Winder et al. 2011; Cloern and Jassby 2012). This regime shift affected the entire estuarine food web, but was most pronounced in the estuary's LSZ. This regime shift provided the impetus for a substantial research effort on the pervasive influence of benthic grazing and its consequences.

SIDEBAR 1

Defining Change

As we have described in the previous sections, many factors have brought about the changes to the Delta food web. These factors have varied in kind from species introductions to landscape and water flow alteration and the time-scales have varied from gradual (Whipple et al. 2012), over decades, to abrupt (Thomson et al. 2010; Alpine and Cloern 1992), over a few months or years. In many respects, the Delta fits the definition of a novel ecosystem. Morse et al. (2014) credit Chapin and Starfield (1997) with the first use of the concept, which is commonly used among ecologists to describe ecosystems with biotic or abiotic characteristics altered by humans (Hobbs et al. 2009, 2013). Morse et al. (2014) have suggested that novel ecosystems should also have crossed

> "an ecological threshold that facilitates a new ecosystem trajectory and inhibits its return to a previous trajectory regardless of additional human intervention. The resulting ecosystem must also be self-sustaining in terms of species composition, structure, biogeochemistry, and ecosystem services. A defining characteristic of a novel ecosystem is a change in species composition relative to ecosystems present in the same biome prior to crossing a threshold."

These additional characteristics make the concept very similar to that of multiple stable states or alternative stable states (Beisner et al. 2003). Interestingly, Morse et al. (2014) do not consider the San Francisco estuary to be a novel ecosystem; however, their consideration of the literature appears limited to a single paper (Carlton and Cohen 1997). The evidence in this paper suggests that the Delta, as well as the entire estuary, meets the definition for a novel ecosystem as defined by Morse et al. (2014).

Another term often applied to change in the estuary, particularly the Delta, is "regime shift" (Moyle and Bennett 2008; Baxter et al. 2010). Regime shifts can be defined as changes in the internal dynamics and feedbacks of an ecosystem that often prevent it from returning to a previous regime, even when the driver that precipitated the shift is reduced or removed (Scheffer et al. 2001; Carpenter 2003; Mac Nally et al. 2014). The undesirable characteristics (for humans) of regime shifts have led to interest in predicting when such shifts might occur (Biggs et al. 2009). Clearly, a system where introduced species have comprehensively replaced native flora and fauna has undergone a regime shift; however, few examples of change in estuarine systems are able to meet all the formal statistical requirements for establishing a regime shift (Mac Nally et al. 2014).

Regardless of various labels and definitions, it is clear that the food web in the Delta and the larger estuary has experienced profound changes in species composition and trophic pathways, with repercussions throughout the ecosystem. Although it is unclear if the current system is stable, the probability of it returning to any previously observed state seems small or nonexistent. This has led to the suggestion of applying the concepts of reconciliation biology (Rosenzweig 2003) to the Delta (Moyle et al. 2012). In the context of reconciliation ecology, managers seek to improve conditions for native species while accepting that the system has been irrevocably altered by human use and will continue to be used to support human goals. So, improving ecosystem conditions for native species in the estuary must happen alongside continuing use of land and water by humans and continuing physical and biological change. Such continuing change will likely include changes in water system management and operations, new invasions, and various physical and biological manifestations of climate change, including increasing temperature stress for sensitive native species (Brown et al. 2013, 2016).

Pelagic primary productivity and phytoplankton biomass are now generally low throughout the northern estuary, but recent work has focused on depressed production in the LSZ (Cloern and Jassby 2012; Kimmerer et al. 2012). Only about half of the spring–summer primary production in the LSZ is attributable to phytoplankton large enough (greater than ~5 µm) to be readily consumed by copepods and clams (Kimmerer et al. 2012). Phytoplankton provide less support to copepods and other consumers since 1993 than before 1993 (Kratina and Winder 2015). Growth and reproduction of all three species of copepod that are abundant during summer in the LSZ are food limited (Kimmerer et al. 2014a).

Over 6 years after the spread of *P. amurensis*, a spate of introductions of copepods and mysids in the fresh to brackish regions of the estuary (Table 2) resulted in a nearly complete change in species composition (Orsi and Walter 1991; Orsi and Ohtsuka 1999; Winder and Jassby 2011) that further altered the food web. The biomass of copepods in the LSZ decreased less than the biomass of phytoplankton, rotifers, or mysids, presumably because of the departure of Northern Anchovy, which had comprised about half of the biomass of planktivorous fish in this region (Kimmerer 2006), and because newly introduced species used resources previously used by *E. affinis*.

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The different copepod species are roughly nutritionally equivalent (Kratina and Winder 2015), but are not equally available to consumers (Meng and Orsi 1991). For example, the most abundant of the newly introduced species, *Limnoithona tetraspina*, is not commonly consumed by fish (Bryant and Arnold 2007; Slater and Baxter 2014), and the mortality rate of adults is very low, presumably because of the small size and cryptic behavior of these copepods (Kimmerer 2015). The copepod *Pseudodiaptomus forbesi*, which now makes up over half of the diet of Delta Smelt and other planktivorous fishes (Bryant and Arnold 2007; Slater and Baxter 2014), is most abundant in freshwater. The LSZ receives *P. forbesi* from freshwater via advection and dispersion, and they tend to be retained in the LSZ through their tidally timed vertical migration behavior (Kimmerer et al. 2014b). *Acartiella sinensis* is consumed by fish (Slater and Baxter 2014) and is apparently able to survive in the LSZ by preying on other copepods, particularly *L. tetraspina* and *P. forbesi* (Slaughter et al. 2016).

Even with the introductions of several mysid species, total mysid abundance and biomass have remained low compared to former abundances of *N. mercedis*. The epibenthic amphipod *Gammarus daiberi*, introduced in 1983, increased in abundance after the introduction of *P. amurensis* (Peterson and Vayssières 2010). Based on results from benthic surveys, it is more abundant in freshwater than in the LSZ (Kimmerer 2004). *Gammarus* spp. generally feed by shredding detritus, although they can be predaceous (Kelly et al. 2002). *G. daiberi* moves into the water column at night and remains on the bottom by day (Kimmerer et al. 2002), which may explain its infrequent occurrence in diets of most visually feeding fishes (Feyrer et al. 2003).

Several hydromedusae (jellyfish, Table 2) have become established in the low-salinity waters of the system (Mills and Rees 2000), raising questions about possible competition with fishes for zooplankton. The introductions likely resulted from ballast water release (Rees and Gershwin 2000). Medusae are seasonally abundant in the harbors and sloughs of the estuary (Rees and Kitting 2002; Schroeter 2008; Wintzer et al. 2011a, 2011c) but are not sampled well by existing sampling programs. They consume copepods, especially nauplii (Wintzer et al. 2011b, 2013), and in Suisun Marsh their diets overlap with those of Threadfin Shad and Delta Smelt (Wintzer et al. 2011c). Medusae were reported in samples taken by the Fall Midwater Trawl Survey during 2001–2011 with an average annual catch per volume of 0.0008 m^{-3} with a maximum of 0.0030 m^{-3} (Osborn and Civiello 2013, catch based on data in their Table 1). Small (<5 mm) medusae were detected in fewer than 5% of zooplankton samples collected with a 150-µm mesh net in channels of the LSZ during spring–summer of 2006–2007 (Kimmerer et al. 2014a; W. Kimmerer, unpublished data, see "Notes"). If further investigations show these low densities to be typical, substantial predatory effects on the zooplankton of open waters seem unlikely.

The changes in lower trophic levels were followed by shifts in diets, distributions, and abundance of many fish species. For example, during 1998–1999, the stomachs of Striped Bass, Splittail *Pogonichthys macrolepidotus*, and three other species in Suisun Marsh were less full than those of fishes caught during 1979–1983 (Feyrer et al. 2003). Further, mysids made up a smaller proportion of the prey of Striped Bass and were a negligible proportion of other common fishes. The magnitudes of declines in fish abundance were positively related to the dietary importance of mysids before the declines (Feyrer et al. 2003). Abundance of Northern Anchovy declined in the LSZ but not at higher salinities, presumably because the fish abandoned this now low productivity area (Kimmerer 2006). Abundance of Striped Bass and Longfin Smelt declined soon after the clam invasion (Kimmerer et al. 2009; Thomson et al. 2010; Mac Nally et al. 2010). In addition, Striped Bass became less abundant in the deep channels and more abundant in shallow nearshore areas, presumably because of better foraging opportunities (Sommer et al. 2011). Delta Smelt are frequently captured in the north Delta (Sommer and Mejia 2013). Because the region was not well sampled until recently, it is unclear whether the high frequency of occurrence in recent samples there reflects a shift of the population toward the north Delta or simply an increase in sampling effort there.

Today: The Pelagic Food Web No Longer Supports Native Fishes

Over approximately the last 15 years the zooplankton species composition has been more stable than in the preceding decades. No introductions of copepods have been reported since 1993 or mysids since 1997 (Table 2), and no previously documented native species went extinct. Notable recent invertebrate invaders include Siberian prawn *Exopalaemon modestus* (Brown and Hieb 2014) and an invasive cladoceran *Daphnia lumholtzi* (Mueller–Solger 2001). More alarmingly to many observers, four pelagic fish species, including the native Delta Smelt and Longfin Smelt, underwent steep declines in abundance in the early 2000s (collectively known as the "pelagic organism decline," [POD]; Sommer et al. 2007; Thomson et al. 2010). The POD may have been the manifestation of another ecosystem-wide regime shift (Baxter et al. 2010) or delayed repercussions of the regime shift that started in 1987. In any case, pelagic habitat in the LSZ and parts of the Delta appears to be less suitable for pelagic fishes than before 1987, and changes in the food web are a likely contributing cause (IEP–MAST 2015; Merz et al. 2016).

In contrast to the relatively high productivity in the LSZ before the *P. amurensis* invasion, this region

Table 2 Selected known introductions of copepods, mysids, and medusae to the San Francisco Estuary since monitoring began. *Eurytemora affinis* is not considered because it has existed in the estuary before monitoring began. Salinity is the reported value where the species was taken, not necessarily where it is most abundant.

Species	Taxon	Date of first capture	Location	Salinity	Likely source	Source
Cordylophora spp.	Hydromedusa	1920s?	Napa and Petaluma rivers, Pittsburg, Antioch	1-16	Ponto-Caspian	Matern and Brown 2005 Folino–Rorem et al. 2009
Blackfordia virginica	Hydromedusa	September 1970	Petaluma, Napa R.	14–17	Black Sea	Mills and Sommer 1995
Deltamysis holmquistae	Mysid	August 1977	Not stated	Not stated	Not stated	Bowman and Orsi 1992
Sinocalanus doerrii	Calanoid copepod	May 1978	Confluence	3.4	Asia	Orsi et al. 1983
Limnoithona sinensis	Cyclopoid copepod	August 1979	Stockton	~0	China	Ferrari and Orsi 1984
Oithona davisae	Cyclopoid copepod	October 1979 or before 1963	Suisun Bay	>12	Japan	Ferrari and Orsi 1984
Pseudodiaptomus marinus	Calanoid copepod	October 1986	Suisun Bay	6-8	Japan	Orsi and Walter 1991
Pseudodiaptomus forbesi	Calanoid copepod	October 1987	San Joaquin R.	~0	China	Orsi and Walter 1991
Aurelia spp.	Scyphomedusa	Spring 1988	Foster City (South Bay lagoon)	Not stated, probably high	Unknown	Greenberg et al. 1996
Acanthomysis aspera	Mysid	August 1992	Suisun Bay	Not stated	Korea, Japan	Modlin and Orsi 1997
Maeotias marginata	Hydromedusa	June 1992	Petaluma R.	10–15	Black Sea	Mills and Sommer 1995
Moerisia lyonsi	Hydromedusa	1993	Petaluma R.	10–15	Black Sea	Mills and Sommer 1995 Mills and Rees 2000 Meek et al. 2013
Hyperacanthomysis longirostris	Mysid	July 1993	Suisun Bay	Not stated	China, Korea?	Modlin and Orsi 1997
Tortanus dextrilobatus	Calanoid copepod	August 1993	Suisun Bay	3.6	China	Orsi and Ohtsuka 1999
Limnoithona tetraspina	Cyclopoid copepod	September 1993	Suisun Bay	1–3.8	China	Orsi and Ohtsuka 1999
Acartiella sinensis	Calanoid copepod	October 1993	Suisun Slough	2.8–4.6	China	Orsi and Ohtsuka 1999
Acanthomysis hwanhaiensis	Mysid	September 1997	San Pablo Bay	10–30	Korea	Modlin and Orsi 2000

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today is a net sink for phytoplankton, organic matter, and zooplankton (Jassby 2008; Kimmerer and Thompson 2014; Kayfetz 2014). Biomass accumulation of phytoplankton can be controlled by grazing. During spring–fall, the grazing rate attributed to different taxa is usually highest for clams (Lucas et al. 2002; Lucas and Thompson 2012; Kimmerer and Thompson 2014), followed in declining order by microzooplankton (York et al. 2011) and mesozooplankton (Kimmerer and Thompson 2014). Phytoplankton biomass is higher in both the freshwater Delta and the seaward higher-salinity areas than in the LSZ, implying that grazing is depressing phytoplankton biomass in the LSZ and the upstream and downstream areas are providing a spatial subsidy to the LSZ (Figure 4) (Kimmerer and Thompson 2014). An excess of bacterial carbon demand over primary production in the LSZ implies a subsidy of organic carbon from the Delta or Suisun Marsh (Hollibaugh and Wong 1996). Mortality of *P. forbesi* and other copepod nauplii from *P. amurensis* grazing in the LSZ is high despite strong escape responses (Kimmerer 2015; Kimmerer and Lougee 2015), and is partially compensated for by a spatial subsidy of copepods from the Delta (Durand 2010; Kayfetz 2014). There has also been a shift from largely herbivorous and omnivorous to more predatory zooplankton species (Orsi and Ohtsuka 1999; Kratina and Winder 2015), which added an additional trophic step to the food web, further decreasing its efficiency and exacerbating food scarcity for pelagic fishes. Phytoplankton, organic matter, and zooplankton from the more productive northern channels of Suisun Marsh may provide part of the seaward subsidy, although long residence time and shallow water may limit the extent of the subsidy if clam grazing is a significant factor in Suisun Marsh (Lucas and Thompson 2012, see "Suisun Marsh" section).

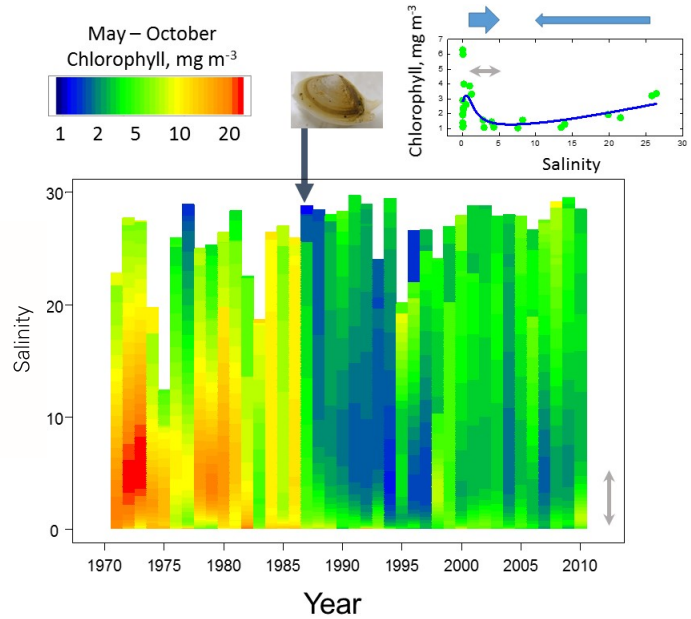

Figure 4 Effect of the invasion of *Potamocorbula amurensis* on phytoplankton in the low salinity zone. Main panel is an image plot showing chlorophyll-*a* concentration (color, scale upper left) vs. salinity and year, averaged over all IEP surveys during May–October. The clam (photograph) became abundant in summer of 1987. Chlorophyll is from a generalized additive model of chlorophyll vs. a smoothed function of salinity and year as a categorical variable. The panel in the upper right shows an example for 2010 with symbols representing data and the line representing the result of smoothing. Double-ended arrows on both graphs show the low salinity zone (salinity 0.5 – 5). Block arrows at top show the direction of net chlorophyll flux as a result of mixing and advection, inferred from the slope of chlorophyll vs. salinity by use of a mixing model. (Modified from Kimmerer and Thompson 2014.)

Does Ammonium Limit Primary Production?

Here, we briefly discuss the potential role of ammonium in suppressing phytoplankton blooms, and whether this might influence higher trophic levels. This topic and other nutrient issues in the Delta and Suisun Bay are addressed in detail elsewhere (Dahm et al., submitted). The theory known as the "ammonium paradox" (Wilkerson et al. 2006, 2015; Dugdale et al. 2007, 2012, 2013) asserts that some phytoplankton can grow faster on nitrate than on ammonium, and therefore inhibition of nitrate uptake by ambient ammonium concentrations enhanced by wastewater discharge can prevent the development of blooms.

This theory has generated considerable controversy among the estuarine research community, partly because experimental work has shown that phytoplankton growth rates can be faster on ammonium than on nitrate in some phytoplankton species (e.g., Dortch 1990; Clark and Flynn 2000). However, the "phytoplankton" is composed of a

very phylogenetically and physiologically diverse group of organisms, making it difficult to generalize statements about the effects of ammonium. In addition, some reports that claim to refute the theory have instead fueled the controversy; for example, Collos and Harrison (2014) examined ammonium toxicity, which is not relevant for this theory. Esparza et al. (2014) examined phytoplankton community composition in a small channel where ammonium concentrations were generally far above the threshold theorized to affect phytoplankton growth, but did not address the response of estuarine phytoplankton to low ammonium concentrations, so those results provide no insights into this theory.

Ammonium may play a role in modulating spring diatom blooms in the Delta and Suisun Bay when clam biomass is low (Dugdale et al. 2012, 2013; Wilkerson et al. 2015). However, clam biomass and grazing rate are usually high enough from late spring to autumn to prevent bloom formation or persistence (Kimmerer and Thompson 2014). During the summer, increased ammonium loads appear to contribute to *Microcystis aeruginosa* blooms (Lehman et al. 2015a).

Moreover, the available data do not support an assertion (Glibert et al. 2011) that the ammonium effect has had a substantial long-term influence on higher trophic levels. For example, chlorophyll concentrations increased in the Delta during the 2000s when ammonium loading and concentrations were increasing (Jassby 2008). Further, phytoplankton biomass, diatom production, zooplankton abundance, and abundance of several fish species resident in the LSZ declined in a brief (1 month to 2 years) period after the spread of the clam *P. amurensis*, from mechanisms that are well understood (Cloern and Jassby 2012) and described above. Even if improved wastewater treatment reduced ammonium loading and increased phytoplankton growth rate, the additional production may be consumed mostly by clams and fail to reach species of concern. An upgrade of the largest wastewater treatment plant and greatest ammonium point source (Jassby 2008) in the Delta from secondary to tertiary treatment is currently under way, and reductions in ammonium (and nitrate) discharge into the Sacramento River at Freeport will start in 2019. This provides an excellent opportunity to greatly reduce uncertainties and controversies about the effects of ammonium discharge on the Delta and Suisun Bay food webs.

Harmful Algal Blooms

M. aeruginosa blooms have been widespread in freshwater and brackish regions in the Delta since 1999. The blooms appear to originate in the San Joaquin and Old rivers, based on the high abundance of *M. aeruginosa* (Lehman et al. 2015a). *Microcystis* species produce hepatotoxic microcystins (Carmichael 1996; Chorus and Bartram 1999; Paerl 2008), and recent research has documented microcystins in zooplankton, amphipods, and fishes (Lehman et al. 2010a). Harm to human and livestock health is also a concern. Because the POD occurred soon after the first observations of *M. aeruginosa* blooms, questions quickly arose about the contribution of these blooms to the POD and to the ongoing poor recruitment of Delta Smelt (IEP–MAST 2015). As a result, considerable effort has been invested to understand the role of the blooms in Delta ecology (Dahm et al., submitted).

Recent research in the estuary has been equivocal regarding the role of *M. aeruginosa* in causing toxic effects to food webs and organisms. Several species of fish suffered sublethal effects when fed *M. aeruginosa* as part of their diet (Acuña et al. 2012a, 2012b). Laboratory studies found that survival of the copepods *E. affinis* and *P. forbesi* was reduced by dissolved microcystin, but the concentrations tested were unlikely to occur in the field (Ger et al. 2009). However, survival of both *E. affinis* and *P. forbesi* was reduced when *M. aeruginosa* exceeded 10% of their diet (Ger et al. 2010). In contrast, survival and reproduction of *P. forbesi* were much less affected when the water used in experiments was obtained from the field, so that it contained a natural assemblage of microorganisms (DuMais 2014).

In addition to releasing cyanotoxins, *M. aeruginosa* blooms can inhibit production of other phytoplankton. *M. aeruginosa* contain gas vesicles that allow them to float to the surface of the water. During periods of high temperature, long water residence time, and low wind speed, *M. aeruginosa* can accumulate at the surface, forming dense mats that shade underlying non-buoyant phytoplankton, which reduces the diversity of the phytoplankton assemblage

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through competition for light (Paerl 1988; Paerl and Huisman 2008). Lehman et al. (2015a) showed that *M. aeruginosa* is able to grow on the high concentrations of ammonium in the Delta. The ability of *M. aeruginosa* to use available ammonium may be an important factor that contributes to the magnitude and frequency of blooms. More detail on Delta nutrient dynamics is provided by Dahm et al. (submitted).

Other cyanobacteria are also present in the Delta, but have been less well studied. Lehman et al. (2010a) found *M. aeruginosa* blooms co-occurred with the cyanobacterium *Aphanizomenon flos-aquae*. During the wet year of 2011, *M. aeruginosa* did not form blooms until late in the year (DuMais 2014), and *A. flos-aquae* and *Dolichospermum* spp. (formerly *Anabaena* spp.) were abundant (Kurobe et al. 2013). Like *Microcystis* spp., *A. flos-aquae* produces toxins that may impair the Delta food web, but unlike *Microcystis* spp., *A. flos-aquae* can fix nitrogen gas. Nitrogen fixation can allow cyanobacteria, which include some harmful algal bloom (HAB) species, to outcompete other phytoplankton species (Schindler 1977). The roles of these cyanobacteria in the Delta food web are unknown.

As long as conditions remain favorable—such as high nutrients, water temperatures, and long residence times—and factors driving those conditions continue to occur—such as climate change, water management, and drought (Paerl and Huisman 2008, 2009)—HABs are likely to continue indefinitely. Nearly 2 decades after they were first observed, HABs are still not routinely monitored quantitatively in the estuary, although qualitative categorical observations (e.g., none, low, medium, high, scum or mats) are made during routine fish and discrete water quality monitoring (IEP–MAST 2015). Quantitative monitoring should be developed and implemented so blooms and their effects on food webs can be better understood.

Under-Studied Components of the Pelagic Food Web

When the Interagency Ecological Program (IEP) zooplankton monitoring program began in 1972, the dominant model of the food web was the linear food chain from phytoplankton through zooplankton to fishes. Consequently, the program was designed to focus on larger zooplankton and phytoplankton. We now know that estuarine pelagic food webs are much more reticulate than this, and that non-photosynthetic microbes are important consumers of phytoplankton and organic matter. Microzooplankton such as ciliates and flagellates overlap in size with phytoplankton, so that their grazing on phytoplankton must be inferred indirectly from experiments (Calbet and Landry 2004; York et al. 2011). Many microbes are mixotrophs, contributing to both primary and secondary production (Flynn et al. 2012).

Archaea and bacteria mediate nearly all biogeochemical processes (Mosier and Francis 2008), and their potentially high production can contribute to higher trophic levels, often through a microzooplankton trophic step (Ederington et al. 1995). The high bacterial carbon demand in Suisun Bay, discussed above, implies a carbon subsidy from other areas and potentially high production of organic matter available to higher trophic levels. In open waters, this carbon source appears to be smaller than that arising directly from phytoplankton (Sobczak et al. 2002, 2005; Mueller–Solger et al. 2002). Similar analyses of carbon sources and processing have not been done for tidal wetlands or tidal marsh channels.

The IEP zooplankton monitoring program has collected pump samples for microzooplankton between 43 and 150 µm and has reported abundance of rotifers, copepod nauplii, and adults of small species such as the copepod *Limnoithona* spp. (Orsi and Mecum 1986; Ferrari and Orsi 1984). However, until 2008, sub-samples were taken for processing that represented < 2 L of sample volume (IEP 2016), such that the counts of copepods and some other taxa in the pump samples were often too low for reliable abundance estimates. Starting in 2008 the effective volume sampled was increased to provide more reliable counts.

The abundance of non-photosynthetic protists (e.g., ciliates and heterotrophic flagellates) and all metazoan zooplankton smaller than 43 µm, has never been routinely monitored in the estuary. Several short-term studies have shown their importance as grazers on phytoplankton (York et al. 2011;

Kimmerer and Thompson 2014) and as food for some zooplankton (Rollwagen Bollens and Penry 2003; Bouley and Kimmerer 2006; Gifford et al. 2007) and clams (Greene et al. 2011). These roles are well known from other marine, estuarine, and freshwater locations (e.g., Calbet and Landry 2004), and the continued neglect of microzooplankton reflects the persistence of the outmoded 1970s conceptual model of a linear food chain that guided the initial design of the long-term monitoring programs in the estuary. It also reflects the difficulty of changing legally mandated, long-term monitoring programs and adding additional components to already expensive monitoring surveys.

Because small metazoa, protists, bacteria and archaea are key ecosystem components, monitoring their abundance and distribution would likely reveal important processes and sources of variation that are currently unknown.

NEW INTEREST IN NON-PELAGIC FOOD WEBS

Tidal Wetlands

By the time scientific data collection began, tidal wetlands were a relatively minor component of the landscape in the Delta (Table 1), and much of the tidal wetland in Suisun Marsh had been converted to managed wetlands (Manfree 2014). Consequently, there are relatively few studies that illustrate food web function in tidal wetlands. Brown (2003) reviewed and summarized the available information but because of the lack of information reached few conclusions on the importance of tidal wetland habitats to fishes. Today, understanding food web processes in tidal wetlands and their interaction with other food webs has gained scientific attention because tidal wetland restoration has been identified as a management action for improving habitat and food web processes for fish species of concern (e.g., EcoRestore c2016). We discuss this new information here, and the potential role of tidal wetlands in subsidizing the proximate open-water food web later.

Stable isotope data have shown that tidal marsh production supports resident species and is consumed by transient species (Grimaldo et al. 2009b; Howe and Simenstad 2011; Schroeter et al. 2015; Young 2016). Juvenile salmon feed in shallow areas throughout the estuary including small remnant wetlands (Grimaldo et al. 2009b). Juvenile salmonids in other Pacific Coast estuaries access tidal marsh for feeding and rearing (Simenstad and Cordell 2000; Bottom et al. 2005); however, it is less clear that pelagic fishes such as Delta Smelt make extensive use of tidal marsh. Delta Smelt probably used tidal channel habitat in the pre-Gold Rush Delta, when tidal channels were a dominant habitat type (Whipple et al. 2012; Robinson et al. 2014), but sampling in the Delta suggests that Delta Smelt are now relatively rare in small tidal channels (Gewant and Bollens 2012). Research from elsewhere in the estuary indicates that channel order and geomorphology can affect how different species of fish use tidal channels (Visintainer et al. 2006). The flooded Liberty Island in the northern Delta is used by Delta Smelt and other fishes (Whitley and Bollens 2014), but it is dominated by open water, with emergent tidal marsh mostly limited to its northern end. However, the fishes captured from that area do have tidal wetland-associated organisms in their diets at times.

Although the ability of transient and resident fishes to feed within tidal wetlands is well established, the dynamics of lower trophic-level organisms are not. Cohen et al. (2014) measured primary production of phytoplankton, benthic microalgae, low marsh, and submerged aquatic vegetation (SAV), in four tidal marshes in the lower Napa and Petaluma rivers of northern San Pablo Bay and in two small tidal marshes in the western Delta (only one had SAV). Primary production per unit area decreased with producer group in this order: low marsh vegetation > SAV > phytoplankton > benthic microalgae. However, relative contributions of the different producer groups varied from site to site, based on the areal coverage of each producer group. Cohen et al. (2014) suggested ammonium inhibition and benthic grazing were possible reasons for low primary production in the Delta wetlands compared to the other sites. A study in fall 2011 (a wet year) near the confluence of Suisun Marsh with Grizzly Bay, indicated highly variable carbon sources among consumers ranging from clams to Striped Bass (Schroeter et al. 2015). Emergent aquatic vegetation and phytoplankton were commonly dominant sources, and SAV was a substantial contributor for amphipods, California bay shrimp, and Striped Bass

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(Schroeter et al. 2015). The addition of introduced species (specifically polychaete worms, shrimp, and amphipods) increased food web complexity, illustrated by isotopic differences from their native counterparts (Schroeter et al. 2015). Similarly, Young (2016) explored food web processes in Lindsey and Cache sloughs in the north Delta. Contributions to consumers of various primary producers, including emergent and submerged vegetation, epiphytic green algae, benthic diatoms, and phytoplankton, were variable seasonally and spatially, and highly dependent on local conditions. The results of Schroeter et al. (2015) and Young (2016) show that there is no single food web structure for tidal wetlands. Instead, food web structure is likely to vary in space and in time, with contributions from multiple primary sources.

Zooplankton abundance in the large channels of Suisun Marsh is similar to that in Suisun Bay. Few differences were detected in zooplankton communities between tidal marshes at Browns Island and Sherman Lake and nearby open waters (Bollens et al. 2014). Although this implies that existing tidal marshes do not support a distinct zooplankton community because of high exchange rates with pelagic habitats, the more remote sloughs of northern Suisun Marsh and the northern Delta may harbor higher abundance because of long residence time.

Submerged Aquatic Vegetation

There is no historical information on the extent of submerged aquatic vegetation (SAV) in shallow subtidal habitat in the Delta–Suisun region. There are native aquatic macrophytes, sago pondweed *Stuckenia pectinata* and widgeongrass *Ruppia maritima* (Whitcraft et al. 2011), so SAV habitat was certainly present. Interest in SAV was stimulated by the observation that a number of introduced species, particularly Largemouth Bass *Micropterus salmoides*, were increasing in abundance as SAV habitat expanded (Brown and Michniuk 2007), with the SAV composed primarily of introduced Brazilian waterweed *Egeria densa* (Hestir 2010). Brown and Michniuck (2007) noted increased occurrence of SAV in the Delta between the early 1980s, when it was first perceived as a problem (Hestir 2010), and the early 2000s. Recent assessments have indicated fluctuation in SAV extent in the Delta within the 2000s (Table 1). During peak SAV biomass in fall, Brazilian waterweed can cover nearly 60% of central Delta waterways (Santos et al. 2011) and 6% to 11% of the total area of Delta waterways (Santos et al. 2016). Conversely, in the brackish Suisun Marsh and Bay regions, the submerged macrophyte community is composed primarily of the natives. The reduced abundance of introduced aquatic macrophytes in brackish areas is likely a result of a low tolerance for salinity (e.g., Borgnis and Boyer 2016).

Brazilian waterweed makes up the vast majority of the SAV biomass in the freshwater Delta because of its bimodal growth pattern, which allows it to overgrow other SAV species in the fall (Santos et al. 2011), and its ability to colonize under low-light conditions (Yarrow et al. 2009) unfavorable to native SAV species (Santos et al. 2012). The invasion and spread of Brazilian waterweed established a new food web. Aquatic macrophytes provide structural complexity and surface area, expanding habitat for epiphytic algae, invertebrates (Schultz and Dibble 2012), and fishes (Brown and Michniuk 2007; Grimaldo et al. 2009b, 2012; Conrad et al. 2016).

A diet and stable-isotope study indicated that nearshore fishes in the Delta (mostly centrarchids) consumed mainly amphipods living on the SAV, thereby gaining energy from SAV and associated epiphytic macroalgae (Grimaldo et al. 2009b). Fishes inhabiting open water (non-vegetated) shoals such as Chinook Salmon and Mississippi Silversides *Menidia beryllina* consumed some food organisms supported by SAV production and may have been foraging in the SAV on high tides. Non-native red swamp crayfish *Procambarus clarkii* may have also increased in abundance because of an increase in suitable habitat within Brazilian waterweed beds, and may also provide an important food source to Largemouth Bass (Nobriga and Feyrer 2007). The role of red swamp crayfish in the SAV food web and its interaction with SAV is an under-studied but important topic, given that the crayfish can affect water quality, sediment resuspension rates, macrophyte growth, and nutrient dynamics in other systems (Matsuzaki et al. 2009).

Foraging in the SAV by fish species normally more abundant in unvegetated shoals or open waters may

provide a path of energy exchange between the SAV and pelagic habitats (Grimaldo et al. 2009b). Mississippi Silversides typically inhabit open-water habitats near the shoreline, but also occur at lower densities offshore (Grimaldo et al. 2012; IEP–MAST 2015). The dietary shift in fishes after the invasion of *P. amurensis*, discussed above, included an increase in consumption of amphipods (Feyrer et al. 2003), which are supported by SAV-based energy sources (Grimaldo et al. 2009b). Thus, food resources originating in SAV may provide some support to fish populations outside of SAV beds. Similarly, as noted above, stable isotope studies in sloughs within areas of tidal wetlands that also contain SAV have shown that the SAV can be an important source of organic matter to consumers in those channels (Schroeter et al. 2015; Young 2016).

E. densa is considered an "ecosystem engineer" (Jones et al. 1994), which can affect other food webs and species through its effects on physical habitat. *E. densa* beds create drag and slow-moving water, reducing turbulence, and increasing net deposition of sediment, thereby increasing water clarity (Yarrow et al. 2009). Hestir et al. (2015) found that, 21% to 70% of the increase in water clarity in the Delta from 1975 to 2008 can be attributed to SAV expansion. The dense canopies of *E. densa* beds shade the water column, contributing to light limitation of phytoplankton and benthic algae. Research from shallow lakes has shown that *E. densa* has seasonal effects on chlorophyll-*a* concentrations, with lower concentrations inside plant beds in spring and fall (Mazzeo et al. 2003). The spread of *E. densa* may also have important but unquantified effects on water-column nutrients; however, the relationship between submerged macrophytes and nutrients is likely complex, because they can obtain and store nutrients from both the sediment and the water column (Boyer and Sutula 2015; Dahm et al., submitted).

Less is known about the food-web effects of invasive floating aquatic vegetation (FAV). Both native (pennywort *Hydrocotyle umbellata*) and introduced (water hyacinth *Eichhornia crassipes* and water primrose *Ludwigia* spp.) species are present in the Delta–Suisun region. These floating species form dense mats at the water surface that limit light penetration, which in turn may limit growth and establishment of SAV (Khanna et al. 2012), as well as growth of phytoplankton and benthic algae. Dissolved oxygen and densities of epibenthic and benthic invertebrates were lower beneath water hyacinth than beneath native pennywort mats in three flooded islands in the Delta (Toft et al. 2003). Senescent plant material beneath the floating mats can create anoxic conditions (Malik 2007); large-scale mechanical shredding of water hyacinth as a control measure is associated with localized fish kills, presumably because of the low dissolved oxygen associated with decomposition (Greenfield et al. 2007). Research on the effects of FAV and associated control measures on food webs, including the potentially allelopathic effects of FAV on phytoplankton (Schultz and Dibble 2012; Shanab et al. 2010), is extremely limited and deserves increased attention.

Floodplain

Similar to other historic habitats, only remnants of seasonally flooded habitats remain (Table 1). Historically, seasonally inundated wetlands included small floodplains along many tributaries to the estuary and large flood basins to its north. The Yolo and Sutter flood bypasses—as well as the Sacramento Deep Water Ship Channel and the northern reaches of the Cache Slough complex in the north Delta—cross and encompass large parts of the historical flood basins (Whipple et al. 2012). Although the bypasses are used mostly for agriculture and flood flow conveyance, they also function as managed flood plains. Smaller managed or restored flood plains also exist in the Delta, for example along the Cosumnes River, a small eastside tributary to the Delta.

The Yolo Bypass has been well studied for the benefits it provides to fishes that use it and for potential subsidies to the north Delta. In 2003, the Yolo Bypass contributed 14% (median) of the phytoplankton biomass (chlorophyll-*a*) exported to the estuary, with only 3% of the river flow through the combined Sacramento River and Yolo Bypass (Lehman et al. 2008). This effect mainly resulted from higher phytoplankton growth rate and longer residence time in the Bypass than in the river (Lehman et al. 2008). However, the actual chlorophyll-*a* flux and its contribution to Delta food webs depend on the extent, duration, and

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timing of flooding. Recent data have suggested that increased flows through Yolo Bypass during the fall rice field drainage are associated with increased chlorophyll-*a* concentrations at Rio Vista (Figure 5). Flooding of Yolo Bypass stimulates rapid production of chironomids, which aestivate in floodplain sediments (Benigno and Sommer 2008). Invertebrate drift in the Yolo Bypass exceeds that observed in the Sacramento River (Sommer et al. 2001, 2004) and the chironomids are a major food source for juvenile salmon (Sommer et al. 2001) in the Bypass. Conversely, there was no difference between floodplain and river in densities of zooplankton, likely because of the low residence time of the water. Similar food web benefits have been documented in the Cosumnes River floodplain, including high phytoplankton, invertebrate, and fish productivity within the floodplain, and biomass exports to adjacent habitats (Ahearn et al. 2006; Grosholz and Gallo 2006; Moyle et al. 2007; Jeffres et al. 2008).

Of course, floodplain habitats are not immune to the effects of species invasions and other stressors. For example, the Siberian prawn became the dominant macroinvertebrate in the perennial ponds and waterways of Yolo Bypass just 1 year after it was first observed (Brown and Hieb 2014). Its ecological effects have not yet been studied in detail, but food web effects are likely. In the Cosumnes River Preserve, which includes restored floodplain and riparian habitat, the highly invasive herb perennial pepperweed *Lepidium latifolium* and non-native redeye bass *Micropterus coosae* pose considerable management challenges (Moyle et al. 2003).

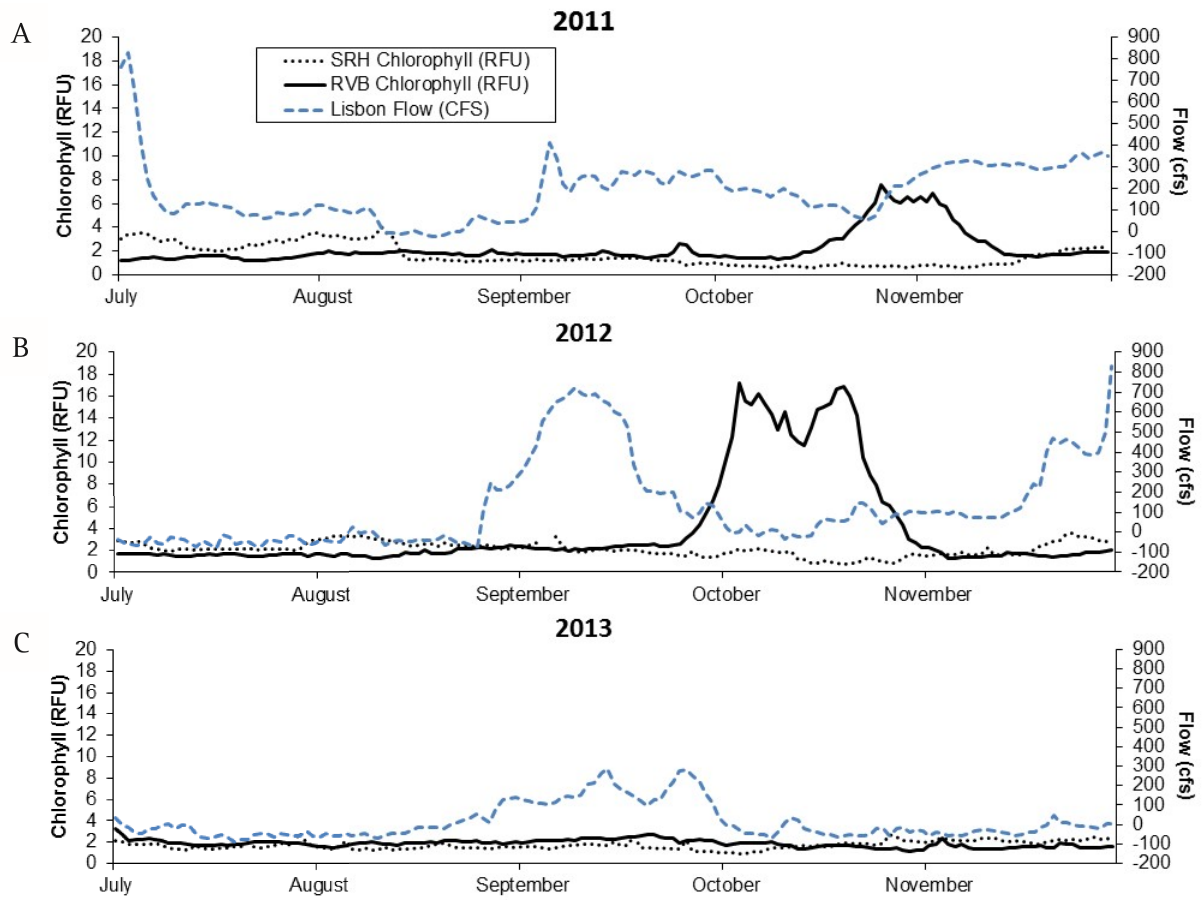

Figure 5 Chlorophyll-*a* concentration, measured as relative florescence units (RFU), in the Sacramento River at Hood (SRH; just south of Freeport; see Figure 1) and the Sacramento River at Rio Vista (RVB) in relation to flow in cubic feet per second (cfs) through Yolo Bypass measured at Lisbon Weir (Lisbon Flow)

REGIONAL VARIATION IN FOOD WEBS ACROSS THE LANDSCAPE

Earlier, we have largely discussed habitat-specific food webs as individual entities; however, across the landscape there is variation in the types and degree of connection among habitat-specific food webs in specific geographic regions (Figure 2). Understanding these geographic differences is important when management strategies and expected outcomes for different parts of the Delta–Suisun system are considered. We omit the LSZ from this discussion because it has been treated as a specific region throughout this paper.

Suisun Marsh

Fishes (Moyle et al. 1986; Meng et al. 1994; Matern et al. 2002; O'Rear and Moyle 2014a, 2014b) and their diets (Feyrer et al. 2003; O'Rear 2012) have been well-studied in Suisun Marsh; however, lower trophic-level function has not been well studied, with the exception of invasive jellyfish (Schroeter 2008; Wintzer et al. 2011b, 2013). Within the context of our conceptual model (Figure 3), Suisun Marsh mainly represents the interaction of a tidal wetland food web, as represented by the smaller sloughs, with the pelagic-benthic food web of the larger channels (Suisun and Montezuma sloughs). The tidal wetlands component includes a perennial connection of smaller Suisun Marsh channels with "fringing marshes" along the edges and small areas of tidal wetland (O'Rear and Moyle 2014a). The smaller sloughs have higher residence times, higher concentrations of phytoplankton and zooplankton, and lower abundances of *P. amurensis* compared to the larger sloughs (O'Rear and Moyle 2014a). *P. amurensis* is most common in upper Suisun Slough, with most of the remaining clams captured in the region of lower Suisun Slough just upstream of the confluence with Grizzly Bay. The interaction between the benthic and pelagic food webs in the larger sloughs appears to be similar to that described in the LSZ.

Seasonal draining of managed wetlands affects Suisun Marsh food webs both positively and negatively. In some cases, draining the ponds can flush large numbers of small fish, such as Threespine Stickleback *Gasterosteus aculeatus*, that can be consumed by predatory fish such as Striped Bass (O'Rear and Moyle 2014a). Conversely, under some conditions, the decomposing organic matter in such drainage water can deplete the oxygen in sloughs, killing fish and reducing habitability of portions of some sloughs (Siegel et al. 2011); however, this situation appears to be improving with management changes (O'Rear and Moyle 2013). The value of the discharged organic matter to the food web is unknown, but it likely includes a great deal of refractory material that is less biologically available to the ecosystem than fresh material such as phytoplankton (Sobczak et al. 2002, 2005).

The small- and large-channel food webs appear to change on several time-scales. O'Rear and Moyle (2013) have noted that over the course of their surveys (started in 1980) fishes have used nearshore habitats for feeding as mysid abundances decline seasonally, consistent with the hypothesis of shifts to nearshore areas and smaller channels for feeding on amphipods. Schroeter (2008) found no change in Striped Bass abundance in small channels and shallow areas, compared to declines in deeper areas of large sloughs.

The relative importance of various primary producers to Suisun Marsh food webs has been little studied. Schroeter et al. (2015) conducted a stable isotope study in lower Suisun Slough, but the study was limited to a few sites during the fall of a single wet year. Primary producers included phytobenthos, SAV, emergent aquatic vegetation, and terrestrial vegetation. Consumers tended to be generalists, incorporating a mixture of primary producer sources into their diet, even those generally thought of as primarily using phytoplankton (e.g., *C. fluminea* and mysids). A study with broader geographic and temporal scope would be useful to understanding how Suisun Marsh functions, and could provide important information for designing restoration projects and projecting outcomes.

Freshwater Delta

For the following discussion, we divide the freshwater Delta into two regions: We define the south-central Delta as the region of the Delta south of the Sacramento River (Figures 1 and 2) and the north Delta as the area north of the Sacramento River,

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emphasizing the Cache Slough complex and Liberty Island, as well as the Sacramento Deep Water Ship Channel and Yolo Bypass.

South–Central Delta

Two food webs dominate the south–central Delta: the pelagic-benthic and SAV. Floating aquatic vegetation (FAV) is also abundant, but only a single study (Toft et al. 2003) has explored the food web effects of FAV. Therefore, we acknowledge that FAV may have large effects, but there are insufficient studies for synthesis. This region also receives a seasonal floodplain subsidy from the Cosumnes River restored flood plain. Studies have shown that the Cosumnes River flood plain can provide important spawning and rearing habitat and food web resources for native fishes (Ahearn et al. 2006; Grosholz and Gallo 2006; Moyle et al. 2007; Jeffres et al. 2008); however, the degree to which this production is transported into the tidal Delta has not been explored. Later, we further address his general topic of floodplain transport to the freshwater Delta (see "North Delta").

Studies in the south-central Delta have been critical to our understanding of clam grazing effects, particularly *C. fluminea*. Studies in the open waters of several flooded islands, e.g., Franks Tract and Mildred Island (Figure 1), documented how grazing by *C. fluminea* could deplete phytoplankton biomass from these areas, and that such effects were situation dependent (Lucas et al. 2002; Lopez et al. 2006). Franks Tract, which is shallow and well-mixed, and supported a population of clams, was consistently a sink for phytoplankton. Conversely, Mildred Island, which was deep and had limited connection to surrounding channels through a few breaches, did not support a large population of clams, and could accumulate phytoplankton biomass; however, the biomass was largely consumed by *C. fluminea* when it was transported out of the island through shallow channels where *C. fluminea* was abundant. These results have been the basis for much of the thinking about flux of organic matter from habitat restoration areas to pelagic habitats (e.g., Lucas and Thompson 2012; Herbold et al. 2014).

Studies in the south-central Delta have also influenced current understanding of SAV, which has invaded channel edges and other shallow habitats. These studies have highlighted changes in the fish community (Brown and Michniuk 2007; Grimaldo et al. 2012; Conrad et al. 2016). This new habitat has also established new food webs (Grimaldo et al. 2009b; Young 2016). Grimaldo et al. (2009b) determined that pelagic phytoplankton, and SAV and associated epiphytic macroalgae, fueled largely separate food webs; however, there was some limited crossover. Invertebrates produced within the SAV, such as amphipods and chironomid pupae, were consumed by fishes, such as Chinook Salmon and Mississippi Silverside, feeding along the edge of SAV beds.

In addition to *C. fluminea* grazing and habitat change, this region is subject to several other possible food web modifications. HABs are generally centered in this region, indicating that organisms are exposed to greater concentrations of these cyanobacteria and their toxins for longer periods of time. Also, there has been periodic concern that water exports from the water projects in the south Delta may entrain large quantities of nutrients and lower trophic-level organisms (Jassby and Powell 1994; Arthur et al. 1996; Durand 2015). Management concerns over entrainment have focused mainly on entrainment of fish (Kimmerer 2008; Brown et al. 2009; Grimaldo et al. 2009a). The effects of diversions on nutrients and lower trophic levels would require consideration of the timing and duration of diversions, hydrodynamics and interactions with *C. fluminea* and the SAV food web.

North Delta

The north Delta has been of much recent interest because of its potential for extensive habitat restoration and because of high frequency of occurrence of Delta Smelt (Sommer and Mejia 2013). Lindsey and Cache sloughs have relatively intact terminal channel networks (Figure 1) that have tidal marsh, backwater, and SAV habitats (Young 2016); however, there is a water diversion near the upper end of Lindsey Slough. Liberty Island provides a large area of open water pelagic habitat. The region provides the pathway from the Yolo Bypass to the Delta, and thus receives episodic inputs of organic material and sediment when Yolo Bypass floods and drains. Invasive species, particularly SAV (Young 2016) and *C. fluminea* (Kramer–Wilt 2010), appear to

be less prevalent than in the south-central Delta. SAV and FAV are present and can be abundant in the channel networks, but the distribution of SAV may be limited by turbidity (Young 2016). The role of *C. fluminea* in north Delta food webs has not been fully evaluated. Overall, the area appears to provide some of the best remaining habitat for native fishes (Moyle et al. 2012; Young et al. 2015), including Delta Smelt (Hammock et al. 2015)

Young (2016) conducted stable isotope analyses in upstream and downstream sites in the channels of Lindsey and Cache sloughs of the north Delta in spring and summer. Pelagic species in the north Delta channels consumed more organic matter of non-phytoplankton origin than those in the south-central Delta. The high degree of separation between pelagic and SAV food webs observed in the south Delta was most similar to conditions in the downstream channel reaches of Cache and Lindsey sloughs, where channels have rip-rapped banks, limited emergent vegetation and strong tidal exchange of water. This suggests that concepts developed in the south-central Delta should be applied to north Delta channel food webs with caution.

Liberty Island provides an expansive area of shallow pelagic habitat that supports an array of native and invasive fishes (Nobriga et al. 2005; Whitley and Bollens 2014). Liberty Island is dominated by tidal marsh at the northern end: connections with larger channels are important at the southern end and western margins. Fish diet studies in the northern tidal marsh area indicate important contributions of tidal marsh habitat to the diets of native and invasive fishes (Whitley and Bollens 2014). Whitely and Bollens (2014) noted that Delta Smelt used tidal wetland-derived prey during some seasons although zooplankton was always dominant in the diet; they did not address diets in the southern area of Liberty Island. The Liberty Island food web deserves additional study, perhaps using stable isotopes.

CAN AQUATIC FOOD WEBS BE MANAGED TO BENEFIT SELECTED SPECIES?

Given the condition of the present-day Delta–Suisun food webs, formulating management actions to provide food web support to fish species of concern—particularly Delta Smelt, Longfin Smelt, and endangered salmonids—is a formidable challenge. There appear to be two major approaches to food web management. First, if primary production is limited by excessive ammonium loading, limiting such loading from wastewater discharge is a potential approach to food web management. The plan for wastewater treatment upgrades and the opportunity this presents for understanding food web processes is discussed above and by Dahm et al., submitted). A second approach to food web management is habitat restoration, particularly of tidal wetlands and flood plains, to provide new production sources for fishes to exploit.

The premise of the restoration approach is that altering areas of the current Delta landscape to more closely resemble historical conditions will restore food web processes that benefit native fishes. Specifically, the expectation for restoration of food webs are two-fold: first, restored areas will produce phytoplankton and zooplankton that will benefit species of concern on-site; and second, food resources produced in restored areas will be exported such that they will subsidize pelagic habitat in adjacent waters or regionally.

A major challenge to achieving the objectives of the restoration approach is that the highly altered state of the ecosystem makes it difficult to predict outcomes, making restoration planning more complex (Seastedt et al. 2008). Species assemblages within novel ecosystems such as the Delta–Suisun system are unique, and environmental stressors differ from those of the historical ecosystem. Thus, restoration projects and their effects on the local and regional food webs must be approached as experiments, beginning with the knowledge of current ecosystem function, having clearly expressed objectives and careful design, and including feasibly measured metrics to determine if projects are achieving stated objectives (Seastedt et al. 2008). An adaptive management framework for restoration projects in the Delta–Suisun system is required by the *Delta Plan* (DSC 2013) and includes all of these elements. This adaptive management framework is crucial for charting and adjusting the progress of floodplain and tidal wetland restoration projects that are intended to support food web processes.

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Floodplain Restoration

Wetland and floodplain restoration efforts are likely to play out differently for food web support simply because tidal wetlands are perennial, and floodplains are only seasonally and episodically inundated, to the extent that their food web effects are likely to be more ephemeral than those of tidal wetlands. However, the data summarized above (Figure 5) suggest that Yolo Bypass can quantifiably contribute to phytoplankton populations in the north Delta and contribute to phytoplankton blooms in the lower estuary. One option for food web management is to adaptively manage Yolo Bypass flows to support the pelagic food web downstream. For example, it may be possible to strategically augment natural high-flow events (via appropriately timed reservoir releases) to achieve Yolo Bypass inundation in winter and early spring to support spring blooms of the type that were common in the historic estuary until approximately the 1970s. Similarly, winter and early-spring Yolo Bypass flooding would likely benefit juvenile salmonids by providing a food-rich habitat during their emigration to the ocean (Sommer et al. 2001). During the autumn rice harvest in the Yolo Bypass, strategic management of the perennial agricultural drainage system could achieve flows out of Yolo Bypass substantial enough to promote phytoplankton blooms downstream of the Bypass (Figure 5). If these phytoplankton blooms support enhanced zooplankton production, such management could promote food web processes to support pelagic species, particularly Delta Smelt. Thus, while floodplain support of downstream food webs is indeed likely to be ephemeral, well-timed adaptive management actions may have beneficial food web results.

Tidal Wetland Restoration

Evaluating the benefits of tidal wetland restoration to fish requires the consideration of several overlapping spatial scales. The first spatial scale is that of the tidal wetland itself; benefits provided within the tidal wetland are available to resident fishes and transient fishes that can access the site. The second spatial scale is the near-field, local scale outside of a specific tidal wetland project but within roughly a tidal excursion (the "tidal footprint" of a restored area). The third spatial scale is regional and depends on tidal dispersive transport from the tidal wetland to more distant channels and bays where food is scarce (e.g., the LSZ). At the near-field-scale, we consider in detail the narrower perspective of a subsidy of food (primarily zooplankton) for native pelagic fishes in open waters, because this is one of the major areas of uncertainty (Herbold et al. 2014). We then take a more general perspective on regional ecosystem restoration. At all scales, characteristics of the wetland itself—such as elevation, vegetation types, inundation regime, colonization by SAV and clams, and connectivity to neighboring areas—are key to its structure and to functions such as productivity, and thus to its ability to support consumer species. To determine if a project is achieving its objectives, each scale of habitat restoration will require scientific monitoring efforts of specific metrics. For example, at the wetland scale, metrics might include densities of food resources and target fish species for management. At the tidal-excursion and regional scales, measurement of plankton fluxes between restoration areas and nearby open waters over the full tidal cycle, may be appropriate. Where possible, comparison of plankton biomass in all areas before and after restoration will also be helpful to evaluate success.

At the scale of the tidal wetland, stable isotope data have clearly shown that tidal wetland production supports resident species and is consumed by transient species (see "Tidal Wetlands"). Clearly, tidal wetland restoration projects are designed to allow fishes to access the newly created habitat, but invasive SAV and FAV may impose a physical or water-quality (e.g., low dissolved oxygen) barrier to fish movement into a restoration site, and SAV will provide habitat for predators that could seriously reduce the survival of fishes of concern. Extensive beds of *E. densa* and FAV, such as water hyacinth, may limit phytoplankton production through competition for light. Studies in Suisun Marsh indicate that smaller channels that are somewhat isolated from larger channels can be very productive (see "Suisun Marsh"); however it is unclear whether individual restoration projects will be large enough to maintain such channel systems. It is also unclear how likely some fishes are to access and use tidal channels within wetland restoration projects. Research from

elsewhere in the estuary indicates that channel order and geomorphology can affect use by different fish species (Visintainer et al. 2006). This uncertainty suggests that access-relevant metrics are needed to evaluate restoration projects. Monitoring metrics for the "opportunity" offered by restored habitat have already been proposed for wetland restoration efforts in the Pacific Northwest (Simenstad and Cordell 2000).

At tidal-excursion and regional scales, the potential for the export of food organisms from restoration sites to surrounding habitats is not well understood. To be used by fish in the surrounding habitats, this export must take the form of zooplankton, non-planktonic aquatic animals (e.g., epi-benthic amphipods and chironomids), or large particles of biologically available detritus. Few studies have examined zooplankton exchange between tidal wetlands and adjacent areas. A marsh at China Camp in San Pablo Bay was a net sink for mysids, probably because of predation within the marsh (Dean et al. 2005). Liberty Island, often cited as a habitat restoration model for Delta Smelt, is a net sink for organic and inorganic material over a whole tidal cycle (Lehman et al. 2015b) and seasonally (Lehman et al. 2010b). Within Liberty Island, limited areas of wetland provide a large proportion of the total phytoplankton production, which can support food web processes locally (Lehman et al. 2015b). Zooplankton fluxes in and out of Liberty Island were sometimes inward and sometimes outward, and strongly related to the tidal cycle (Lehman et al. 2010b).

Of the handful of studies of zooplankton flux to and from shallow estuarine areas outside of the estuary, all show evidence of import and none of export except for planktonic larvae of the wetlands' benthic residents (Carlson 1978; Kimmerer and McKinnon 1989; Brucet et al. 2005, 2010; Badosa et al. 2006; Mazumder et al. 2009; Cooper et al. 2012). Fluxes of zooplankton into shallow areas likely result from consumption of zooplankton by small fish that seek food and shelter there, which has been shown in estuaries and lakes (e.g., Fulton 1985; Cryer and Townsend 1988; Gliwicz and Rykowska 1992; White 1998; Jeppesen et al. 1998).

Although phytoplankton is not directly consumed by fishes of concern, it can support secondary production that can be consumed by fishes; however, the likelihood of such a subsidy is uncertain. Lucas and Thompson (2012) described the complex interactions among residence time, depth, and grazing rates of invasive clams, and their combined influence on phytoplankton in shallow restoration sites. The principal lesson of that study was that benthic grazing can control the sign of the relationship between residence time and biomass. Without information on all three values, the outcome of restoration actions is difficult to predict.

Wetland restoration to enhance beneficial food web processes at the regional scale has been discussed in other estuaries. In Delaware Bay, stable isotope data have shown that several marine transient fishes benefit from production that originates in salt marshes, without necessarily occupying them (Litvin and Weinstein 2003; Weinstein et al. 2014). Based on these indirect benefits, researchers have strongly advocated for adopting a "whole estuary" approach to wetland restoration, in which tidal wetlands are considered as part of a larger "habitat mosaic," and their functional connections with adjacent habitats are considered in the restoration planning phase (Weinstein and Litvin 2016). In the Delta–Suisun system, much of the tidal wetland restoration planning occurs at the single project level. To adopt the "whole estuary" approach proposed by Weinstein and Litvin (2016), the potential production of all wetland restoration projects—and their contribution to adjacent waters within their tidal excursion—would be considered jointly and at a landscape scale. The advantages of this approach may be the identification of (1) potential food web benefits that are apparent only with the joint contributions of proximate restoration areas, and (2) the need for restoration in other areas that are not yet planned.

Regardless of the scale of the planning approach, if tidal wetlands are to be restored to support pelagic fishes, much work is required to determine how to design restoration programs that are likely to achieve that purpose. The long-term sustainability of the benefits of restoration over future decades should also be considered, given the likelihood of colonization by introduced clams, SAV, and FAV, and the anticipated use of the area by the target species. The challenges

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to achieving substantial zooplankton export suggest that this objective of restoration should be approached with a careful, step-wise experimental approach that includes hydrodynamic modeling, analysis of the effects of wetland vegetation and bathymetry on zooplankton production, and behavioral studies of zooplankton and their predators. In addition, studies of phytoplankton and nutrient fluxes will be necessary to determine if they support zooplankton production in open waters, or merely provide more food for clams.

INTO THE FUTURE: EXPECTATIONS FOR CONTINUED CHANGE AND SCIENCE NEEDS

Continued changes in the Delta food web should be expected. Although the pace of species introductions has declined, species invasions still occur in the estuary and its watershed. A likely future invertebrate invader is quagga mussel, which has already invaded several reservoirs in California. Quagga mussels and closely related zebra mussels can have effects on aquatic ecosystems at least as severe as that of *P. amurensis* in the estuary (Strayer 2009). The high calcium requirements of quagga and zebra mussels may limit their distributions to areas outside the influence of the Sacramento River (Cohen 2008). The ultimate distribution and severity of the food web effects of such an invasion are difficult to predict, especially given the high current grazing rates of clams.

Successful zooplankton introductions into the estuary have been associated with drought (Winder et al. 2011). Drought conditions are often associated with higher temperatures, salinity intrusions deep into the Delta, and low flows that could favor newly arriving species over native species, although abundance, growth, and reproductive rates of copepods in the estuary do not respond to changes in freshwater flow (Kimmerer et al. 2014). Also, the analysis of Winder et al. (2011) used a 3-year lag between drought and establishment, which is very long for species with life cycles of a few weeks. Ballast-water regulations that require at-sea exchange have been reasonably effective at limiting the supply of potential invaders (Choi et al. 2005), and no new zooplankton invasions have been documented. Further work on the conditions that favor introductions of zooplankton and other organisms would help clarify what has happened in the past, and provide information that would inform expectations for the future.

The expected effects of climate change on the Delta are addressed by in detail by Dettinger et al. (2016). Ecologically, the effects of climate change in the watershed (Yates et al. 2008; Cloern et al. 2011; Thompson et al. 2012; Null et al. 2013) and the estuary (Cloern et al. 2011; Brown et al. 2013, 2016) have largely been considered on a species-specific basis. Statewide, native species appear more susceptible to climate change than invasive species (Moyle et al. 2013). There have been several assessments of tidal marsh sustainability in the context of estimated rates of sea level rise (Orr et al. 2003; Stralberg et al. 2011; Swanson et al. 2013), but the outcomes have generally not been considered in the context of food webs.

The effects of sea level rise and concurrent salinity intrusion on food webs must be examined in the context of local topography and land use, regional human activities including management, and the vulnerability of Delta levees to failure (Mount and Twiss 2005). If tidal and seasonal marshes are given room to migrate landward as sea level rises, changes to the landscape and associated food web processes would likely be relatively minimal. If edges are hardened with seawalls or levees, sea level rise will more likely result in marsh drowning and the conversion of tidal marsh to subtidal habitats, with accompanying changes in trophic processes. Salinity intrusion would likely little affect food web processes in the open waters of the estuary because pelagic species move with the water, and other species move with the salinity gradient, either actively or through death and colonization. However, the geographic extent and location of waters with a specific salinity, such as the LSZ, would change, with possible effects on species abundance. Efforts to model and predict the outcomes of changes in aquatic habitat from climate change would help to indicate where habitat conservation and restoration should be focused.

The uncertainties in predicting the effects of climate change, the outcomes of management actions, and the occurrence of unexpected events such as levee failures should not be interpreted as a reason not to proceed with efforts to improve conditions for species

of concern. The continued development of modeling capacity (e.g., Cloern et al. 2011; Rose et al. 2013; Kimmerer et al. 2014b) and ecological understanding (IEP–MAST 2015; Kimmerer and Thompson 2014) can be applied to scenarios of future change (e.g., Cloern et al. 2011). Combined with monitoring and research in an adaptive management framework, implementing new management actions should improve our ability to understand what the future Delta and its food web will look like.

CONCLUSION

Over the last 2 decades our understanding of the structure and changes in Delta–Suisun food webs has improved, but the relative importance of various ecosystem drivers in causing those changes is unclear. These uncertainties urgently need to be resolved to support effective management actions that will halt or reverse the declines in species abundance and otherwise improve aquatic habitat. Management of a few drivers is clearly more feasible than simultaneous management of a large number of drivers; however, the quest for a ranking of drivers or selection of a single "key" driver is futile because they all matter at different times, in different places, and in different and often interactive ways (NRC 2012; IEP–MAST 2015).

Below, we identify the topics that we believe merit the initiation of research programs to identify effective management approaches that will support beneficial food webs. Our recommendations are presented in the order they appeared in the preceding sections, and *we do not prioritize them*.

1. **Clarify the causes of low pelagic biomass.** The relative contributions of clam grazing, light limitation and ammonium inhibition in limiting the accumulation of phytoplankton biomass should be resolved through a dedicated effort, including experimental and modeling components. Monitoring and research associated with expected decreases in ammonium inputs to the Sacramento River should be a key part of this program to inform the integration effort and to determine if any benefits are sustained over time.

2. **Monitor and investigate harmful algal blooms (HABs).** Despite the high frequency of HABs, we still lack a systematic monitoring program to document HAB distribution, abundance, and toxicity. Additional research on the effects of HABs on organisms of interest under field conditions would be useful to define the level of concern for aquatic resources and identifying management actions that might be effective. A monitoring program for HABs should be designed and implemented as soon as possible.

3. **Modernize the monitoring program.** Maintaining current long-term monitoring is essential. There is, however, a growing disconnect between what the existing monitoring programs provide and what is needed for effective management of the changing system. Most important, current monitoring focuses almost entirely on abundance and distribution of species, or indices of species groups such as chlorophyll-*a* concentrations. There is very little monitoring of process rates or fluxes, which are necessary to understand how drivers influence species of concern. Major habitats (e.g., tidal wetlands and SAV) and species groups (e.g., HABs, SAV, FAV, jellyfish, microzooplankton, and bacteria) are not being systematically monitored. Preparation for short-term studies during unusual or extreme events—such as the wet year of 2011 (Brown et al. 2014), the current drought, or the large phytoplankton bloom in spring 2016—would also be beneficial. Finally, effort is needed on an ongoing basis to incorporate modern methods into long-term monitoring.

4. **Conduct tidal wetland restoration to benefit native species of concern as an experimental program.** This is likely the most urgent issue because large investments are being made in planning and implementation without parallel efforts to fully understand outcomes. Too many uncertainties remain for confident predictions of the outcomes of restoration, especially at the scale of the Delta. Therefore, large-scale restoration should be implemented as adaptive management experiments, which will require considerable additional effort and funding beyond those required to simply construct wetlands. Adoption of an experimental approach integrated across the whole estuary or Delta but addressing all spatial scales discussed above, as well as different

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wetland characteristics and configurations, would help to achieve maximum benefit from the time, money, energy and resources being invested. Although conceptual models are being developed and monitoring protocols designed and tested (IEP–TWMPWT 2016), a framework is needed to predict outcomes, synthesize results, or standardize monitoring.

5. **Study the functions of submerged and floating aquatic vegetation (SAV and FAV).** The importance of SAV to consumers of fish in Suisun Marsh and the north Delta tidal channels suggests that Delta–Suisun food webs are more thoroughly linked across the landscape than previously thought. Further, we lack established concepts about the role of FAV. A unified study should be designed to better understand the relative importance of SAV and FAV, as well as other habitat-specific food webs. This recommendation interacts with recommendation 4.
6. **Study the contributions of floodplains.** Determine the extent and fate of floodplain contributions to Delta food webs. This study should focus on Yolo Bypass, which provides a large area.
7. **Model regional processes.** It is unclear if individual, uncoordinated restoration projects can contribute to improvement of pelagic habitats in a specific region or across the Delta–Suisun region as a whole. Such processes should be explored using suitable simulation models to determine if significant long-term benefits seem likely.
8. **Expand efforts at interdisciplinary analysis and synthesis.** Ongoing analysis and synthesis of new knowledge should be an ongoing part of any sustained scientific effort, including the efforts outlined above. Such analysis and synthesis can lead to new understanding, and identify important data gaps (e.g., Brown et al. 2014; Herbold et al. 2014; IEP–MAST 2015). These analyses should increasingly apply modern modeling and statistical tools to improve the reliability and utility of results (e.g., Feyrer et al. 2007; Thomson et al. 2010).

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