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**Keywords:**
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**Abstract:**

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Aquatic trophic interactions in the upper San Francisco Estuary are synthesized here as a conceptual food web model, using over 35 years of scientific research, and highlighting key uncertainties for restoration. The food web was created as part of the Delta Regional Ecosystem Restoration Implementation Program to evaluate the benefits of restoration actions. Historic changes to the hydrology and geomorphology of the region have decreased ecosystem resiliency. More recently, pressures from water export, alien species introductions, and nutrient loading have disrupted the food web and increased the vulnerability of pelagic and juvenile fishes. One of the key features of the contemporary food web is a decoupling of pelagic and the detrital pathways. Low production and high mortality of phytoplankton since the 1980s have led to declines of pelagic organisms, including zooplankton, mysids, and planktivorous fish. In contrast, detrital pathways support abundant epibenthic invertebrates, such as amphipods and crayfish, which have become a dominant food source for adult demersal and piscivorous fish. Fishes that are obligate to the pelagic web will likely continue to decline, although fishes able to use the detrital pathway may be more robust. Fishes with pelagic larvae may be vulnerable to recruitment failures if they are unable to obtain planktonic food during the critical period of their ontological development. Options for increasing pelagic production at large scales are limited, but may include management of clams, nutrient ratios, and off-channel habitat subsidies. Restorations at small to intermediate scales may produce pelagic food, but volumetric constraints will limit the extent of subsidies. Creating spatial opportunities where pelagic and detrital food webs can re-integrate may offer some opportunities for local recruitment, and species able to use localized detritally-based webs will benefit strongly from such activities.

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SAN FRANCISCO ESTUARY & WATERSHED SCIENCE
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RESEARCH

# A Conceptual Model of the Aquatic Food Web of the Upper San Francisco Estuary

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## ABSTRACT

Aquatic trophic interactions in the upper San Francisco Estuary are synthesized here as a conceptual food web model, using over 35 years of scientific research, and highlighting key uncertainties for restoration. The food web was created as part of the Delta Regional Ecosystem Restoration Implementation Program to evaluate the benefits of restoration actions. Historic changes to the hydrology and geomorphology of the region have decreased ecosystem resiliency. More recently, pressures from water export, alien species introductions, and nutrient loading have disrupted the food web and increased the vulnerability of pelagic and juvenile fishes. One of the key features of the contemporary food web is a decoupling of pelagic and the detrital pathways. Low production and high mortality of phytoplankton since the 1980s have led to declines of pelagic organisms, including zooplankton, mysids, and planktivorous fish. In contrast, detrital pathways support abundant epibenthic invertebrates, such as amphipods and crayfish, which have become a dominant food source for adult demersal and piscivorous fish. Fishes that are obligate to the pelagic web will likely continue to decline, although fishes able to use the detrital pathway may be more robust. Fishes with pelagic larvae may be vulnerable to recruitment failures if they are unable to obtain planktonic food during the critical period of their ontological development. Options for increasing pelagic production at large scales are limited, but may include management of clams, nutrient ratios, and off-channel habitat subsidies. Restorations at small to intermediate scales may produce pelagic food, but volumetric constraints will limit the extent of subsidies. Creating spatial opportunities where pelagic and detrital food webs can re-integrate may offer some opportunities for local recruitment, and species able to use localized detritally-based webs will benefit strongly from such activities.

## KEY WORDS

Sacramento–San Joaquin Delta; Suisun Bay; San Francisco Estuary; foodweb; pelagic; detritus; invertebrates; fish; restoration; Pelagic Organism Decline

## INTRODUCTION

Restoration of aquatic habitat in the upper San Francisco Estuary (the estuary) is being planned in hopes of reversing historic declines of native fish (Herbold et al. 2014). Much of the success of these projects will hinge on whether restoration can provide food and refuge across the life cycle of these organisms, improving trophic interactions that are currently impaired. The anthropogenic degradation of the ecosystem of the modern estuary has proceeded by stages (Lund et al. 2007). In the 19th century, the estuary was transformed by the influx of gold mining sediments, the reclamation of emergent marsh to agriculture, and the straightening and hardening of slough habitat for flood control. The resulting simplified hydrology and geomorphology benefited development, but amounted to a loss of aquatic habitat and ecosystem resiliency, leading to the extinction of the endemic thicktail chub (*Gila crassicauda*) by the early 20th century (Miller et al. 1989).

Many subsequent aquatic stressors have accompanied development of central California. The highly modified landscape of the upper estuary has less ability to absorb ecosystem stressors because of the loss of habitat heterogeneity (Moyle et al. 2010). But because scientific monitoring of the system did not begin until the 1960s, the initial and irreversible loss of ecosystem resilience is difficult to separate from subsequent stressors that have led to sometimes puzzling and precipitous declines in native and introduced species alike.

These declines correspond with changes in multiple environmental conditions, including droughts, increased water diversions, flow pattern changes, nitrogen inputs, pesticide use, and alien species introductions (Mount et al. 2012). Decreased food reliability and quality for planktonic species have almost certainly resulted from a mix of recent and historic stressors (Meng and Orsi 1991; Orsi and Mecum 1996; Müeller–Solger et al. 2002; Winder and Jassby 2010). A decrease in pelagic production in the 1980s is ascribed to the invasion of the clam *Potamocorbula amurensis*. In the 2000s, another steep decline in pelagic production and fishes became known as the "pelagic organism decline," (POD) and remains not fully explained. It includes special-status native fishes such as delta smelt (*Hypomesus transpacificus*) and longfin smelt (*Spirinchus thaleichthys*), and naturalized species such as striped bass (*Morone saxatilis*) and threadfin shad (*Dorosoma petenense*) (Sommer et al. 2007; Mac Nally et al. 2009). Other native and endemic fishes are in decline, including winter-run Chinook salmon (*Oncorhynchus tshawytscha*) and southern green sturgeon (*Acipenser medirostris*). In contrast, a suite of introduced centrarchid fishes have become abundant and may prey upon or compete with native fishes (Turner 1966; Grimaldo et al. 2004; Brown and Michniuk 2007).

Implementation of regional restoration is expected to increase the capacity of the aquatic food web to support pelagic fishes (Herbold et al. 2014). However, uncertainty remains about the scale and direction of the response of the food web to restoration. The following qualitative conceptual model of the aquatic food web of the upper estuary, including Suisun Bay and the Sacramento–San Joaquin Delta (the Delta), was produced to assist conservation and management decisions (Gilbert 1980; Mills et al. 1993; Polis et al. 1997). It synthesizes over 35 years of ecosystem research into the Driver–Linkage–Outcome format used in the Delta Regional Ecosystem Restoration Implementation Program (DRERIP) (DiGennaro et al. 2012). To manage complexity and help isolate uncertainties, the model has been divided into seven separate diagrams that emphasize: abiotic drivers (Diagram 1); nutrient supply to phytoplankton (Diagram 2); primary production to grazers (Diagram 3); detrital and microbial production to grazers (Diagram 4); secondary production to predators (Diagram 5); piscivory (Diagram 6); and an overall synthesis (Diagram 7). Incorporating food web knowledge into habitat restoration and management decision may help to clarify goals and expectations while optimizing benefits.

## METHODS

### Study System

The trophic interactions of the low-salinity and tidal freshwater aquatic habitats of the upper estuary are described here. The physical geography of this region includes the Sacramento–San Joaquin Delta; the confluence of the Sacramento and San Joaquin rivers; and Suisun Bay and Marsh. There are distinct regional differences in the upper estuary (Whipple et al. 2012; Durand 2014). The north Delta is an ebb-dominated tidal system influenced by fresh water flows from the Sacramento River and the Yolo Bypass. It supports a mix of native and alien species that respond to seasonal and annual changes in flow, including anadromous and migratory fish. The south Delta relies on freshwater inputs from the San Joaquin River and cross-Delta diverted flows from the Sacramento River, which are then subject to export. The region is characterized by low flows and high residence time, resembling a tidal lake. It is dominated by invasive organisms, including the Asian clam *Corbicula fluminea*, invasive aquatic weeds, and alien centrarchid fishes such as largemouth bass (*Micropterus salmoides*). The western Delta and Suisun Bay are characterized by the interaction of fresh water flows with tidal marine influences, creating a brackish estuarine mixing zone. Brackish water limits the westward range of *C. fluminea*, which is supplanted by the salt-tolerant overbite clam *P. amurensis*. Suisun Bay is bordered by Suisun Marsh, which is characterized by a mosaic of fresh water managed wetlands and brackish tidal channel networks, and supports a diverse assembly of native and alien species (Moyle et al. 1986).

## Model Components

Ecological relationships are described using a Driver–Linkage–Outcome approach similar to that used in the DRERIP process for Ecosystem Conceptual Models (DiGennaro et al. 2012). Drivers are physical or chemical effects on food web processes. Intermediate outcomes are species population responses to the drivers, at different trophic levels, via the associated linkages. Fish population responses are the final outcomes. Linkages are the arrows in the diagrams that describe the reciprocal influence of drivers, intermediate outcomes, and outcomes.

The direction, size, color, and pattern of the linkages together describe ecological outcomes: that is, potential population increase or decrease. Linkages are imbued with attributes that describe the nature of the relationship, including the magnitude (indicated by line size); scientific understanding (line color); predictability (line pattern); and direction (arrows = positive, clubs = negative) of the effect (Figure 1). Criteria for levels were standardized for all the DRERIP models (DiGennaro et al. 2012), and adapted to the food web model (Table 1).

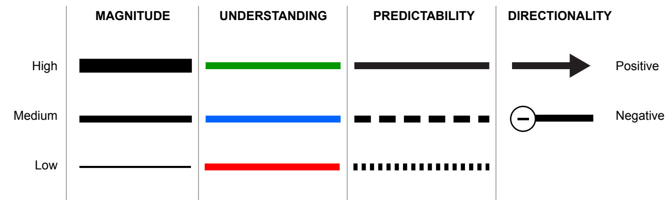

**Figure 1 Key to symbols.** Each linkage is imbued with symbols that indicate magnitude (line thickness), scientific understanding (line color), predictability (line pattern) and directionality (line terminus shape) of the effect. Positive population level effects include carbon and nutrient flows, or bottom-up effects. Negative population effects include grazing and predation, or top-down effects. Two-headed lines mean that an effect is symmetrically reciprocal. Separate lines indicate that one or more aspects of the magnitude, understanding or predictability are asymmetrical.

Each diagram represents a different trophic step, described in detail, along with relevant references to facilitate further investigation. The **blue** band on the top includes the pelagic web, the **grey** band on the bottom the detrital organic carbon web, and the white interior band includes carbon and nutrient sinks.

Populations can be understood to be limited when large clubs or many clubs are directed at them. For example, in Diagram 3, *Linkage 3.14* shows strong limitation of diatoms by bivalves. This limitation may resonate up the food web, so that the effect of *Linkage 3.11* from diatoms to zooplankton also will be limited by clam grazing, as will the effect of *Linkage 5.11* (Diagram 5) from zooplankton to plankton-feeding fishes.

Linkages refer to all sub-categories that a box may include. For example, Diagram 4, *Linkage 4.29* refers to all microzooplankton (ciliates, rotifers, etc.) in the grey and yellow box. In contrast, *Linkage 4.25* refers only to the relationship between Ciliates and *Limnoithona*.

**Table 1** Criteria for levels used in linkage [a]

| Level | Magnitude | Understanding | Predictability |
|---|---|---|---|
| Ranked linkage characteristics | Size of population response | Level of scientific understanding | The likelihood that a population will respond consistently |
| High | Sustained major population level effect; the driver contributes substantially to population productivity, abundance, or spatial distribution | Based on peer-reviewed studies from within the system and scientific reasoning supported by most experts within the system | Outcome largely unconstrained by ecosystem or external variability, or under specific conditions indicated by model |
| Medium | Sustained minor population effect | Based on peer review studies from outside the system and corroborated by non-peer-reviewed studies within the system | Outcome is dependent on ecosystem or external variability |
| Low | Effect limited to small population fraction, or minor influence on productivity, or limited spatio-temporal effects | Based on peer reviewed-research within the system or elsewhere | Outcome is greatly dependent on ecosystem or external variability |

a. Source: DiGennaro et al. 2012.

## Food Web Assumptions

Food webs are model representations of complex trophic interactions found in nature (Polis and Strong 1996; Dunne et al. 2002). From highly simplified (Elton 1927) to reticulate (Lafferty et al. 2008) models, food webs rely on simplifying assumptions about membership, currency, and feeding strategies. Topological food webs, such as the one presented here, are simplified, qualitative descriptions of interspecific interactions. Below are key assumptions of this model.

1. **Relative importance of linkages remains consistent.** Hydrodynamics can create periods of co-occurrence and separation among pelagic and benthic organisms, such as grazing clams and pelagic prey (Lopez et al. 2006; Thompson et al. 2008). Flows also structure interactions, as when overland flows deliver trophic subsidies (Sommer et al. 2001; Lehman et al. 2007). Periods of low flow may support phytoplankton blooms in regions of high residence time (Glibert et al. 2014). Although trophic relationships are influenced by regional, seasonal, and inter-annual availability, we assumed for the purposes of the model that the relative strength of linkages does not change.
2. **Linkages describe population-level responses.** The model captures functional trophic relationships on a population level, and summarizes understanding and uncertainties. Each linkage has a positive direction (an arrow) indicating population increase, and a negative direction (a club) indicating population decrease (Puccia and Levins 1985). The positive arrow parallels the flow of carbon and nutrients to higher trophic levels. The negative arrow generally represents predation.
3. **Linkages emphasize trophic relationships that increase or reduce food supply for fish.** Fish are integrators of ecosystem function (Vadeboncoeur et al. 2002; Vander Zanden and Vadeboncoeur 2002), and of particular importance in the estuary because of declines (Sommer et al. 2007; Mac Nally et al. 2009). Choices about inclusion in the food web were based upon direct or indirect importance to fish populations. Phytoplankton are discussed as an important food pathway to pelagic grazers. Zooplankton are important to nearly all species of juvenile fishes and to planktivorous and filter-feeding adult fishes. The invasive clams *P. amurensis* and *C. fluminea* are included because of their known impact on phyto- and zooplankton populations (Kimmerer 1996, 2006). Epibenthic invertebrates are included because they are well-represented in fish diets, and because of evidence that amphipods have replaced the native mysid (*Neomysis mercedis*) as an important food source (Kjelson and

Fisher 1982; Feyrer et al. 2003; Dean et al. 2005; Nobriga and Feyrer 2008; O'Rear 2012).

4. **No distinctions are made between native and alien species.** Introductions of alien species to the estuary have been occurring since the early 1800's, such that alien species make up 40% to 100% of species, 97% of the total number of organisms, and up to 99% of the biomass in certain habitats of the estuary (Cohen and Carlton 1998). The effect of introduced invertebrates ranges from complete integration to the food web (the copepod *Pseudodiaptomus forbesi*), to deep disruption (the overbite clam *P. amurensis*). Because possibilities for removal of established aliens are often limited (Kimmerer 2004), the food web includes species currently naturalized to the upper estuary, regardless of origin.

## FOOD WEB DIAGRAMS

### Diagram 1—Main Physical Drivers

Estuaries are defined by the hydrodynamics of freshwater and saltwater across geomorphic structure (Elliott and McLusky 2002; Potter et al. 2010). Complex hydrodynamics affect nearly every aspect of the food web (Weissburg and Zimmer–Faust 1993; Kimmerer et al. 1998; Kimmerer 2002; Jones et al. 2009; Enright 2010, unreferenced, see "Notes"). Unlike physical structure, hydrodynamic features change with inflow and tides (Monismith et al. 2002; Enright 2008, 2010, unreferenced, see "Notes"). Differences in physical mobility change the manner in which organisms confront their environment: planktonic organisms are subject to tidal movement, and are less subject to abrupt changes in water quality; benthic organisms are less affected by tide, but must cope with water quality changes (Kimmerer et al. 2001; Kimmerer 2004).

### *1.10 Hydrodynamics*

Estuarine hydrodynamics result from the interaction of directional fresh water inputs and bi-directional, tidally-driven marine influences (Potter et al. 2010), affecting turbidity, salinity, water quality, and stratification, as well as the transport of water quality constituents and nutrients (Elliott and McLusky 2002). There are large, well-understood, and predictable direct effects of hydrodynamics (*Driver 1.10*) on pelagic food web constituents, including phytoplankton (*Linkage 1.11*), zooplankton (*Linkage 1.12*), planktonic fish (*Linkage 1.13*), microbial organisms (*Linkage 1.14*), and detritus (*1.15*). The effect of hydrodynamics on pelagic hydromedusae may be of moderate importance, understanding, and predictability (*Linkage 1.16*). Hydrodynamic effects of key importance are residence time and its obverse, transport (Herrgesell et al. 1981; Kimmerer 2002a, 2002b; Moyle et al. 2010). Long residence times can induce blooms of phytoplankton and zooplankton by retaining organisms in a suitable environment. Extended residence time can also contribute to bloom cessation, when nutrients are drawn down below the Redfield ratio (an indicator of productive capacity, indicated by the molar ratio of $^{106}C:^{16}N:^{1}P$ [Redfield 1958]). Shorter residence times imply increased transport of nutrients and organisms within or out of the estuary. In the estuary, the magnitude of water movement by tidal action is generally much greater than the magnitude of flow (Schoellhamer 2000, 2002; Kimmerer 2004). Because of this, tidal dynamics slow net flow through the upper estuary during much of the year, thereby increasing residence times.

Estuarine turbidity maxima (ETMs) are mixing zones that result from interactions between suspended particles, fresh and brackish water, and geomorphic complexity (Cloern 1996). Mixing zones retain sediment, phytoplankton and zooplankton, creating opportunities for trophic linkages to occur in that space (Fisher et al. 1988). ETMs can occur at multiple locations, and move tidally. The western end of Suisun Bay has a geographically fixed ETM as the result of flows interacting with a sill near Benicia (Schoellhamer 2000).

Tidal exchange is the amount of water that is advected in and out of a slough by tidal action (Williams et al. 2002; Williams and Orr 2002; Ritter et al. 2008). As tidal magnitude varies, so too will the tidal exchange of any given slough or region, creating changing residence times across the tidal cycle and across different landforms. This pattern of mixed residence times allows biological production

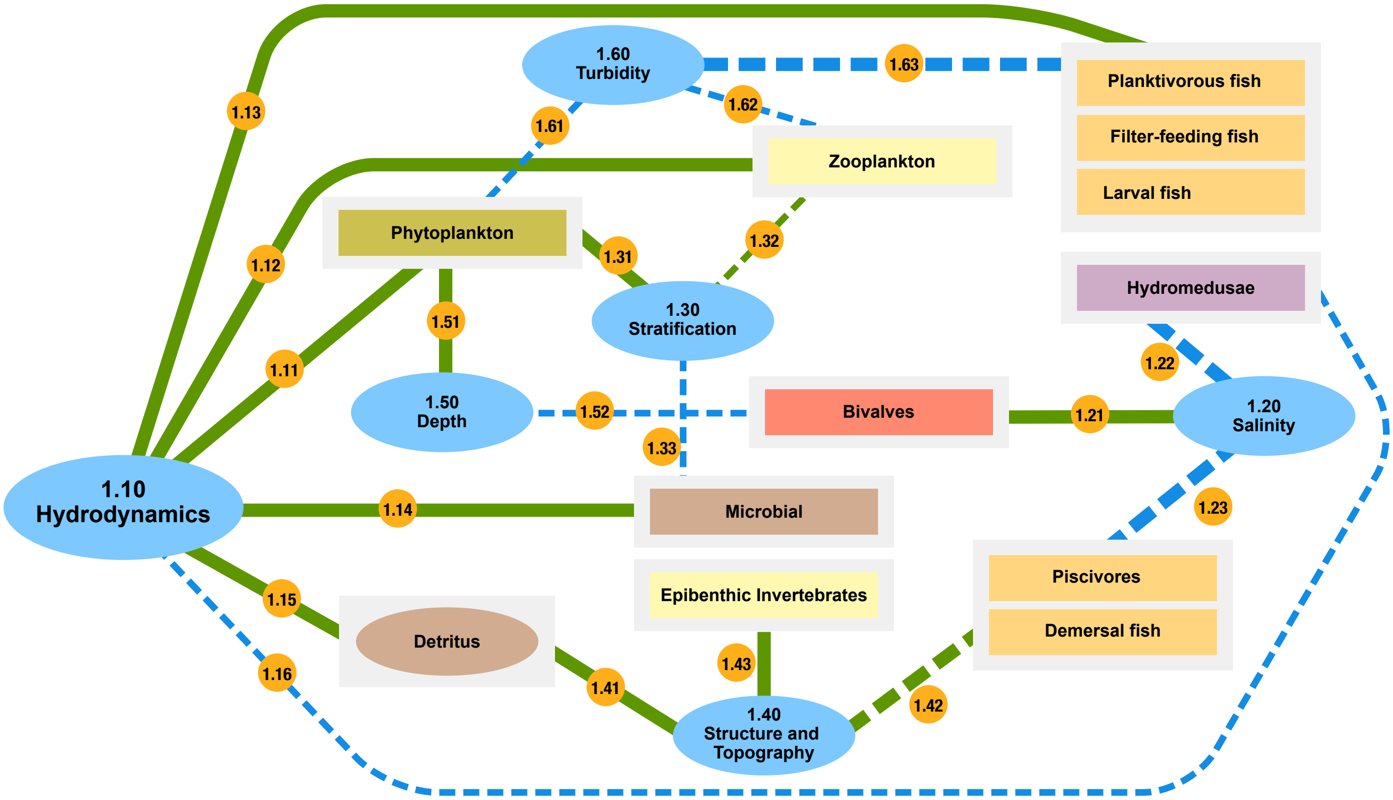

**Diagram 1 Physical drivers and biotic responses.** Key drivers are Hydrodynamics, Salinity, and Structure, and Topography. Lines indicate dominant linkages. Directionality omitted because each physical driver may have positive, negative, or non-linear influence on outcomes.

to be accumulated and then exported, with periodic exchanges of new water and nutrients (Enright 2008, unreferenced, see "Notes"; Enright et al. 2013). The channelization of sloughs for flood control shortens them relative to tidal excursion. As a result, water and particles in these sloughs likely have greatly reduced residence times, allowing for little biomass accumulation, as constituents are more rapidly advected away (Enright 2006, unreferenced, see "Notes").

Hydrodynamics in the Delta create high-nutrient, low-velocity, low-turbidity, warm-water environments that support harmful algal blooms (largely *Microcystis sp.*) (Jacoby et al. 2000; Lehman et al. 2005, 2008) and the establishment of nuisance aquatic vegetation (largely *E. densa* and *Eichhornia crassipes*) (Brown and Michniuk 2007; Sousa et al. 2009, 2010; Yarrow et al. 2009). Stands of *E. densa* alter the physical structure of Delta channels and support the colonization of non-native fishes such as sunfish (*Centrarchidae*), which are often able to outcompete or prey upon native fishes (See 2.30 Structure, below) (Grimaldo and Hymanson 1999; Grimaldo et al. 2004; Nobriga et al. 2005; Nobriga and Feyrer 2007; Ferrari et al. 2014).

Water diversions occur throughout the Delta for urban and agricultural use (Nichols et al. 1986). In-Delta diversions are numerous, and remove and return large quantities of water (Lund et al. 2007). The principal water exporters are the state and federal pumping facilities in the south Delta. Along with water, these facilities remove nutrients, primary and secondary production, and fish. The magnitude of these exports periodically reverses flow in the Old River and Middle River branches of the San Joaquin River, and redirects water from the Sacramento River across the Delta to the south. Non-diverted fresh water, nutrients and production leave the Delta as outflow via Suisun Bay (Kimmerer 2004).

Changes in direction of flow from a seaward direction to a cross-Delta direction may have the largest effects on Suisun Bay, which receives less flow since large diversions began in the 1960s (Moyle et al. 2010). This may have reduced turbidity and food availability in the Suisun region. If plankton production is density-dependent, then removal by export or outflow may be replaced by in situ productivity. If production is not density-dependent, then export may result in lower phytoplankton and zooplankton abundance. Considerable uncertainty remains about this problem (Jassby et al. 2002; Kimmerer 2002a, 2002b; Kimmerer 2004; Jassby 2008; Kimmerer et al. 2009).

## 1.20 Salinity

Salinity (*Driver 1.20*) shows an important, well understood, and predictable linkage to bivalves (*1.21*), and important, moderately understood, and moderately predictable linkages to hydromedusae (*1.22*), piscivores, and demersal fish (*1.23*). Although virtually all organisms in the estuary respond to salinity, shifting distribution and abundance as salinity changes, organisms with a stationary life stage are more vulnerable to halide stress.

Salinity defines the aquatic structure of an estuary by influencing hydrodynamics, including stratification, circulation, and mixing zones (Kimmerer 2002b; Kimmerer 2004). Salinity generally decreases in the landward direction, although some low flow regions near the Stockton deep water ship channel and the Sacramento Deep Water Ship Channel may exhibit inverted patterns of salinity, with increased salinity occurring landward during hot, dry periods (from evaporation of agricultural drainage water) (Conomos et al. 1985).

Estuarine assemblages are dominated by species that can tolerate some osmotic stress. Species diversity may be high because salinity can form a gradient within which different species may coexist without direct competition or interference (Wagner 1999; Martino and Able 2003). Seasons or years of high fresh water outflow expand low-salinity or freshwater habitat (Kimmerer 2004). The converse occurs during low flows; low-salinity habitat can become very limited where the Sacramento River becomes constrained by geomorphology and levees. This expansion or contraction may affect both planktonic and fixed organisms (Moyle et al. 2010, but see Kimmerer et al. 2009).

Generally, salinity changes are most stressful on stationary benthic organisms. These organisms may be subjected to tidal or seasonal shifts in salinity that limit their range or their ability to forage and reproduce (Kimmerer 2004). Both of the invasive clams *P. amurensis* and *C. fluminea* are reciprocally limited by salinity: the former by fresh water (below ~2 psu) and the latter by brackish water (above ~2 psu) (Carlton et al. 1990; Nichols et al. 1990; Hymanson et al. 1994). The mechanism of limitation is thought to act on the recruitment stage, when clam larvae are most vulnerable to halide stress; adults have mechanical and physiological mechanisms to resist salinity stress (Paganini et al. 2010; Miller and Stillman 2013; Miller et al. 2014). Clam management using salinity will require varying salinity at critical times and for extended durations, and the contraction of one population may be met with the expansion of the other complementary population. Other species may be more readily constrained by salinity. The aquatic plants *E. densa* and *E. crassipes* are limited to the mostly freshwater region east of Browns Island (Haller et al. 1974; Hauenstein and Ramirez 1986).

## 1.30 Stratification

Stratification (*Driver 1.30*) has an important, well understood and predictable effect on primary productivity (*Linkage 1.31*), by maintaining phytoplankton in the photic zone, above the critical depth at which mixing below the surface causes a net loss of production through respiration (Cloern 1996). Stratification can also insulate against bivalve grazing, and accelerate the draw-down of ammonium ($NH_4$) (Diagram 2, *Linkage 2.33*), both of which can otherwise interfere with bloom formation. Figure 2 shows how different stratification depths can affect net primary production (Lucas et al. 2002).

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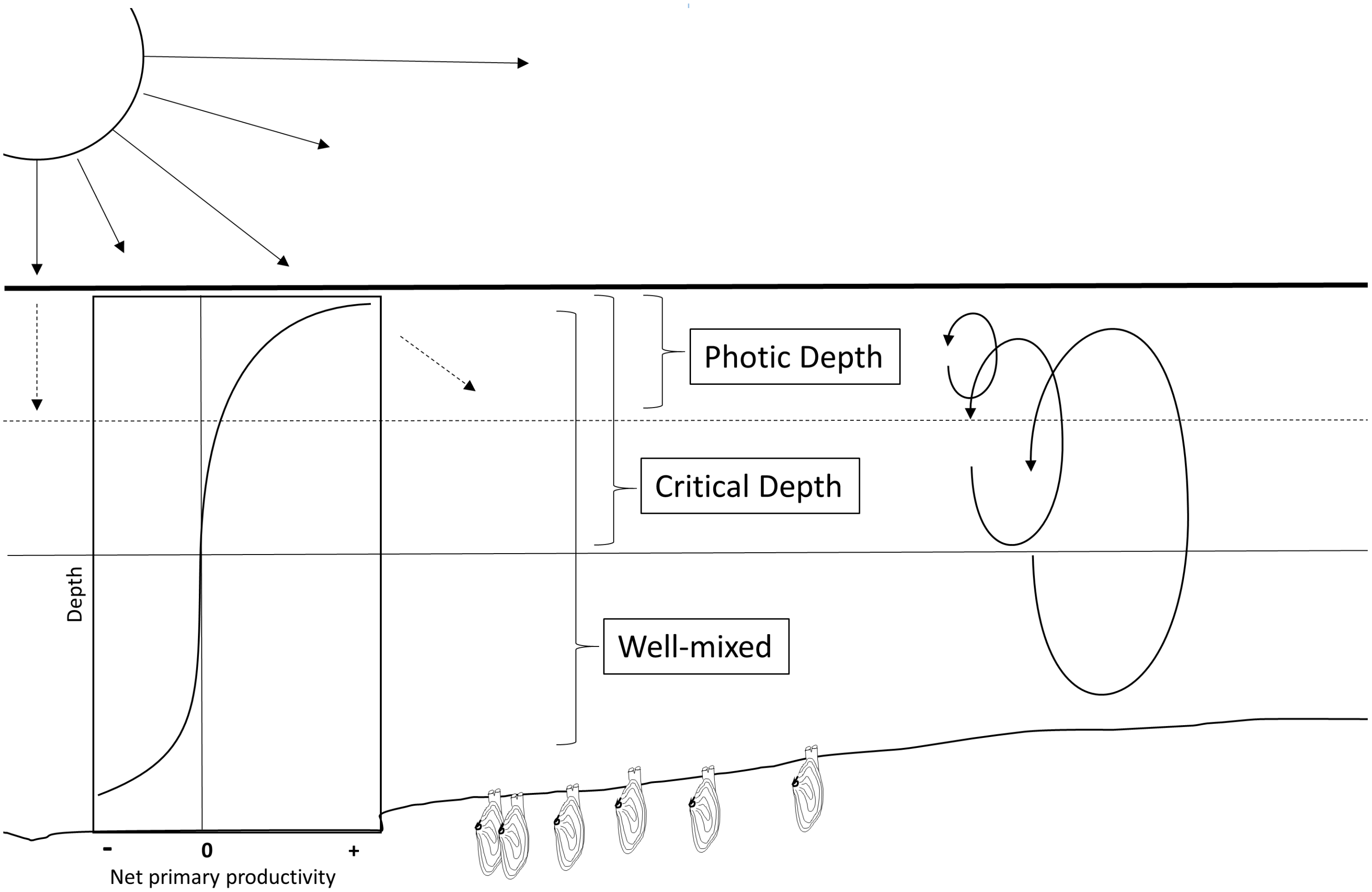

**Figure 2 Effects of stratification, mixing, and grazing on phytoplankton production.** Photic depth is the depth to which photosynthetically active radiation can penetrate, supporting active photosynthesis in phytoplankton. Sverdrup critical depth is the depth at which mixing of phytoplankton causes photosynthesis and respiration to balance, resulting in zero net primary production. When the water column is vertically well-mixed, phytoplankton productivity may become negative (i.e., respiration exceeds photosynthesis), high mortality may occur from clam grazing, and ammonium draw-down cannot occur. Stratification isolates phytoplankton in the upper water column, facilitating blooms.

Because the doubling time of diatoms (a particularly nutritious form of phytoplankton) occurs on the order of days, stratification must exist for at least a few days to promote bloom formation (Kimmerer 2004). The linkage with zooplankton (*1.32*) is of moderate importance, and although it is well understood, it has only moderate predictability because the response time of zooplankton is much greater than the response time of phytoplankton. The linkage to microzooplankton (*1.33*) is expected to function similarly to that for zooplankton, but there is less scientific understanding of this relationship. Zooplankton and microzooplankton may benefit from stratification when phytoplankton food sources become concentrated (Lopez et al. 2006; Cloern 2007).

### *1.40 Structure and Topography*

Geomorphology constrains tides and flows, creating the complex hydrodynamics that typify an estuary, including salinity gradients, residence time variation, mixing zones and stratification (Enright et al. 2013). At large scales, the geomorphology of the estuary creates distinct ecological regions (Whipple et al. 2012). These regions are separated by long straits (Sacramento River, Carquinez Strait) that provide corridors for species such as Sacramento splittail (*Pogonichthys macrolepidotus*), migrating salmonids, smelt, and sturgeon (Kjelson and Fisher 1982; Schaffter and Kohlhurst 1997; Moyle et al. 2004; Feyrer et al. 2005; Sommer et al. 2011).

Structure at intermediate scales includes floodplains, wetlands, and ponds, which may have local effects on salinity, turbidity, stratification, residence time, temperature, productivity and dissolved oxygen (Enright and Culberson 2009; Lehman et al. 2009; Enright et al. 2013). For example, emergent wetlands influence local water quality and food production (Simenstad et al. 1999; Howe and Simenstad 2007, 2011). Ponds can create low dissolved oxygen conditions in adjacent sloughs, or export food subsidies (O'Rear and Moyle 2010; O'Rear 2012). Floodplains (such as the Yolo Bypass or Cosumnes River) may provide large seasonal food subsidies to the Delta in the form of detritus (derived from aquatic and terrestrial vegetation), phytoplankton and zooplankton (Sommer et al. 2001; Lehman et al. 2007). The Sacramento River, as the largest single input into the upper estuary, has large regional influence, and is likely a major source of detrital subsidies to the region (Jassby 2008) (*Linkage 1.41*).

On small scales, physical structure such as gates, pilings, submersed aquatic vegetation (SAV) and large wood offer opportunities for both resident and non-resident fishes to forage and find habitat (*Linkage 1.42*). Centrarchid fishes use vertical structure like woody debris and vegetation for refuge and foraging (Grimaldo and Hymanson 1999; Nobriga et al. 2005; Ferrari et al. 2014); catfish create burrows in muddy banks (Moyle 2002); and striped bass probably use flow fronts and eddies created by water flow against structures (2013 in-person conversation with T. O'Rear, unreferenced, see "Notes").

Wood benefits native and non-native fishes by providing structure for both hunting and hiding (Everett and Ruiz 1993; Robertson and Crook 1999). Wood is rare in the estuary because most waterways are maintained for transit by various government agencies, and many levees are required to be free of trees to meet federal flood-control standards. Most hard physical structure is in the form of riprapped levees, which favor benthic fishes such as prickly sculpin (*Cottus asper*) and gobies (*Gobiidae*) (unpublished data); and to a lesser degree by pilings and docks, which favor predators such as sunfish, largemouth bass, and striped bass (Helfman 1981; Hurst and Conover 2001).

Structure provides substrate to many epibenthic invertebrates (*Linkage 1.43*). Invertebrates like corophiids and other amphipods colonize nearly all hard structure, and a variety of aquatic epiphytic invertebrates colonize vegetation (Brown and May 2000), leading to foraging opportunities for organisms at higher trophic levels (Everett and Ruiz 1993; Robertson and Crook 1999; Sindilariu et al. 2006).

Once established, *E. densa* facilitates non-native fishes to the exclusion of most natives (Grimaldo and Hymanson 1999). It exerts strong physical control over the system; dense stands can slow flow, increase temperature, and reduce turbidity. Alien largemouth bass and other centrarchids use *E. densa* for foraging, outcompeting native fishes (such as Sacramento perch, *Archoplites interruptus*) (Moyle 2002), or directly preying upon them (such as splittail) (Brown 2003).

### 1.50 Depth

Depth (*Driver 1.50*) can regulate the circulation of phytoplankton below the photic zone, creating differences in production between shallow and deep water (*Linkage 1.51*) (Lucas et al. 2002). Because photosynthetically active radiation (PAR) attenuates as a function of water depth and turbidity, the rate of photosynthesis declines with depth. As photosynthesis decreases, net productivity decreases, eventually becoming negative because of plant respiration. The depth at which net photosynthesis is equal to net respiration is called the critical depth (Sverdrup 1953; Lucas et al. 1998). In shallow areas, phytoplankton are usually maintained above the critical depth, resulting in net production. In deeper water, phytoplankton may circulate below the critical depth and lose carbon through respiration, unless stratification occurs. Biomass accumulation in shallow water may

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SIDEBAR 1

### Key Uncertainties: Physical Drivers

- The effect of physical transport across boundaries of spatially distinct regions of localized production (from ponds, floodplains, etc.) on pelagic production
- The disposition of ETMs in the upper estuary and their effect on localized food webs
- The effect of water diversions and export on nutrient concentration, phytoplankton and zooplankton abundance
- The effect of small-scale structure on predation and refuge-seeking
- Physical limits on clam distributions
- Regional differences in turbidity and food web effects

be preserved by a trophic cascade in which foraging sturgeon, splittail, and diving ducks limit clam abundance and release grazing pressure on phytoplankton (Richman and Lovvorn 2004) (*Linkage 1.52*). Shallow water production that is exported to deeper channels may subsidize those lower-production, heterotrophic environments (Lucas et al. 2002; Lopez et al. 2006).

### *1.60 Turbidity*

Turbidity (*Driver 1.60*) is a measurement of light attenuation through the water column by sediment, organic matter, phytoplankton, or any other advected material. Turbidity is generally decreasing in the estuary (i.e., clarity is increasing), as historic hydraulic mining sediments continue to be removed and new inputs are limited (Wright and Schoellhamer 2004). There are distinct regions of turbidity differences in the upper estuary (Durand 2014). The lowest turbidity values are found in the central Delta, which are on average < 10 NTU. The highest values are found in the north Delta and Suisun Marsh, and average well over 30 NTU. However, turbidity has large seasonal variability, with lower values in summer.

Turbidity is of moderate importance to phytoplankton (*Linkage 1.61*) and zooplankton (*Linkage 1.62*). High turbidity can decrease the photic zone and the critical depth, resulting in lower rates of net primary production (Cloern 1987). However, phytoplankton blooms have tended to decrease at least since 2000, in spite of low turbidity, suggesting that phytoplankton are limited by some other mechanism (Kimmerer 2004). Some organisms, including planktivorous fish (*Linkage 1.63*) may rely upon turbidity for foraging and protection from predators (Bennett and Burau 2015). For example, delta smelt may use turbidity to assist with visual discrimination of prey during feeding (Lott 1998; Nobriga 2002; Baskerville–Bridges et al. 2003).

## Diagram 2—Nutrient Supply to Phytoplankton

Nutrient supply is one of many factors that control the rate of production. Hydrodynamics control transport and residence time of nutrients and phytoplankton. Uptake rates of nutrients are influenced by light availability and attenuation from depth and turbidity. Stratification can control both the refresh rate of nutrients and the circulation of phytoplankton below the photic zone. Despite nutrient availability, the upper estuary has relatively low phytoplankton production and biomass compared to other estuaries (Boynton et al. 1982; Nixon et al. 1986; Jassby et al. 2002; Wilkerson et al. 2006). The cause of this continues to be debated, but it is probably a function of multiple, interacting stressors including: historic loss of shallow water habitat and dendritic channel networks, as well as contemporary changes to turbidity, hydrodynamics, water export, benthic grazers, and nutrient loading (Mount et al. 2012).

Phytoplankton in the upper estuary are dominated by diatoms and microflagellates (Lehman and Smith 1991; Müeller–Solger et al. 2002). *Linkage 2.11* shows the important, well understood, and predictable effect of silica on diatoms and the small reciprocal effect of diatoms on silica. *Linkages 2.21* and *2.22* show the important, well understood and predictable effect of nitrate ($NO_3$) on diatoms and microflagellates, with small reciprocal effects. Regions downstream of the Sacramento River are generally

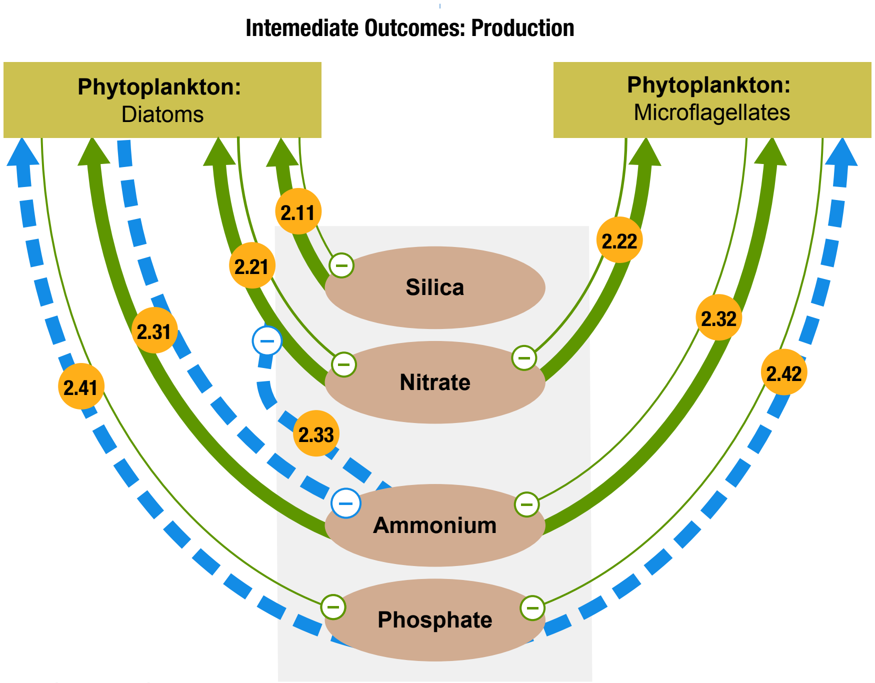

**Diagram 2** Nutrient supply to phytoplankton

unlimited by nitrogen because of anthropogenic inputs deriving primarily from waste water treatment facilities (WWTFs) (Hager and Schemel 1992). This may not be the case north of the confluence of the Sacramento River and the Sacramento Deep Water Ship Channel (SDWSC), around Liberty Island, where nutrient inputs may be more limited (2014 in-person conversation with R. Dahlgren, unreferenced, see ”Notes”). Areas with limited exchange or high uptake may have sufficient resident time to draw down nutrients, slowing primary production.

*Linkages 2.31* and *2.32* show uptake of $NH_4$ by diatoms and microflagellates. $NH_4$ has increased in the upper estuary since the Clean Water Act of 1972, as a result of required secondary treatment at WWTF’s (Jassby 2008). $NH_4$ may inhibit diatom use of $NO_3$ through a mechanism of preferential uptake (*Linkage 2.33*) (Dugdale et al. 2007), but diatoms exhibit lower rates of production when using $NH_4$. The threshold value for $NO_3$ inhibition in the estuary occurs at $NH_4$ concentrations greater than $1\,\mu mol\ L^{-1}$, with complete inhibition above $NH_4$ concentrations of $4\,\mu mol\ L^{-1}$. For certain phytoplankton species, particularly some diatom species, $NO_3$ uptake may be linear (or biphasic), while $NH_4$ uptake shows classical Michaelis–Menten kinetics, saturating at concentrations above $5\,\mu mol\ L^{-1}$ $NH_4$. Thus, when other conditions are favorable for growth, phytoplankton may still contend with high $NH_4$ concentrations, which inhibit access to $NO_3$, keeping N uptake and biosynthesis low, and disrupting the formation of blooms (Dugdale et al. 2007). Optimal conditions for diatom production may occur only during stratification of the water column. Since stratification isolates the water body, phytoplankton $NH_4$ draw-down can occur, relieving inhibition of $NO_3$ uptake, allowing bloom formation as a result of high primary production rates. This process may occur also in embayments or sloughs, wherever a water body can become sufficiently isolated to cause plankton to draw down $NH_4$ in situ. This has become an increasingly rare event, happening in Suisun Bay only rarely since 2000, although a minor bloom occurred in Suisun Bay during 2014 (Glibert et al. 2014). Blooms can continue until they are broken up by increased flows, turbulence from wind—causing mixing—or drawdown of nutrients by the phytoplankton bloom itself.

*Linkages 2.41* and *2.42* show the important, moderately well-understood, and moderately predictable effect of phosphate ($PO_4$) on phytoplankton. The

SIDEBAR 2

### Key Uncertainties: Nutrient Supply to Phytoplankton

- Nitrogen availability in the north Delta.
- The conditions that support $NH_4$ inhibition of phytoplankton.
- Uptake of nitrogen by competing submersed, floating, and emergent wetland plants.
- The effect of nutrients, nutrient ratios, temperature and turbidity on phytoplankton
- Blooms and species composition.
- The cause of harmful algal blooms and their effect on upper trophic levels.

reciprocal effect shows the small effect of drawdown on $PO_4$, suggesting that it is unlikely to be limiting in the brackish upper estuary. However, $PO_4$ may be limiting in some fresh water regions because of high N:P ratios, resulting from secondary treatment in WWTFs. (Van Nieuwenhuyse 2007).BUnder some conditions in late summer and fall, cyanobacteria such as the noxious *Microcystis sp*. can be common (Lehman et al. 2008). Harmful algal blooms may be related to high concentrations of $NH_4$ (Lehman et al. 2010). *Microcystis* is known to be toxic to both invertebrates and vertebrates; although toxicity has been demonstrated on copepods in the laboratory, it is unknown whether it can cause population-level effects on zooplankton abundance (Ger et al. 2009, 2010).

## Diagram 3—Primary Production to Grazers

Phytoplankton are considered to be the chief engine of food production in open water bodies such as oceans, lakes, and reservoirs. In contrast, the food webs of lotic systems are driven primarily by riparian-derived allochthonous production. Estuarine aquatic food webs are a complex mix of both pelagic and intertidal marsh production (Jassby et al. 1993; Jassby and Cloern 2000; Sobczak et al. 2002, 2005).

Phytoplankton species composition probably shifts seasonally and annually with prevailing conditions, although taxonomic analysis is limited in most studies (Lehman 2000). Differences in the nutritional content of phytoplankton may affect development times, egg production rates, and recruitment success of zooplankton grazers (Müeller–Solger et al. 2002; Sobczak et al. 2002; Glibert et al. 2011). Diatoms are able to complete the general physiological requirements of many zooplankton (Müeller–Solger et al. 2002; Jassby et al. 2003).

*Linkage 3.11* shows the large, well-understood, predictable effect of diatoms on zooplankton. Although zooplankton are known to graze down blooms in some lacustrine and marine systems, zooplankton have a small reciprocal effect on diatoms in the upper estuary, largely because diatoms are limited by low production and by *Linkage 3.14*, the symmetrical, important, well-understood, predictable effect between bivalves and diatoms. This linkage represents the ability of the clams *P. amurensis* and *C. fluminea* to clear phytoplankton from the water column, limiting it for competitors. *Linkage 3.12* shows the low importance of diatoms to filter-feeding fish (such as clupeids) and a small reciprocal effect on diatoms. *Linkage 3.13* shows the moderately important, well-understood, predictable benefit of diatoms to epibenthic invertebrates, and the small effect on diatoms. Mysids feed upon diatoms during juvenile stages, but have declined since competition for phytoplankton increased with the introduction of *P. amurensis*. The amphipod *Gammarus daiberi* may use benthic diatoms in addition to other food sources.

Microflagellates, generally too small for calanoid copepods, may be used supplementally by smaller species (Gifford et al. 2007) such as the cyclopoid copepod *L. tetraspina*, as shown in *Linkage 3.21*; the reciprocal effect is minor. *Linkage 3.22* shows that microflagellates are a potentially important source of food for micro-zooplankton, including rotifers, ciliates, and flagellates, with a small reciprocal effect on the abundance of microflagellates. *Linkage 3.23* shows that microflagellates may be an important secondary food source for bivalves. The reciprocal effect of bivalves on microflagellates is potentially quite large, suggesting that bivalves are an important sink for most phytoplankton, and have a key role in limiting blooms.

Phytoplankton blooms occur when production is greater than loss to advection, grazing, or other mortality

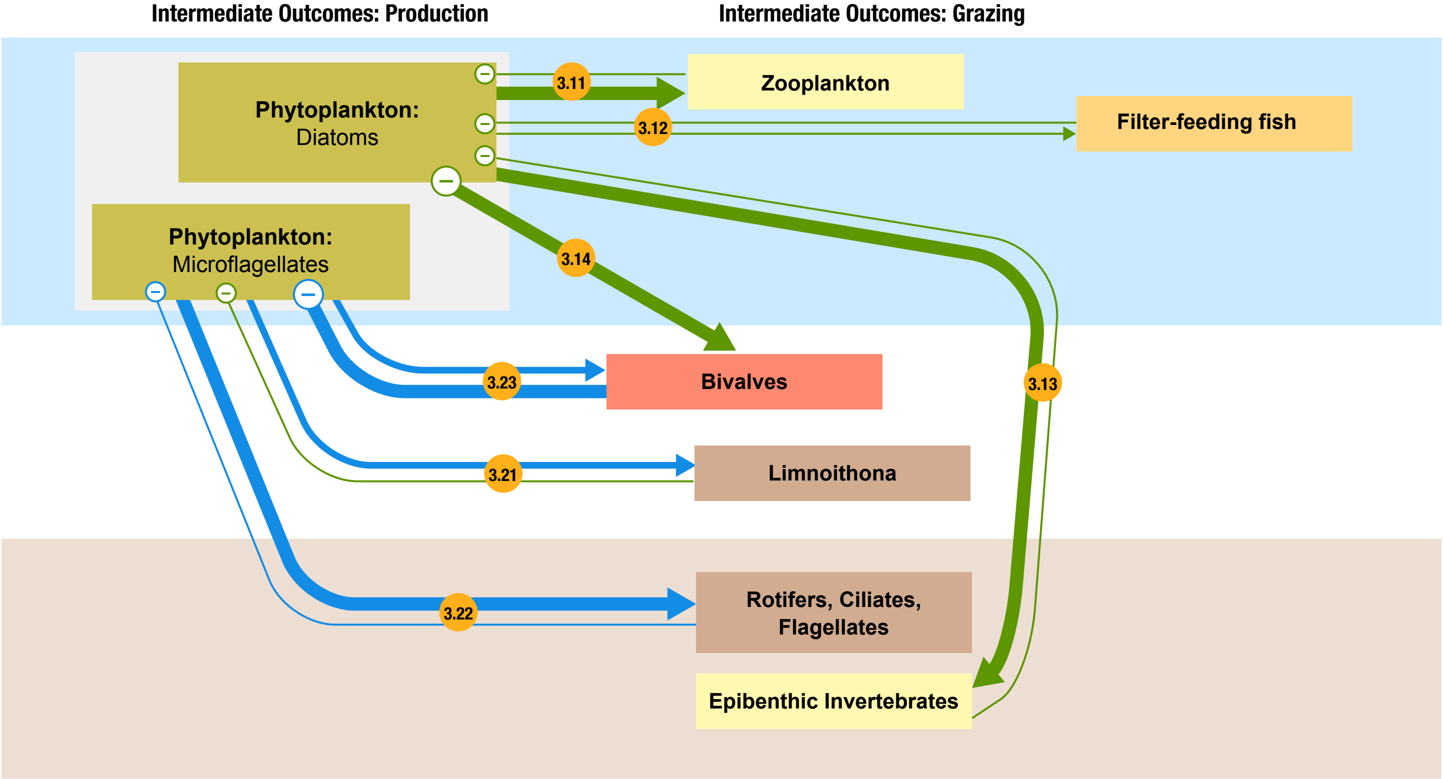

**Diagram 3** Primary production to grazers

(Cloern 1996). High abundance of phytoplankton can promote growth and reproduction for secondary producers (Carpenter et al. 1987, 2001). Maximum feeding during blooms can accelerate zooplankton survival, development, and egg production (Mullin and Brooks 1970a; Mullin and Brooks 1970b). Zooplankton are capable of grazing down blooms in lakes (Carpenter et al. 1987), but it is difficult to show similar activity in the estuary where conditions are more dynamic (York et al. 2013). However, although intensive zooplankton grazing can occur in response to phytoplankton blooms, clam grazing is persistent and chronic, and can prevent bloom formation. This is because the clams use multiple food sources, and can persist for an extended time (>6 months) without feeding (Werner and Hollibaugh 1993; Greene et al. 2011).

Phytoplankton is generally low in the upper estuary, and diatom blooms have been rare in Suisun Bay since about 1987 (Dugdale et al. 2013). Bloom formation probably requires at least some of the following conditions:

- Nutrient levels cannot be limiting. This means that a Redfield ratio of $^{106}$N:$^{16}$P:$^{1}$C must be present (Boynton et al. 1982; Cloern 1999).
- $NH_4$ may need to be lower than 4 ug $L^{-1}$. (Dugdale et al. 2007).
- Mixing below the photic zone (or critical depth) must stop, which generally implies a cessation of aeolian (wind-driven) mixing (Cloern 1987; Jassby et al. 2002; Cloern 2007; Cloern and Jassby 2010).
- Grazing pressure must be released. When grazing is intense from the invasive clams *P. amurensis* and *C. fluminea*, blooms tend not to form even when production is high, because consumption is higher than production (Alpine and Cloern 1992).

Clam grazing pressure can be released by two mechanisms. First, temporary release from pressure occurs when stratification causes phytoplankton to be confined to the upper layer of the water column and insulated from the benthos, eliminating grazing pres-

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SIDEBAR 3

### Key Uncertainties: Primary Production to Grazers

- The relative contribution of factors that suppress phytoplankton growth rates
- Relative sources of phytoplankton mortality in different regions of the Delta, Suisun Bay, and Suisun Marsh
- The effect of phytoplankton species composition on zooplankton production
- The effect of ephemeral phytoplankton blooms on zooplankton production
- The rate of consumption and dispersion of localized blooms originating in shallow water

sure during the stratification event (Alpine and Cloern 1992; Lucas et al. 2002; Thompson 2005). The second mechanism of release occurs by trophic cascade, when predation by waterfowl, sturgeon, and splittail reduces-the clam population (Poulton et al. 2002; Richman and Lovvorn 2004; Kogut 2008). Waterfowl predation explain the low abundance of clams in some shallow water areas; and it is here that potentially productive blooms may form and be "exported" to adjacent habitat (Cloern 2007). However, shoal blooms such as these are likely to be either rapidly dispersed because of the dynamic estuarine environment, or consumed in the heterotrophic deeper channels which continue to hold clams (Thompson et al. 2007).

## Diagram 4—Detrital Organic Carbon and Microzooplankton Supply to Grazers

Phytoplankton provide an efficient transfer of carbon to higher trophic levels (requiring fewer steps, with less inter-trophic energy loss). However, nearly five times as much detritus is imported into the Delta from allochthonous sources than originates from phytoplankton growth, (Sobczak et al. 2002; Sobczak et al. 2005). Allochthonous sources of detritus include carbon from marshes, agriculture, soil, pond production, WWTFs, and riparian and woodland corridors. Autochthonous sources include dead phytoplankton and zooplankton, dead aquatic vegetation (both floating and submersed), dead fish and other aquatic organisms, fecal matter and clam pseudofeces (Jassby and Cloern 2000). Most of this material is likely to be processed in the microbial food web, and possibly by some macroinvertebrates and demersal fishes.

The main direct linkages to detrital organic matter occur with microbial organisms and invertebrates. *Linkage 4.11* shows the important, but only moderately understood transformation of detritus by microbes, including bacteria, flagellates, rotifers, and ciliates. It is through this pathway that most detritus is made available to higher trophic levels, but some uncertainty remains as to how much detrital carbon becomes biologically available. Bacteria are the main consumers of detritus and dissolved organic carbon (Mann 1988; Landry and Calbet 2004), making it available in a particulate form. Bacterial production can be ingested and used by other organisms in the food web, such as ciliates (*Linkage 4.12*) and rotifers (*Linkage 4.13*) (Arndt 1993; Holst et al. 1998; Rollwagen–Bollens and Penry 2003; Gifford et al. 2007). Rotifers may also feed upon flagellates (*Linkage 4.14*).

*Linkage 4.16* shows the moderate, poorly understood use of detrital organic carbon by zooplankton; copepods may rely on a variety of food sources (Islam et al. 2005; Islam and Tanaka 2006). For example, *E. affinis* and *Sinocalanus doerri* do not use phytoplankton exclusively, supplementing their diets substantially with particulate organic matter or ciliates (Gasparini and Castel 1997; Merrell and Stoecker 1998; Gasparini et al. 1999; Islam et al. 2005). Zooplankton have a small effect on the pool of detritus. *Linkage 4.17* shows a minor reciprocal effect from detritus to *L. tetraspina*.

*Linkage 4.18* indicates that bivalves may have a symmetric, poorly understood, and moderate effect on detritus. Clams may both consume detritus and contribute to the detrital pool through pseudofeces elimination or death. *Linkage 4.19* shows the direct pathway, of minor importance, from detritus directly to demersal fishes such as catfish or suckers, which incidentally or intentionally ingest it while feeding on other organisms.

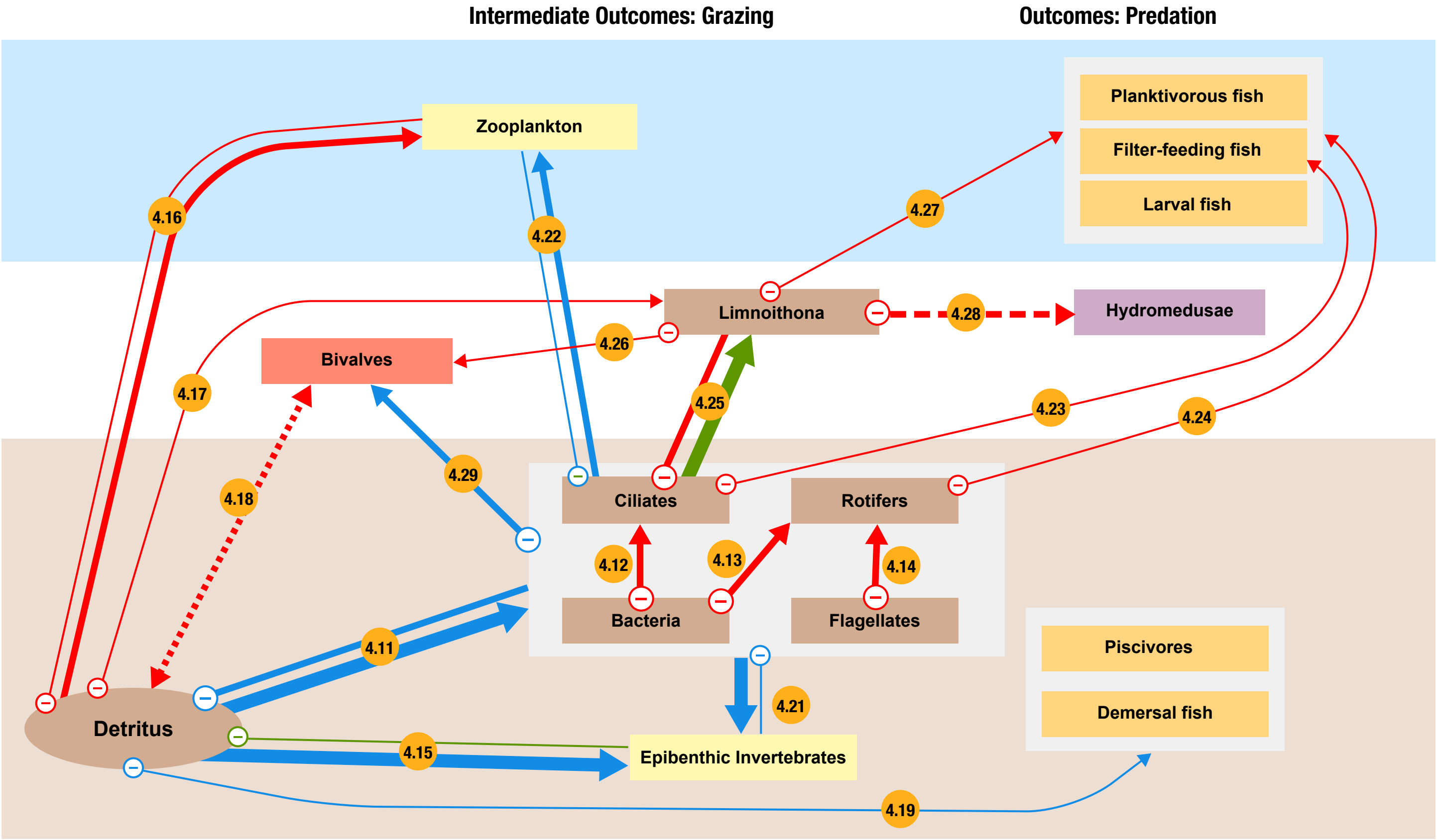

**Diagram 4** Detrital organic carbon and microbial production to grazers

Microbial organisms offer pathways to higher trophic levels through epibenthic invertebrates, zooplankton, and bivalves. The microbial loop is highly important to epibenthic organisms (*Linkage 4.21*), offering a parallel, indirect pathway to the direct pathway from detritus seen in *Linkage 4.15*. Benthic invertebrates, particularly amphipods, feed on detritus and microbes, forming an important food supply to fish (Feyrer et al. 2003). Before the decline in plankton in the 1980s, the main macroinvertebrate prey for fishes was the formerly abundant mysid *N. mercedis*, which feeds on phytoplankton and zooplankton (Orsi and Knutson 1979). This represents a shift in resource use pathways for fishes, as a response to changing food availability (Simenstad et al. 1999; Howe and Simenstad 2011).

Because of their relatively large sizes, ciliates and rotifers provide a moderate food source for both zooplankton (*Linkage 4.22*) and an occasional food source for plankton feeding fish (*Linkages 4.23* and *4.24*). *Limnoithona tetraspina* uses motile microbial prey (*Linkage 4.25*) (Bouley and Kimmerer 2006; Gifford et al. 2007), linking it to the detrital food web, rather than the pelagic (phytoplankton-based) food web. The abundance of detritally-derived carbon in the estuary may give it an advantage as an invader. Although *L. tetraspina* is the dominant copepod in the LSZ in terms of both abundance and biomass (Bouley and Kimmerer 2006), it is not well-used by bivalves (*Linkage 4.26*) or planktivorous fish (*Linkage 4.27*). This is likely because of phenology, behavior, size, or nutritive content (Sullivan 2010; Winder and Jassby 2010); whatever the underlying mechanism, *L. tetraspina* acts largely as a carbon and nutrient sink. *Linkage 4.28* suggests a pathway from *L. tetraspina* to hydromedusae, but the latter bloom unpredictably, and this relationship is poorly understood.

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SIDEBAR 4

### Key Uncertainties: Detrital Organic Carbon and Microzooplankton Supply to Grazers

- Relative contribution of pelagic and detrital carbon among feeding guilds in fish
- The function and efficiency of the microbial web in processing detritus
- Nutritional differences between mysids and amphipods
- The extent to which copepods *E. affinis* and *P. forbesi* rely upon detritally derived carbon and the microbial loop
- The extent to which clams use, recycle, and sequester detritally-derived carbon
- Contribution of aquatic vegetation, emergent marsh vegetation, agriculture, and riverine sources to bioavailable detritus

Microbial organisms form a moderately important secondary food source for bivalves (*Linkage 4.29*). This supplemental food source may prevent clam populations from becoming food-limited during periods of low phytoplankton production (Werner and Hollibaugh 1993).

## Diagram 5—Secondary Production to Predators

Invertebrates form a critical linkage from primary production and organic detritus to higher trophic levels. Pelagic invertebrates such as zooplankton are important to nearly all juvenile fishes during their first feeding. As most fish grow, they progress to larger foods, such as mysids, amphipods and other epibenthic invertebrates. Filter feeders such as American (*Alosa sapidissima*) and threadfin (*Dorosoma petenense*) shad, and planktivores such as delta and longfin (*Spirinchus thaleichthys*), smelt remain largely tied to the pelagic food web, although they use epibenthic organisms such as mysids at least periodically (Moyle et al. 1992; Feyrer et al. 2003; Feyrer et al. 2007; Slater and Baxter 2014).

*Linkage 5.11* shows the well-understood and predictable path of zooplankton to plankton-feeding fishes. Zooplankton species assembly has shifted considerably since the 1980s, when the introduced *P. forbesi* replaced the naturalized *E. affinis* as the dominant calanoid copepod in the upper estuary (Orsi and Walter 1991; Winder and Jassby 2010). By the 2000s calanoid copepods appeared to be in decline in many parts of Suisun Bay because of food limitation (Orsi and Mecum 1986; Kimmerer et al. 2005) and competition with clams for phytoplankton (Kimmerer et al. 2014); direct predation of copepod nauplii by clams (*Linkage 5.12*) (Kimmerer et al. 1994; Durand 2010); inadequate nutrition resulting from a shift in phytoplankton assembly (Winder and Jassby 2010); and advection and loss from the system by export or outflow (Kimmerer 2004). In addition, large copepods (*Linkage 5.13*), mysids (*Linkage 5.14*) and hydromedusae (*Linkage 5.15*) prey upon other zooplankton, and may have a moderate and periodic effect.

Fish declines after 2002, during the POD, appear to mirror declines in zooplankton, although it is uncertain whether the relationship is causal or merely correlative (Mac Nally et al. 2009). Presumably, low zooplankton density limits fish foraging effectiveness. Zooplankton make up an important part of most larval fish diets during the critical period of their ontogenetic development from yolk-sac larvae to juvenile stage (Nobriga 2002; Nobriga and Feyrer 2007). During this period, zooplankton blooms of sufficient magnitude must occur in proximity to larval fish to allow successful transition to the first feeding. If a juvenile fish fails to find food during this window, it will die; if a cohort is unable to find food during this stage, it may cause recruitment failure at the population level (Hjort 1926, but see Houde 2008).

As juvenile fish grow, they begin to exploit larger prey. Thus, most planktivorous, demersal, and piscivorous fish begin preying on epibenthic organisms (*Linkages 5.21* and *5.22*), in effect, switching to the detrital food web (Heubach and McCready 1963; Thomas 1967; Meng and Orsi 1991; Garz 1999; Simenstad et al. 2000; Nobriga and Feyrer 2008). Epibenthic invertebrates include amphipods, isopods, mysids, and crayfish, and appear to derive much of their support from detritus, mediated by microbes. As piscivorous fish grow, they will opportunistically take small fish when available, but gut content analyses

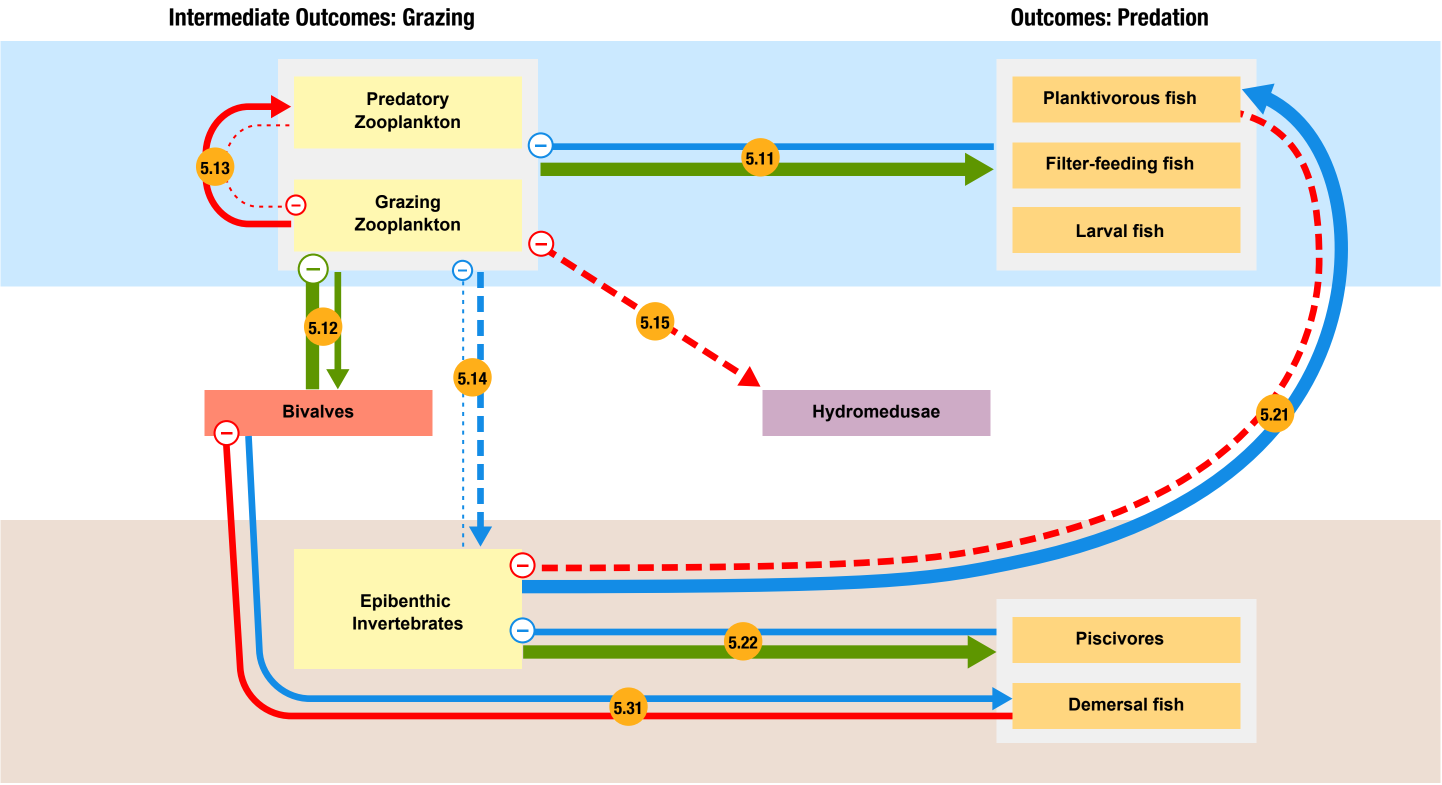

**Diagram 5** Secondary production to predators

show continued exploitation of epibenthic invertebrates, even in larger fish such as striped bass and largemouth bass. For largemouth bass, red swamp crayfish (*Procambarus clarkii*) can be the dominant food item (Simenstad et al. 2000; Nobriga and Feyrer 2007; Ferrari et al. 2014). *Linkage 5.31* shows the effect of predation by demersal fish on bivalves, which can be importantly locally, but has little control on the overall abundance of clams.

The native mysid *N. mercedis* may represent a lost link of larger epibenthic organisms to the pelagic phytoplankton-derived web (Feyrer et al. 2003). Mysids are dependent upon phytoplankton during juvenile development, switching to invertebrate prey as adults (Baldo Kost and Knight 1975). Mysid decline may be due to the decline in phytoplankton production (Orsi and Mecum 1986), competition for food with benthic grazers, loss of habitat, and competition with introduced invertebrate species (Orsi and Knutson 1979; Knutson and Orsi 1983; Orsi and Mecum 1996; Feyrer et al. 2003).

## Diagram 6—Piscivory

Fish tend to be opportunistic predators, and food resource utilization shifts with ontogenetic development and size. Although prey types have been well established for many fishes, it is difficult to predict prey preference and the ecological role of piscivores in structuring prey populations. Most fish have a Type-III functional response to prey abundance, which suggests a density-dependent relationship: fish will capitalize on highly abundant organisms until they become scarce, then switch to a more abundant food source (Kimmerer 2004). Because prey switching is common, the role of piscivores in controlling other fish populations is not well established (Nobriga and Feyrer 2007). Moreover, although predation may often be the proximate cause of mortality, the ultimate cause may be an interactive stressor on prey populations, such as ambient toxicity, loss of habitat, or food depletion (Grossman et al. 2013). The influence of predation and interactive drivers may also change regionally.

SIDEBAR 5

### Key Uncertainties: Secondary production to predators

- Predation effects and niche partitioning in calanoid copepods, particularly *E. affinis* and *P. forbesi*
- The effect of predatory *Acartiella sinensis* on calanoid copepod populations
- Spatial and temporal effects of zooplankton abundance on recruiting juvenile fish success
- The role of predators in controlling clam abundance
- The importance to fish of large invertebrates such as crayfish
- The effectiveness of amphipods as a replacement for the native mysid *Neomysis mercedis* in fish diets

Low abundance of delta and longfin smelt and other small planktonic fishes offer limited foraging opportunities to piscivores (Nobriga and Feyrer 2007; Nobriga et al. 2013), but threadfin shad probably remain a source of pelagic food for striped bass (Nobriga and Feyrer 2008). *Linkage 6.11* shows the link between smaller plankton-consuming fishes and larger piscivores and demersal fish. The linkage is probably of moderate importance to both predators and prey populations, such that predators may at times have moderate control over prey populations. Delta and longfin smelt populations are probably less affected by predation than by food limitation; although endangered salmon are likely to be limited by physical changes to the upper estuary watershed (e.g., export pumping, turbidity changes, loss of habitat) (Lindley and Mohr 2003; Nobriga et al. 2005). Outmigrating salmon smolts may be particularly vulnerable at predation hotspots, but the population-level effect on returning adults is difficult to assess in light of habitat modification and the uncertain effect of ocean conditions (Grossman et al. 2013). *Linkage 6.21* describes the linkage between palatable demersal fishes (such as gobies and prickly sculpin) and predatory fishes such as Sacramento pikeminnow, striped bass and largemouth bass (Nobriga and Feyrer 2007, 2008).

Successful threadfin shad, splittail, and salmon spawning may provide large numbers of larval fishes to predators, especially during years of high fresh water inflow (Daniels and Moyle 1983; Moyle et al. 2004; Feyrer et al. 2005, 2006, 2007). During these years, many millions of splittail juveniles are salvaged at the south Delta export pumps, suggesting high spawning potential when these fish have access to winter floodplains. Abundant larvae and juveniles are likely to provide a major source of food for other fishes such as striped bass, largemouth bass, and catfish. The alien Mississippi silversides may be an important predator of Delta smelt eggs and larvae, because of the foraging characteristics of silversides and overlap in distribution with presumed smelt spawning habitat, but no quantitative data exist (Bennett and Moyle 1996; Bennett 2005; Baerwald et al. 2012). *Linkage 6.12* shows the periodic but poorly understood availability of larval fish to planktivorous fish. *Linkage 6.13* shows the small, but poorly known and unpredictable effect of hydromedusae predation on larval fish. This effect stems in part from the tendency of hydromedusae to bloom during dry years, when spawning success is low for many fishes.

## Diagram 7—Synthesis

The upper estuary ecosystem is fueled by two food web pathways that supply asymmetrical support to fishes. The paths differ in productivity and mechanics. Although the pelagic food web is energetically efficient, it is now limited by at least two main factors: nutrient constituents that lower productivity (Dugdale et al. 2007), and benthic grazers that keep pelagic biomass low (Cohen et al. 1984; Foe and Knight 1985; Kimmerer et al. 1994; Kimmerer 2006). While the detrital food web is potentially vast, it may be energetically less efficient because of the many trophic steps required to reach fish (Canuel and Rau 1995; Jassby and Cloern 2000; Sobczak et al. 2002, 2005) and it may lack nutritive benefits provided by pelagic productivity (Müeller–Solger et al. 2002; Winder and Jassby 2010). Nonetheless, fishes that use the detrital food web as adults appear to be less

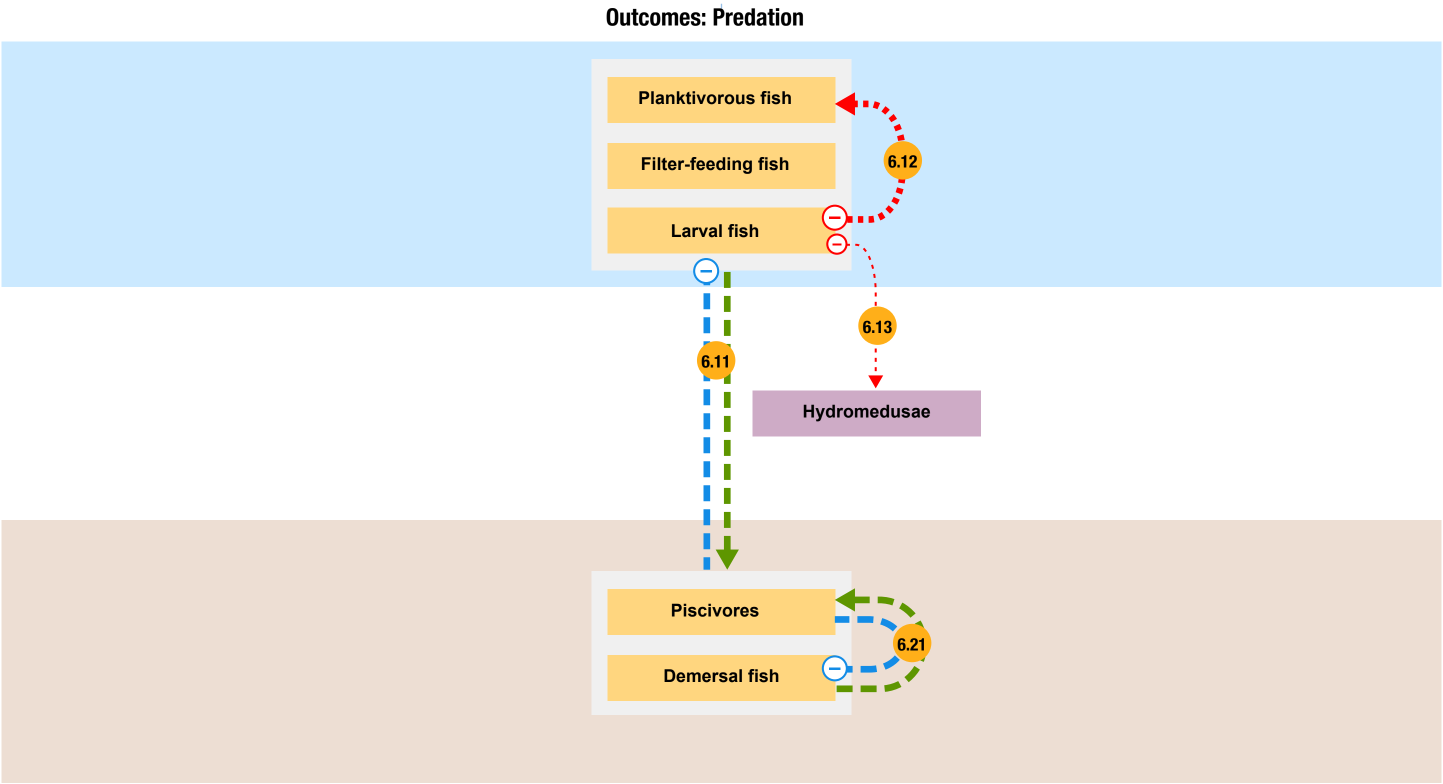

**Diagram 6** Piscivory

vulnerable than fishes that rely mainly on the pelagic web.

The traditional pelagic food web model has 3 to 4 trophic levels that contain phytoplankton–zooplankton–fish. Phytoplankton, particularly diatoms, support zooplankton (such as the calanoid copepods *E. affinis* and *P. forbesi*) (Sautour et al. 1996; Breitburg et al. 1999; Tan et al. 2004) and mysid larvae (including the once dominant *N. mercedis*) (*Linkage 3.11*) (Siegfried and Kopache 1980; Bernát et al. 1994; Froneman 2001). These planktonic invertebrates in turn support planktivorous fishes (such as delta smelt) and filter-feeding fishes (such as threadfin shad) (*Linkage 5.11*) (Kjelson 1971; Domermuth and Reed 1980; Bernát et al. 1994; Lott 1998; Feyrer et al. 2009). This pelagic web also supports larvae of fishes at the critical period in their ontogenetic development when they are transforming from the yolk stage to the first feeding stage (Nobriga 2002; Nobriga and Feyrer 2007). Larvae must be in spatial and temporal proximity to a bloom in order to successfully transform into juveniles (Hjort 1926).

However, since the 1980s, the engine of productivity has been greatly modified. Two species of bivalves rapidly expanded their range (Carlton et al. 1990; Nichols et al. 1990) and began effectively competing with zooplankton for phytoplankton (*Linkage 3.14*) (Thompson 2005), as well as preying directly on zoo-

**SIDEBAR 6**

## Key Uncertainties: Piscivory

- The place of predation as an ultimate or proximate cause of mortality
- The relative importance of piscivory in structuring prey fish populations
- The relative importance of planktivory and food limitation on prey fish populations
- The effect of interactive factors on proximate mortality from predation
- The relative importance of invertebrate and fish in the diets of predatory fish

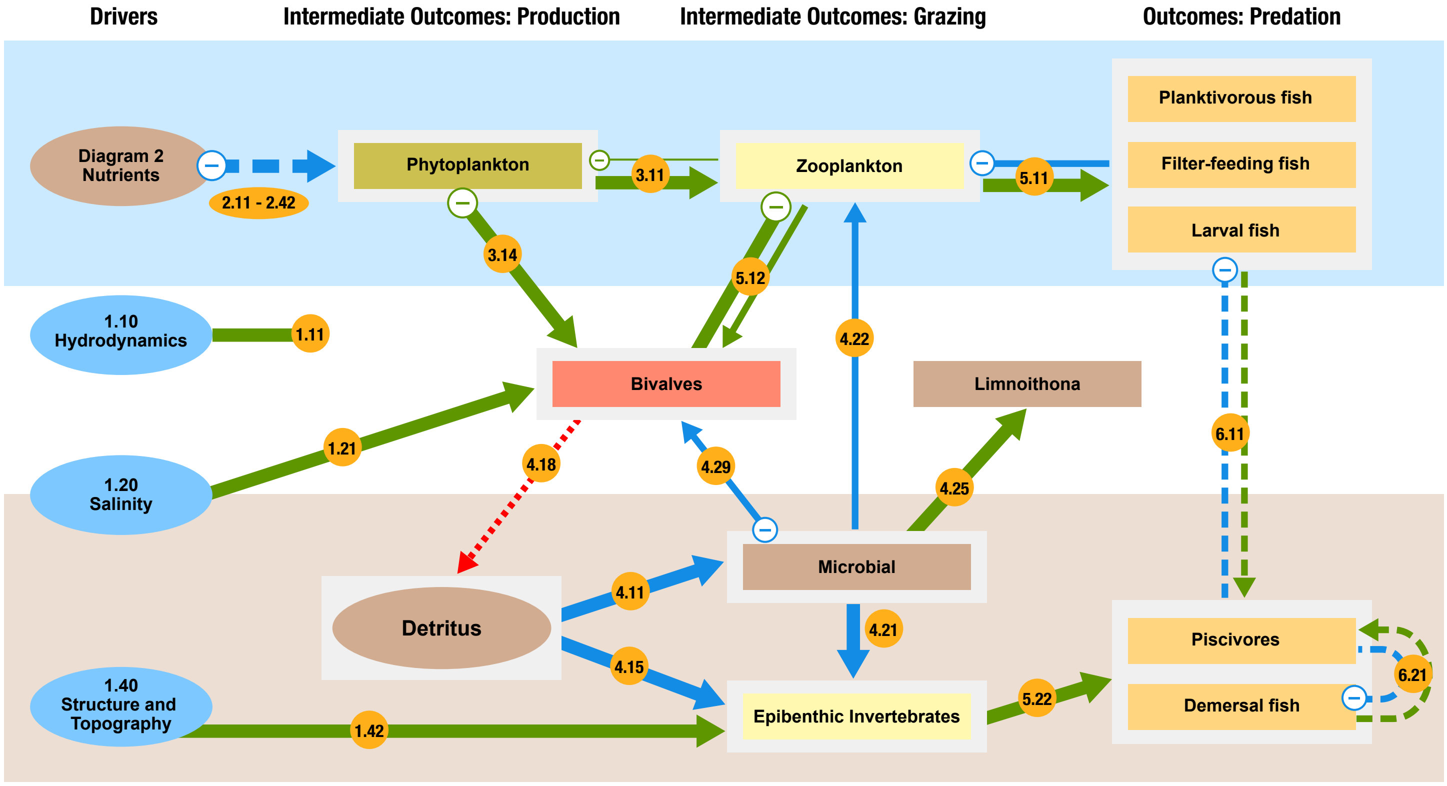

**Diagram 7** Conceptual model of key drivers and linkages

plankton larvae (*Linkage 5.12*) (Durand 2010; Greene et al. 2011). The zooplankton community shifted as new species invaded and established species became rarer. Submersed and floating aquatic vegetation expanded into extensive tracts that provided new kinds of habitat and food resources. In addition, nutrient dynamics may have changed (*Linkages 2.11-2.42*) (Glibert et al. 2011). Although nutrients are generally non-limiting downstream of Freeport on the Sacramento River, $NH_4$ discharge from WWTFs increased, suppressing $NO_3$ uptake and overall diatom growth (Dugdale et al. 2007). Decreasing discharges of $PO_4$ may have led to nutrient limitation of phytoplankton in the northern Delta (Van Nieuwenhuyse 2007).

As a result, both primary production and biomass are low when compared to historical levels and to other estuaries (Cleorn 1987; Jassby et al. 2002), which leads to frequent food limitation in zooplankton and other pelagic organisms (Bennett and Hinton 1995; Orsi and Mecum 1996; Müeller-Solger et al. 2002; Kimmerer et al. 2002), including fishes at higher trophic positions. The Delta Smelt population is federally listed as an endangered species, and the longfin smelt is listed as a California threatened species. Northern anchovy (*Engraulis mordax*), although not threatened, are rare in Suisun Bay, occurring more commonly in the western San Francisco Bay and off shore, where, presumably, they are less food-limited (Kimmerer 2006). Declines of planktivorous fish suggest a greatly decreased contribution to piscivores (*Linkage 6.11*).

Small, localized blooms have continued to occur in marshes and terminal sloughs with high residence time. Such events may be beneficial to larval fishes that co-occur with the bloom. However, there may be little benefit for open water fishes because (1) the blooms are so isolated that they do not occur where the fish are, or (2) the blooms are diluted, dispersed or grazed before they can make significant contributions to the broader systemic food web (Kimmerer 2004). Historically, multiple blooms were likely to occur at different spatial and temporal locations, maximizing opportunities for grazing by higher trophic levels. Because of simplified channel network morphology, fewer opportunities exist for favorable conditions to occur in a way that will support the pelagic food web (Moyle et al. 2010) (*Linkage 1.11*).

In contrast, the parallel detrital organic carbon web is fueled by a large reservoir of decaying matter derived from autochthonous phytoplankton and allochthonous production from marshes, agriculture and upstream riparian habitat (Jassby and Cloern 2000). Sources include emergent and submersed vegetation, stubble from rice fields, tidal and seasonal wetland plants, soil runoff from storm events and agriculture water returns, WWTFs, and decaying organisms of all kinds, including clams (Sobczak et al. 2002). The detrital food web supports a many-tiered microbial community comprised of bacteria, rotifers, ciliates, and microflagellates (*Linkage 4.11*); and an epibenthic invertebrate community comprised of amphipods and isopods, aquatic insects, caridean shrimp, mysids, Crangon shrimp, and crayfish (*Linkages 4.15* and *4.21*) (Baldo Kost and Knight 1975; Simenstad et al. 1999; Sobczak et al. 2005; Howe and Simenstad 2011; York et al. 2013). The larger of these organisms are a major food source for most demersal and piscivorous fishes (including resident and transient natives, and non-native centrarchid sunfish and bass) (*Linkage 5.22*) (Heubach and McCready 1963; Meng and Orsi 1991; Nobriga and Feyrer 2007; Nobriga and Feyrer 2008; Ferrari et al. 2014). Demersal fish likewise form a moderately important contribution to piscivores (*Linkage 6.21*).

Recruiting juvenile fishes pass through the critical period at first feeding (driven by pelagic productivity, *Linkage 5.11*), and subsequently switch to larger invertebrate prey, such as amphipods, that are derived from the detrital organic carbon web, at *Linkage 5.22*. Although epibenthic invertebrates are poorly studied, they account for a large proportion of organisms in adult fish guts of some species (Nobriga and Feyrer 2007; Nobriga and Feyrer 2008; O'Rear 2012). Many of these invertebrates are associated with physical structure (*Linkage 1.42*), including clam shells, tree branches, rock surfaces, and SAV. The invasive aquatic weed *E. densa* harbors a high density of invertebrates and aquatic insects (Ferrari et al. 2014). Caridean and *Crangon* shrimp are found on soft-bottomed habitats, and crayfish are associated with burrows in soft bottoms or rocky rip-rap on levees. Invasive bivalves may also provide additional hard structure for amphipods.

Historically, the pelagic and detrital organic carbon food webs may have been tightly coupled. Ontogenetic shifts in the diets of larval fishes and the native mysid (which uses diatoms during juvenile development, switching to omnivory as an adult [Baldo Kost and Knight 1975; Orsi and Knutson 1979]) represent these couplings. Mysids were once an important source of food for a wide variety of planktivorous, demersal, and piscivorous fishes. However, the decline in pelagic production that resulted from clam grazing effectively caused a corresponding decline in mysid populations (Orsi and Mecum 1996). Mysid-feeding fish switched to more available prey, such as amphipods, which are connected to the detrital web, essentially decoupling these fish from pelagic productivity, except for a brief period during ontogenetic development. Fishes that were not able to decouple from the pelagic web, such as delta smelt and northern anchovy, have declined or moved, respectively (Kimmerer 2006).

As a result, pelagic productivity has become increasingly "grounded": removed from circulation and sequestered into the benthos, where it remains until clams excrete it as pseudofeces, release it through death, or are eaten by fish or birds. Clams are either a sink for phytoplankton-derived carbon (*Linkage 3.14*), or they re-route it through to the detrital web (*Linkages 4.18* and *4.29*). There are few opportunities for grounded carbon to return to the pelagic web, except through microbial production that supplies the cyclopoid copepod *L. tetraspina* (*Linkage 4.25*) and some calanoid copepods (*Linkage 4.22*) with supplemental support. Although *L. tetraspina* is the numerical and biomass dominant copepod in the LSZ, it is not an important prey item for fishes (Slater and Baxter 2014), which may account for its high abundance (Bouley and Kimmerer 2006). Thus, *L. tetraspina* is probably grounded back into the detrital web, or advected out of the system.

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## CONCLUSIONS AND MANAGEMENT OPTIONS

The food web of the upper estuary has been altered by a variety of human-induced changes to the physical, chemical, and biological environment. These changes, when linked to climate variability (such as droughts) and a broad palette of species invasions, have created a novel ecosystem with a suite of organisms that is still in the process of sorting winners and losers. The transformation is the culmination of over 100 years of constant anthropogenic manipulations and is largely irreversible. That is, no clear and attainable restoration point exists for most of the upper estuary. Although restoration activities will need to reference historical conditions, novel approaches will be required to implement functionality. Currently, much restoration is designed to "plug and play," under the assumption that built habitats will interact appropriately with hydrodynamic conditions and attract a desirable suite of species (i.e., those targeted for conservation). This assumption is reinforced by the lack of active monitoring of newly restored sites in the system.

In addition to active monitoring, which will allow managers access to information to evaluate the success of restorations, managers will likely need to embrace active management. Although adaptive management is a system of updating management choices from experimental approaches, active management requires deliberate decisions about short- and long-term goals for the restoration. Most successful restorations will be integrated with tools that maximize configurability of physical structure, tidal and flow energy, hydrologic residence time, and species colonization. Strategies for active management of food web properties will vary considerably from large-scale to small-scale projects.

Manipulation of pelagic food productivity on a large scale will remain challenging. A few examples have been cited of broad-scale system response to flow changes. The Yolo Bypass, an off-channel causeway used for diverting Sacramento River flows across a floodplain, may contribute to phytoplankton blooms at times (Lehman et al. 2007), but there remain uncertainties as to how these inputs affect downstream food web dynamics and higher trophic levels.

**SIDEBAR 7**

### Key Uncertainties: Synthesis

- Nutritional differences between pelagic and detrital webs
- Dynamics of the critical period: when linkages occur
- The importance of plankton blooms that are concentrated in geomorphic features such as backwater sloughs or ponds
- Scale at which restoration projects or floodplains support export of food
- The role of aquatic vegetation to invertebrate and detrital production
- The degree to which grounded carbon is recycled back into the pelagic food web

For example, the response of chlorophyll to flow differs between the Delta and Suisun Bay, likely because of the effects of intensive clam grazing in Suisun Bay (Jassby 2008). As a result, low flows in the Delta may promote local phytoplankton abundance, while reducing inputs to Suisun Bay. Conversely, higher Delta flows may increase inputs to Suisun Bay, while lowering standing chlorophyll in the Delta. An exception to this appears to have occurred in 2014, when low flows combined with other requisite conditions to support a phytoplankton bloom in both the Delta and Suisun Bay (Glibert et al. 2014).

One of the hypothesized requisites for bloom formation is low concentrations of $NH_4$. In conjunction with temperature and residence time, $NH_4$ may influence the production rate and species composition of phytoplankton. Requiring WWTFs to reduce $NH_4$ inputs may increase production rates of desirable phytoplankton in the Delta, but the evidence for this remains equivocal. Other factors may interact to keep phytoplankton abundance low.

For example, in addition to high rates of productivity, bloom formation requires a period of low mortality. Clam grazing restricts this condition across large tracts of the upper estuary. However, some regions may be relatively free from clam grazing pressure, particularly regions in the north Delta and in Suisun Marsh, and localized blooms may occur in these areas that can provide short-term spatial subsidies. These blooms often appear to dissipate by the time they reach Suisun Bay, either because of intensive grazing or dispersal. Currently, no comprehensive strategies exist for managing clams. Salinity (*Linkage 1.21*) could be manipulated on a system-wide scale, which would reduce (temporarily) the distribution of clams in freshwater and the LSZ, but a large volume of water is required to move the salinity field, and periodic oscillations in brackish water or fresh water would be required to knock out the complementary species once established.

Restorations at intermediate scales that include complex channel networks, such as Suisun Marsh, may be manipulated to control flows and salinity. The benefits of manipulation include opportunities for active management of pelagic production, using appropriate engineering of hydrodynamics and channel morphology. Localized production of phytoplankton and zooplankton may provide nursery support to recruiting fishes. However, trade-offs occur with changes in scale: although the hydrodynamics are subject to greater control because less water is involved, smaller volumes limit export to the surrounding region. In addition, even if regions of high production can be engineered, such schemes will require effective ways to manage clams in order for blooms to develop.

Small-scale, localized restorations in ponds or terminal sloughs frequently support high concentrations of both phytoplankton and zooplankton. Resident fishes and invertebrates may recruit to such habitats under the proper conditions, if there is sufficient connectivity. However, scaling is again important: ponds offer a high degree of control over a relatively small volume of water, limiting the effect of export from such habitats.

Intermediate- to small-sized interventions may be very effective at supporting (1) localized high-productivity pelagic environments that offer recruitment and nursery opportunities for fish, and (2) detrital food webs that support late-stage juvenile and adult fishes. In particular, marsh-based restorations will effectively support the latter, while offering limited support for the former, unless two assumptions are met: (1) that sites can be engineered hydrodynamically to promote sufficient residence time and exchange with the surrounding water body, and (2) that pelagic fish are sufficiently abundant or behaviorally plastic to target and use the habitats. Even if true, the likelihood of benefits accruing for pelagic fish may only increase when a threshold of restoration sites along appropriate physical and biological estuarine gradients is surpassed.

The difficulty of system-wide manipulations that can control productivity, clam grazing, SAV establishment, and undesirable introduced species strongly supports the idea that local restoration projects should be prioritized. To support and inform management, it may be desirable to establish some restorations with configurable structures, such as gates, that allow sites to be periodically drained, dried, and remanipulated as necessary. Configurability allows factors like residence time, temperature, turbidity, nutrients, and species assembly to be manipulated simultaneously to maximize benefits to the local food web. Such highly managed sites may also provide refuges for vulnerable species on short to long time-scales.

In spite of most restoration efforts, delta smelt are likely to remain very limited. Extreme events offer high probabilities for forcing extinction. This is in part because pelagic, open water fishes integrate ecosystem conditions across a broad axis of the estuary both in time and space, and weak linkages (such as the decline of pelagic productivity) will be felt strongly at some point in the life history of these fishes. Species that are able to make facultative shifts to features of a localized detrital web are likely to be more robust to future events. Fishes such as splittail, that are migratory but rely on a highly productive floodplain for spawning and recruitment, and local conditions for summer–fall residency, may be resilient, as may be fishes that feed on the abundant epibenthic organisms that comprise the bulk of the upper estuary food web. These fish will benefit from small restoration projects and much can be done to secure their populations.

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## REFERENCES

Alpine AE, Cloern JE. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnol Oceanogr 37:946–955. doi: *http://dx.doi.org/10.4319/lo.1992.37.5.0946*

Arndt H. 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. Hydrobiologia 255/266:231–246. doi: *http://dx.doi.org/10.1007/BF00025844*

Baerwald MR, Schreier BM, Schumer G, May B. 2012. Detection of threatened delta smelt in the gut contents of the invasive Mississippi silverside in the San Francisco Estuary using TaqMan assays. Trans Am Fish Soc 141:1600–1607. doi: *http://dx.doi.org/10.1080/00028487.2012.717521*

Baldo Kost AL, Knight AW. 1975. The food of *Neomysis mercedis* Holmes in the Sacramento–San Joaquin Estuary. Calif Fish Game 61:35–46.

Baskerville–Bridges B, Lindberg JC, Doroshov SI. 2003. The effect of light intensity, alga concentration, and prey density on the feeding behavior of delta smelt larvae. Am Fish Soc Symp 39:219–228.

Bennett WA. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. San Franc Estuary Watershed Sci [Internet]. [cited 2015 Jun 12];3(2). doi: *http://www.escholarship.org/uc/item/0725n5vk* doi: *http://dx.doi.org/10.15447/sfews.2005v3iss2art1*

Bennett WA, Hinton DE. 1995. Larval striped bass condition in a drought-stricken estuary: evaluating pelagic food-web limitation. Ecol Appl 5:680–692. doi: *http://dx.doi.org/10.2307/1941977*

Bennett WA, Moyle PB. 1996. Where have all the fishes gone? Interactive factors producing fish declines in the Sacramento San Joaquin Estuary. In: Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): AAAS, Pacific Division. p. 519–542.

Bennett W, Burau JR. 2015. Riders on the storm: selective tidal movements facilitate the spawning migration of threatened Delta Smelt in the San Francisco Estuary. Estuaries Coasts 3:826–835. doi: *http://dx.doi.org/10.1007/s12237-014-9877-3*

Bernát N, Köpcke B, Yasseri S, Thiel R, Wolfstein K. 1994. Tidal variation in bacteria, phytoplankton, zooplankton, mysids, fish and suspended particulate matter in the turbidity zone of the Elbe estuary; interrelationships and causes. Netherland J Aquat Ecol 28:467–476. doi: *http://dx.doi.org/10.1007/BF02334218*

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Mar Ecol Prog Ser 324:219–228. doi: *http://dx.doi.org/10.3354/meps324219*

Boynton WR, Kemp WM, Keefe CW. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In: Kennedy VS, editor. Estuarine comparisons. New York (NY): Academic Press. p. 69–91.

Breitburg DL, Sanders JG, Gilmour CC, Hatfield CA, Osman RW, Riedel GF, Seitzinger SP, Sellner KG. 1999. Variability in responses to nutrients and trace elements, and transmission of stressor effects through an estuarine food web. Limnol Oceanogr 44:837–863. doi: *http://dx.doi.org/10.4319/lo.1999.44.3_part_2.0837*

Brown LR. 2003. Will tidal wetland restoration enhance populations of native fishes? San Franc Estuary Watershed Sci [Internet]. [cited 2015 May 20];1(1). Available from: *http://escholarship.org/uc/item/2cp4d8wk* doi: *http://dx.doi.org/10.15447/sfews.2003v1iss1art2*

Brown LR, May JT. 2000. Macroinvertebrate assemblages on woody debris and their relations with environmental variables in the lower Sacramento and San Joaquin River drainages, California. Environ Monit Assess 64:311–329. doi: *http://dx.doi.org/10.1023/A:1006482800472*

Brown LR, Michniuk D. 2007. Littoral fish assemblages of the alien-dominated Sacramento–San Joaquin Delta, California, 1980–1983 and 2001–2003. Estuaries Coasts 30:186–200. doi: *http://dx.doi.org/10.1007/BF02782979*

Canuel EA, Rau GH. 1995. Molecular and isotopic tracers used to examine sources of organic matter and its corporation into the food webs of San Francisco Bay. Limnol Oceanogr 40:67–81. doi: *http://dx.doi.org/10.4319/lo.1995.40.1.0067*

Carlton JT, Thompson JK, Schemel LE, Nichols FH. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. 1. Introduction and dispersal. Mar Ecol Prog Ser 66:81–94. doi: *http://www.int-res.com/articles/meps/66/m066p081.pdf*

Carpenter SR, Cole JJ, Hodgson JR, Kitchell JF, Pace ML, Bade D, Cottingham KL, Essington TE, Houser JN, Schindler DE. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. Ecol Monogr 71:163–186. doi: *http://dx.doi.org/10.1890/0012-9615(2001)071[0163:TCNALP]2.0.CO;2*

Carpenter SR, Kitchell JF, Hodgson JR, Cochran PA, Elser JJ, Elser MM, Lodge DM, Kretchmer D, He X, Von Ende CN. 1987. Regulation of lake primary productivity by food web structure. Ecology 68:1863–1876. doi: *http://dx.doi.org/10.2307/1939878*

Cloern JE. 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. Cont Shelf Res 7:1367–1381. doi: *http://dx.doi.org/10.1016/0278-4343(87)90042-2*

Cloern JE. 1996. Phytoplankton bloom dynamics in coastal ecosystems: a review with some general lessons from sustained investigation of San Francisco Bay, California. Rev Geophys 34:127–168. doi: *http://dx.doi.org/10.1029/96RG00986*

Cloern JE. 1999. The relative importance of light and nutrient limitation of phytoplankton growth: A simple index of coastal ecosystem sensitivity to nutrient enrichment. Aquat Ecol 33:3–16. doi: *http://dx.doi.org/10.1023/A:1009952125558*

Cloern JE. 2007. Habitat connectivity and ecosystem productivity: Implications from a simple model. Am Nat 169:E21–E33. doi: *http://dx.doi.org/10.1086/510258*

Cloern JE, Jassby AD. 2010. Patterns and scales of phytoplankton variability in estuarine–coastal ecosystems. Estuaries Coasts 33:230–241. doi: *http://dx.doi.org/10.1007/s12237-009-9195-3*

Cohen AN, Carlton JT. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555–558. doi: *http://dx.doi.org/10.1126/science.279.5350.555*

Cohen RR, Dresler PV, Phillips EJ, Cory RL. 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. Limnol Oceanogr 29:170–180. doi: *http://dx.doi.org/10.4319/lo.1984.29.1.0170*

Conomos TJ, Smith RE, Gartner JW. 1985. Environmental setting of San Francisco Bay. Hydrobiologia 129:1–12. doi: *http://dx.doi.org/10.1007/BF00048684*

Daniels RA, Moyle PB. 1983. Life history of the splittail (Cyprinidae: *Pogonichthys macrolepidotus*) (Ayres) in the Sacramento–San Joaquin Estuary. US Natl Mar Fish Bull 81:647–654.

Dean AF, Bollens SM, Simenstad C, Cordell J. 2005. Marshes as sources or sinks of an estuarine mysid: demographic patterns and tidal flux of *Neomysis kadiakensis* at China Camp marsh, San Francisco Estuary. Estuar Coast Shelf Sci 63:1–11. doi: *http://dx.doi.org/10.1016/j.ecss.2004.08.019*

DiGennaro B, Reed D, Swanson C, Hastings L, Hymanson Z, Healey M, Siegel S, Cantrell S, Herbold B. 2012. Using conceptual models in ecosystem restoration decision making: an example from the Sacramento–San Joaquin River Delta, California. San Franc Estuary Watershed Sci [Internet]. [cited 2015 Mar 05];10(3). Available from: *http://escholarship.org/uc/item/3j95x7vt* doi: *http://dx.doi.org/10.15447/sfews.2012v10iss3art1*

Domermuth RB, Reed RJ. 1980. Food of juvenile American shad, *Alosa sapidissima*, juvenile blueback herring, *Alosa aestivalis*, and pumpkinseed, *Lepomis gibbosus*, in the Connecticut River below Holyoke Dam, Massachusetts. Estuaries 3:65–68. doi: *http://dx.doi.org/10.2307/1351936*

Dugdale RC, Wilkerson FP, Hogue VE, Marchi A. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. Estuar Coast Shelf Sci 73:17–29. Available from: *http://dx.doi.org/10.1016/j.ecss.2006.12.008*

Dugdale RC, Wilkerson FP, Parker AE. 2013. A biogeochemical model of phytoplankton productivity in an urban estuary: the importance of ammonium and freshwater flow. Ecol Model [Internet]. [cited 2014 Jan 26];263:291–307. Available from: *http://www.sciencedirect.com/science/article/pii/S0304380013002779*

Dunne JA, Williams RJ, Martinez ND. 2002. Food-web structure and network theory: The role of connectance and size. Proc Natl Acad Sci 99:12917–12922. doi: *http://dx.doi.org/10.1073/pnas.192407699*

Durand J. 2010. Determinants of calanoid copepod recruitment failure in the San Francisco Estuary [M.S. thesis]. [San Francisco (CA)]: San Francisco State University.

Durand JR. 2014. Restoration and reconciliation of novel ecosystems: Open water habitat in the Sacramento–San Joaquin Delta [Ph.D. dissertation]. [Davis (CA)]: University of California, Davis.

Elliott M, McLusky DS. 2002. The need for definitions in understanding estuaries. Estuar Coast Shelf Sci 55:815–827. doi: *http://dx.doi.org/10.1006/ecss.2002.1031*

Elton CS. 1927. Animal ecology. Chicago (IL): University of Chicago Press. 296 p.

Enright C, Culberson SD. 2009. Salinity trends, variability, and control in the northern reach of the San Francisco Estuary. San Franc Estuary Watershed Sci [Internet]. [cited 2015 May 20];7(2). Available from: *http://escholarship.ucop.edu/uc/item/0d52737t* doi: *http://dx.doi.org/10.15447/sfews.2009v7iss2art3*

Enright C, Culberson SD, Burau JR. 2013. Broad timescale forcing and geomorphic mediation of tidal marsh flow and temperature dynamics. Estuaries Coasts 36:1319–1339. doi: *http://dx.doi.org/10.1007/s12237-013-9639-7*

Everett RA, Ruiz GM. 1993. Coarse woody debris as a refuge from predation in aquatic communities. Oecologia 93:475–486. doi: *http://dx.doi.org/10.1007/BF00328954*

Ferrari MCO, Ranåker L, Weinersmith KL, Young MJ, Sih A, Conrad JL. 2014. Effects of turbidity and an invasive waterweed on predation by introduced largemouth bass. Environ Biol Fishes 97:79–90. doi: *http://dx.doi.org/10.1007/s10641-013-0125-7*

Feyrer F, Herbold B, Matern SA, Moyle PB. 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. Environ Biol Fishes 67:277–288. doi: *http://dx.doi.org/10.1023/A:1025839132274*

Feyrer F, Sommer T, Harrell W. 2006. Managing floodplain inundation for native fish: production dynamics of age-0 splittail (*Pogonichthys macrolepidotus*) in California's Yolo Bypass. Hydrobiologia. 573:213–226. doi: *http://dx.doi.org/10.1007/s10750-006-0273-2*

Feyrer F, Sommer T, Hobbs J. 2007. Living in a dynamic environment: variability in life history traits of age-0 splittail in tributaries of San Francisco Bay. Trans Am Fish Soc 136:1393–1405. doi: *http://dx.doi.org/10.1577/T06-253.1*

Feyrer F, Sommer TR, Baxter RD. 2005. Spatial-temporal distribution and habitat associations of age-0 splittail in the lower San Francisco estuary watershed. Copeia 2005:159–168. doi: *http://dx.doi.org/10.1643/CE-04-187R1*

Feyrer F, Sommer T, Slater SB. 2009. Old school vs. new school: status of threadfin shad (*Dorosoma petenense*) five decades after its introduction to the Sacramento–San Joaquin Delta. San Franc Estuary Watershed Sci [Internet]. [cited 2011 Mar 11];7(1). Available from: *http://escholarship.ucop.edu/uc/item/4dt6p4bv* doi: *http://dx.doi.org/10.15447/sfews.2009v7iss1art3*

Fisher TR, Harding Jr LW, Stanley DW, Ward LG. 1988. Phytoplankton, nutrients, and turbidity in the Chesapeake, Delaware, and Hudson estuaries. Estuar Coast Shelf Sci 27:61–93. doi: *http://dx.doi.org/10.1016/0272-7714(88)90032-7*

Foe C, Knight A. 1985. The effect of phytoplankton and suspended sediment on the growth of *Corbicula fluminea* (Bivalvia). Hydrobiologia 127:105–115. doi: *http://dx.doi.org/10.1007/BF00004190*

Froneman PW. 2001. Feeding ecology of the mysid, *Mesopodopsis wooldridgei*, in a temperate estuary along the eastern seaboard of South Africa. J Plankton Res 23:999–1008. doi: *http://dx.doi.org/10.1093/plankt/23.9.999*

Garz R. 1999. Density dependent growth and diet changes in young-of-the-year striped bass (*Morone saxatilis*) in the Sacramento–San Joaquin Delta. IEP Newsletter [Internet]. [cited 2014 Jan 27];12:22–24. Available from: *http://www.water.ca.gov/iep/newsletters/1999/1999_contents-winter.cfm*

Gasparini S, Castel J. 1997. Autotrophic and heterotrophic nanoplankton in the diet of the estuarine copepods *Eurytemora affinis* and *Acartia bifilosa*. J Plankton Res 19:877. Available from: *http://dx.doi.org/10.1093/plankt/19.7.877*

Gasparini S, Castel J, Irigoien X. 1999. Impact of suspended particulate matter on egg production of the estuarine copepod, *Eurytemora affinis*. J Mar Syst 22:195–205. doi: *http://dx.doi.org/10.1016/S0924-7963(99)00041-X*

Ger KA, Teh SJ, Baxa DV, Lesmeister S, Goldman CR. 2010. The effects of dietary *Microcystis aeruginosa* and microcystin on the copepods of the upper San Francisco Estuary. Freshw Biol 55:1548–1559. doi: *http://dx.doi.org/10.1111/j.1365-2427.2009.02367.x*

Ger KA, Teh SJ, Goldman CR. 2009. Microcystin-LR toxicity on dominant copepods *Eurytemora affinis* and *Pseudodiaptomus forbesi* of the upper San Francisco Estuary. Sci Total Environ 407:4852–4857. doi: *http://dx.doi.org/10.1016/j.scitotenv.2009.05.043*

Gifford SM, Rollwagen–Bollens G, Bollens SM. 2007. Mesozooplankton omnivory in the upper San Francisco Estuary. Mar Ecol Prog Ser 348:33–46. doi: *http://dx.doi.org/10.3354/meps07003*

Gilbert LE. 1980. Food web organization and conservation of Neotropical diversity. In: Soulé ME, Wilcox BA, editors. Conserv Biol Evol–Ecol Perspect Sunderland (MA): Sinauer Associates, Inc.; p. 11–33.

Glibert PM, Dugdale RC, Wilkerson F, Parker AE, Alexander J, Antell E, Blaser S, Johnson A, Lee J, Lee T, et al. 2014. Major – but rare – spring blooms in 2014 in San Francisco Bay Delta, California, a result of the long-term drought, increased residence time, and altered nutrient loads and forms. J Exp Mar Biol Ecol 460:8–18. doi: *http://dx.doi.org/10.1016/j.jembe.2014.06.001*

Glibert PM, Fullerton D, Burkholder JM, Cornwell JC, Kana TM. 2011. Ecological stoichiometry, biogeochemical cycling, invasive species, and aquatic food webs: San Francisco Estuary and comparative systems. Rev Fish Sci 19:358–417. doi: *http://dx.doi.org/10.1080/10641262.2011.611916*

Greene VE, Sullivan LJ, Thompson JK, Kimmerer WJ. 2011. Grazing impact of the invasive clam *Corbula amurensis* on the microplankton assemblage of the northern San Francisco Estuary. Mar Ecol Prog Ser 431:183–193. doi: *http://dx.doi.org/10.3354/meps09099*

Grimaldo LF, Miller RE, Peregrin CM, Hymanson ZP. 2004. Spatial and temporal distribution of native and alien ichthyoplankton in three habitat types of the Sacramento–San Joaquin Delta. Am Fish Soc Symp [Internet]. [cited 2014 Jan 24];39:81–96. Available from: *http://wwwdwr.water.ca.gov/aes/docs/Grimaldo_et_al_2004.pdf*

Grimaldo L, Hymanson Z. 1999. What is the impact of the introduced Brazilian waterweed *Egeria densa* to the Delta ecosystem? IEP Newsletter [Internet]. [cited 2014 Apr 02];12:43–5. Available from: *http://www.water.ca.gov/iep/newsletters/1999/1999_contents-winter.cfm*

Grossman GD, Essington T, Johnson B, Miller J, Monsen NE, Pearsons TN. 2013. Effects of fish predation on salmonids in the Sacramento River–San Joaquin Delta and associated ecosystems [Internet]. Davis (CA): Workshop Report for California Fish Wildlife/Delta Stewardship Council/NMFS. Available from: *http://deltacouncil.ca.gov/docs/effects-fish-predation-salmonids-sacramento-river-san-joaquin-delta-and-associated-ecosystems*

Hager S, Schemel L. 1992. Sources of nitrogen and phosphorus to northern San Francisco Bay. Estuaries Coasts 15:40–52. doi: *http://dx.doi.org/10.2307/1352708*

Haller WT, Sutton DL, Barlowe WC. 1974. Effects of salinity on growth of several aquatic macrophytes. Ecology 55:891–894. doi: *http://dx.doi.org/10.2307/1934427*

Hauenstein E, Ramirez C. 1986. The influence of salinity on the distribution of *Egeria densa* in the Valdivia river basin, Chile. *Arch Für Hydrobiol* [Internet]. [cited 2009 Nov 17];107:511–519. Available from: *http://repositoriodigital.uct.cl/handle/10925/946*

Helfman GS. 1981. The advantage to fishes of hovering in shade. Copeia 2:392–400. doi: *http://dx.doi.org/10.2307/1444228*

Herbold B, Baltz DM, Brown L, Grossinger R, Kimmerer W, Lehman P, Simenstad CS, Wilcox C, Nobriga M. 2014. The role of tidal marsh restoration in fish management in the San Francisco Estuary. San Franc Estuary Watershed Sci [Internet]. [cited 2015 Jan 02];12(1). Available from: *http://escholarship.org/uc/item/1147j4nz* doi: *http://dx.doi.org/10.15447/sfews.2014v12iss1art1*

Herrgesell PL, Kohlhorst DW, Miller LW, Stevens DE. 1981. Effects of freshwater flow on fishery resources in the Sacramento–San Joaquin Estuary. In: Cross R, Williams D, editors. Proc Natl Symp Freshw Inflow Estuaries. Washington, D.C.: U.S. Fish and Wildlife Service. p. 71–108.

Heubach W, McCready AM. 1963. Food of young-of-the-year striped bass (*Roccus saxatilis*) in the Sacramento–San Joaquin River system. Calif Fish Game 49:224–239.

Hjort J. 1926. Fluctuations in the year classes of important food fishes. J Cons [Internet]. 1:5–38. Available from: *http://icesjms.oxfordjournals.org/content/1/1/5.full.pdf*

Holst H, Zimmermann H, Kausch H, Koste W. 1998. Temporal and spatial dynamics of planktonic rotifers in the Elbe Estuary during spring. Estuar Coast Shelf Sci 47:261–273. doi: *http://dx.doi.org/10.1006/ecss.1998.0364*

Houde ED. 2008. Emerging from Hjort's shadow. J Northwest Atl Fish Sci 41:53–70. doi: *http://dx.doi.org/10.2960/J.v41.m634*

Howe ER, Simenstad CA. 2007. Restoration trajectories and food web linkages in San Francisco Bay's estuarine marshes: a manipulative translocation experiment. Mar Ecol Prog Ser 351:65. doi: *http://dx.doi.org/10.3354/meps07120*

Howe ER, Simenstad CA. 2011. Isotopic determination of food web origins in restoring and ancient estuarine wetlands of the San Francisco Bay and Delta. Estuaries Coasts 34:597–617. doi: *http://dx.doi.org/10.1007/s12237-011-9376-8*

Hurst TP, Conover DO. 2001. Activity-related constraints on overwintering young-of-the-year striped bass (*Morone saxatilis*). Can J Zool 79:129–136. doi: *http://dx.doi.org/10.1139/z00-189*

Hymanson ZP, Mayer D, Steinbeck J. 1994. Long-term trends in benthos abundance and persistence in the upper Sacramento–San Joaquin Estuary: summary report, 1980–1990. Sacramento (CA): Interagency Ecological Program for the San Francisco Bay/Delta Estuary.

Islam MS, Tanaka M. 2006. Spatial variability in nursery functions along a temperate estuarine gradient: role of detrital versus algal trophic pathways. Can J Fish Aquat Sci 63:1848–1864. doi: *http://dx.doi.org/10.1139/F06-086*

Islam MS, Ueda H, Tanaka M. 2005. Spatial distribution and trophic ecology of dominant copepods associated with turbidity maximum along the salinity gradient in a highly embayed estuarine system in Ariake Sea, Japan. J Exp Mar Biol Ecol 316:101–115. doi: *http://dx.doi.org/10.1016/j.jembe.2004.11.001*

Jacoby JM, Collier DC, Welch EB, Hardy FJ, Crayton M. 2000. Environmental factors associated with a toxic bloom of *Microcystis aeruginosa*. Can J Fish Aquat Sci 57:231–240. doi: *http://dx.doi.org/10.1139/f99-234*

Jassby A. 2008. Phytoplankton in the upper San Francisco Estuary: Recent biomass trends, their causes and their trophic significance. San Franc Estuary Watershed Sci [Internet]. [cited 2012 Oct 02];6(1). Available from: *http://www.escholarship.org/uc/item/71h077r1* doi: *http://dx.doi.org/10.15447/sfews.2008v6iss1art2*

Jassby A, Cloern J, Müeller–Solger A. 2003. Phytoplankton fuels Delta food web. Calif Agric 57:104–109. doi: *http://dx.doi.org/10.3733/ca.v057n04p104*

Jassby AD, Cloern JE. 2000. Organic matter sources and rehabilitation of the Sacramento–San Joaquin Delta (California, USA). Aquat Conserv Mar Freshw Ecosyst 10:323–352. doi: *http://dx.doi.org/10.1002/1099-0755(200009/10)10:5<323::AID-AQC417>3.0.CO;2-J*

Jassby AD, Cloern JE, Cole BE. 2002. Annual primary production: patterns and mechanisms of change in a nutrient-rich tidal ecosystem. Limnol Oceanogr 47:698–712. doi: *http://dx.doi.org/10.4319/lo.2002.47.3.0698*

Jassby AD, Cloern JE, Powell TM. 1993. Organic carbon sources and sinks in San Francisco Bay: variability induced by river flow. Mar Ecol Prog Ser 95:39–54. Available from: *http://www.int-res.com/articles/meps/95/m095p039.pdf*

Jones N, Thompson J, Arrigo K, Monismith S. 2009. Hydrodynamic control of phytoplankton loss to the benthos in an estuarine environment. Limnol Oceanogr 54:952–969. doi: *http://dx.doi.org/10.4319/lo.2009.54.3.0952*

Kimmerer W. 2004. Open water processes of the San Francisco Estuary: from physical forcing to biological responses. San Franc Estuary Watershed Sci [Internet]. [cited 2008 Mar 30];2(1). Available from: *http://escholarship.org/uc/item/9bp499mv* doi: *http://dx.doi.org/10.15447/sfews.2004v2iss1art1*

Kimmerer W, Gross E, MacWilliams M. 2009. Is the response of estuarine nekton to freshwater flow in the San Francisco Estuary explained by variation in habitat volume? Estuaries Coasts 32:375–389. doi: *http://dx.doi.org/10.1007/s12237-008-9124-x*

Kimmerer WJ. 1996. Changes in the zooplankton of the San Francisco Bay estuary since the introduction of the clam *Potamocorbula amurensis*. In: Hollibaugh JT, editor. San Francisco Bay: the ecosystem San Francisco (CA): AAAS, Pacific Division. p. 403–425.

Kimmerer WJ. 2002a. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Mar Ecol Prog Ser 243:39–55. doi: *http://dx.doi.org/10.3354/meps243039*

Kimmerer WJ. 2002b. Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. Estuaries 25:1275–1290. doi: *http://dx.doi.org/10.1007/BF02692224*

Kimmerer WJ. 2006. Response of anchovies dampens effects of the invasive bivalve Corbula amurensis on the San Francisco Estuary foodweb. Mar Ecol Prog Ser 324:207–218. doi: *http://dx.doi.org/10.3354/meps324207*

Kimmerer WJ, Burau JR, Bennett WA. 1998. Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. Limnol Oceanogr 43:1697–1709. doi: *http://dx.doi.org/10.4319/lo.1998.43.7.1697*

Kimmerer WJ, Cowan J, Miller LW, Rose KA. 2001. Analysis of an estuarine striped bass population: effects of environmental conditions during early life. Estuaries 24:557–575. doi: *http://dx.doi.org/10.2307/1353257*

Kimmerer WJ, Ferm N, Nicolini MH, Peñalva C. 2005. Chronic food limitation of egg production in populations of copepods of the genus *Acartia* in the San Francisco estuary. Estuaries 28:541–550. doi: *http://dx.doi.org/10.1007/BF02696065*

Kimmerer WJ, Gartside E, Orsi JJ. 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Mar Ecol Prog Ser 113:81–93. Available from: *http://www.int-res.com/articles/meps/113/m113p081.pdf*

Kimmerer WJ, Ignoffo TR, Slaughter AM, Gould AL. 2014. Food-limited reproduction and growth of three copepod species in the low-salinity zone of the San Francisco Estuary. J Plankton Res 36:722–735. doi: *http://dx.doi.org/10.1093/plankt/fbt128*

Kjelson MA. 1971. Selective predation by a freshwater planktivore, the threadfin shad, *Dorosoma petenense* [Ph.D. dissertation]. Davis (CA): University of California, Davis.

Kjelson MA, Fisher FW. 1982. Life history of fall-run juvenile Chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento–San Joaquin Estuary, California. In: Kennedy VS, editor. Estuarine comparisons. New York (NY): Academic Press. p. 393–411.

Knutson ACJ, Orsi JJ. 1983. Factors regulating abundance and distribution of the shrimp *Neomysis mercedis* in the Sacramento–San Joaquin Estuary. Trans Am Fish Soc 112:476–485. doi: *http://dx.doi.org/10.1577/1548-8659(1983)112<476:FRAADO>2.0.CO;2*

Kogut NJ. 2008. Overbite clams, *Corbula amurensis*, defecated alive by white sturgeon, *Acipenser transmontanus*. Calif Fish Game [Internet]. 94:143–149. Available from: *https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=47383&inline=1*

Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, Dunne JA, Johnson PT, Kuris AM, Marcogliese DJ. 2008. Parasites in food webs: the ultimate missing links. Ecol Lett 11:533–546. doi: *http://dx.doi.org/10.1111/j.1461-0248.2008.01174.x*

Landry MR, Calbet A. 2004. Microzooplankton production in the oceans. ICES J Mar Sci J Cons 61:501–507. doi: *http://dx.doi.org/10.1016/j.icesjms.2004.03.011*

Lehman P. 2000. Phytoplankton biomass, cell diameter, and species composition in the low salinity zone of Northern San Francisco Bay Estuary. Estuaries Coasts 23:216–230. doi: *http://dx.doi.org/10.2307/1352829*

Lehman P, Teh S, Boyer G, Nobriga M, Bass E, Hogle C. 2010. Initial impacts of *Microcystis aeruginosa* blooms on the aquatic food web in the San Francisco Estuary. Hydrobiologia 637:229–248. doi: *http://dx.doi.org/10.1007/s10750-009-9999-y*

Lehman PW, Boyer G, Hall C, Waller S, Gehrts K. 2005. Distribution and toxicity of a new colonial *Microcystis aeruginosa* bloom in the San Francisco Bay Estuary, California. Hydrobiologia 541:87–99. doi: *http://dx.doi.org/10.1007/s10750-004-4670-0*

Lehman PW, Boyer G, Satchwell M, Waller S. 2008. The influence of environmental conditions on the seasonal variation of *Microcystis* cell density and microcystins concentration in San Francisco Estuary. Hydrobiologia 600:187–204. doi: *http://dx.doi.org/10.1007/s10750-007-9231-x*

Lehman PW, Mayr S, Mecum L, Enright C. 2009. The freshwater tidal wetland Liberty Island, CA was both a source and sink of inorganic and organic material to the San Francisco Estuary. Aquat Ecol 44:359–372. doi: *http://dx.doi.org/10.1007/s10452-009-9295-y*

Lehman PW, Smith RW. 1991. Environmental factors associated with phytoplankton succession for the Sacramento–San Joaquin Delta and Suisun Bay Estuary, California. Estuar Coast Shelf Sci 32:105–128. doi: *http://dx.doi.org/10.1016/0272-7714(91)90009-Z*

Lehman PW, Sommer T, Rivard L. 2007. The influence of floodplain habitat on the quantity and quality of riverine phytoplankton carbon produced during the flood season in San Francisco Estuary. Aquat Ecol 42:363–378. doi: *http://dx.doi.org/10.1007/s10452-007-9102-6*

Lindley ST, Mohr MS. 2003. Modeling the effect of striped bass (*Morone saxatilis*) on the population viability of Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*). Fish Bull [Internet]. [cited 2014 Jan 27];101. Available from: *http://fishbull.noaa.gov/1012/10lindle.pdf*

Lopez C, Cloern J, Schraga T, Little A, Lucas L, Thompson J, Burau J. 2006. Ecological values of shallow-water habitats: Implications for the restoration of disturbed ecosystems. Ecosystems 9:422–440. doi: *http://dx.doi.org/10.1007/s10021-005-0113-7*

Lott J. 1998. Feeding habits of juvenile and adult delta smelt from the Sacramento–San Joaquin River Estuary. Interag Ecol Program Newsl [Internet]. 11:14–19. Available from: *http://www.water.ca.gov/iep/newsletters/1998/IEP-winter-1998.cfm*

Lucas LV, Cloern JE, Koseff JR, Monismith SG, Thompson JK. 1998. Does the Sverdrup critical depth model explain bloom dynamics in estuaries? J Mar Res 56:375–415. doi: *http://dx.doi.org/10.1357/002224098321822357*

Lucas LV, Cloern JE, Thompson JK, Monsen NE. 2002. Functional variability of habitats within the Sacramento–San Joaquin Delta: restoration implications. Ecol Appl 12:1528–1547. doi: *http://dx.doi.org/10.1890/1051-0761(2002)012[1528:FVOHWT]2.0.CO;2*

Lund JR, Hanak E, Fleenor W, Howitt R, Mount J, Moyle P. 2007. Envisioning futures for the Sacramento–San Joaquin Delta. San Francisco (CA): Public Policy Institute of California. Available from: *http://www.ppic.org/main/publication.asp?i=671*

Mac Nally R, Thomson J, Kimmerer W, Feyrer F, Newman K, Sih A, Bennett W, Brown L, Fleishman E, Culberson S, others. 2009. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modelling (MAR). Ecol Appl 20:1417–1430. doi: *http://dx.doi.org/10.1890/09-1724.1*

Mann KH. 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. Limnol Oceanogr. 33:910–930.

Martino EJ, Able KW. 2003. Fish assemblages across the marine to low salinity transition zone of a temperate estuary. Estuar Coast Shelf Sci 56:969–987. doi: *http://dx.doi.org/10.1016/S0272-7714(02)00305-0*

Meng L, Orsi JJ. 1991. Selective predation by larval striped bass on native and introduced copepods. Trans Am Fish Soc 120:187–192. doi: *http://dx.doi.org/10.1577/1548-8659(1991)120<0187:SPBLSB>2.3.CO;2*

Merrell JR, Stoecker DK. 1998. Differential grazing on protozoan microplankton by developmental stages of the calanoid copepod *Eurytemora affinis* Poppe. J Plankton Res 20:289. doi: *http://dx.doi.org/10.1093/plankt/20.2.289*

Miller NA, Chen X, Stillman JH. 2014. Metabolic Physiology of the invasive clam, *Potamocorbula amurensis*: the interactive role of temperature, salinity, and food availability. PloS One 9:e91064. doi: *http://dx.doi.org/10.1371/journal.pone.0091064*

Miller N, Stillman J. 2013. Seasonal and spatial variation in the energetics of the invasive clam *Corbula amurensis* in the upper San Francisco Estuary. Mar Ecol Prog Ser 476:129–139. Available from: *http://www.int-res.com/articles/meps_oa/m476p129.pdf* doi: *http://dx.doi.org/10.3354/meps10149*

Miller RR, Williams JD, Williams JE. 1989. Extinctions of North American fishes during the past century. Fisheries 14:22–38. doi: *http://dx.doi.org/10.1577/1548-8446(1989)014<0022:EONAFD>2.0.CO;2*

Mills LS, Soulé ME, Doak DF. 1993. The keystone-species concept in ecology and conservation. BioScience 43:219–224. doi: *http://dx.doi.org/10.2307/1312122*

Monismith SG, Kimmerer W, Burau JR, Stacey MT. 2002. Structure and flow-induced variability of the subtidal salinity field in northern San Francisco Bay. J Phys Oceanogr 32:3003–3019. doi: *http://dx.doi.org/10.1175/1520-0485(2002)032<3003:SAFIVO>2.0.CO;2*

Mount J, Bennett W, Durand J, Fleenor W, Hanak E, Lund J, Moyle P. 2012. Aquatic ecosystem stressors in the Sacramento–San Joaquin Delta. San Francisco (CA): Public Policy Institute of California. Available from: *http://www.ppic.org/content/pubs/report/R_612JMR.pdf*

Moyle PB. 2002. Inland fishes of California. Berkeley (CA): University of California Press.

Moyle PB, Baxter RD, Sommer TR, Foin TC, Matern SA. 2004. Biology and population dynamics of Sacramento splittail (*Pogonichthys macrolepidotus*) in the San Francisco Estuary: A review. San Franc Estuary Watershed Sci [Internet]. [cited 2013 Nov 18];2(2). Available from: *http://escholarship.ucop.edu/uc/item/61r48686* doi: *http://dx.doi.org/10.15447/sfews.2004v2iss2art3*

Moyle PB, Bennett WA, Fleenor WE, Lund JR. 2010. Habitat variability and complexity in the upper San Francisco Estuary. San Franc Estuary Watershed Sci [Internet]. [cited 2015 May 15];8(3). Available from: *http://escholarship.org/uc/item/0kf0d32x* doi: *http://dx.doi.org/10.15447/sfews.2010v8iss3art1*

Moyle PB, Daniels RA, Herbold B, Baltz DM. 1986. Patterns in distribution and abundance of a noncoevolved assemblage of estuarine fishes in California. Fish Bull [Internet]. 84:105–117. Available from: *http://fishbull.noaa.gov/841/moyle.pdf*

Moyle PB, Herbold B, Stevens DE, Miller LW. 1992. Life history and status of delta smelt in the Sacramento–San Joaquin Estuary, California. Trans Am Fish Soc 121:67–77. Available from: *http://www.tandfonline.com/action/showCitFormats?doi=10.1577/1548-8659(1992)121<0067:LHASOD>2.3.CO;2*

Müeller–Solger AB, Jassby AD, Müller–Navarra DC. 2002. Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento–San Joaquin River Delta). Limnol Oceanogr 47:1468–1476. doi: *http://dx.doi.org/10.4319/lo.2002.47.5.1468*

Mullin MM, Brooks ER. 1970a. Growth and metabolism of two planktonic, marine copepods as influenced by temperature and type of food. Mar Food Chains 74:95. Available from: *http://books.google.com/books?hl=en&lr=&id=Wn2gcNvYNrsC&oi=fnd&pg=PA74&dq=Calanus+feeding+mullin&ots=vDDFCQXRDi&sig=dmoI5JRVlwIfDcXGKKnQLI-A4a4*

Mullin MM, Brooks ER. 1970b. The effect of concentration of food on body weight, cumulative ingestion, and rate of growth of the marine copepod *Calanus helgolandicus*. Limnol Oceanogr 15:748–755. doi: *http://dx.doi.org/10.4319/lo.1970.15.5.0748*

Nichols FH, Cloern JE, Luoma SN, Peterson DH. 1986. The modification of an estuary. Science 231:567–567. doi: *http://dx.doi.org/10.1126/science.231.4738.567*

Nichols FH, Thompson JK, Schemel LE. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. 2. Displacement of a former community. Mar Ecol Prog Ser 66:95–101. Available from: *http://www.int-res.com/articles/meps/66/m066p095.pdf*

Van Nieuwenhuyse EE. 2007. Response of summer chlorophyll concentration to reduced total phosphorus concentration in the Rhine River (Netherlands) and the Sacramento–San Joaquin Delta (California, USA). Can J Fish Aquat Sci 64:1529–1542. doi: *http://dx.doi.org/10.1139/F07-121*

Nixon SW, Oviatt CA, Frithsen J, Sullivan B. 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. J Limnol Soc South Afr 12:43–71. doi: *http://dx.doi.org/10.1080/03779688.1986.9639398*

Nobriga M, Feyrer F, Baxter R, Chotkowski M. 2005. Fish community ecology in an Altered River delta: Spatial patterns in species composition, life history strategies, and biomass. Estuaries Coasts 28:776–785. doi: *http://dx.doi.org/10.1007/BF02732915*

Nobriga ML. 2002. Larval delta smelt diet composition and feeding incidence: Environmental and ontogenetic influences. Calif Fish Game [Internet]. 88:149–164. Available from: *http://wwwdwr.water.ca.gov/aes/docs/Nobriga_2002.pdf*

Nobriga ML, Feyrer F. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento–San Joaquin Delta. San Franc Estuary Watershed Sci [Internet]. [cited 2009 Nov 16];5(2). Available from: *http://escholarship.org/uc/item/387603c0* doi: *http://dx.doi.org/10.15447/sfews.2007v5iss2art4*

Nobriga ML, Feyrer F. 2008. Diet composition in San Francisco Estuary striped bass: does trophic adaptability have its limits? Environ Biol Fishes 83:495–503. doi: *http://dx.doi.org/10.1007/s10641-008-9376-0*

Nobriga ML, Loboschefsky E, Feyrer F. 2013. Common predator, rare prey: exploring juvenile striped bass predation on delta smelt in California's San Francisco Estuary. Trans Am Fish Soc 142:1563–1575. doi: *http://dx.doi.org/10.1080/00028487.2013.820217*

O'Rear TA. 2012. Diet of an introduced estuarine population of white catfish in California [M.S. thesis]. [Davis (CA)]: University of California, Davis.

O'Rear T, Moyle P. 2010. Trends in fish and invertebrate populations of Suisun Marsh: January 2009 — December 2009. Davis (CA): University of California, Davis.

Orsi JJ, Knutson AC. 1979. The role of mysid shrimp in the Sacramento–San Joaquin Estuary and factors affecting their abundance and distribution. In: Conomos TJ, editor. San Francisco Bay: the urban estuary. San Francisco (CA): AAAS, Pacific Division. p. 401–408.

Orsi JJ, Mecum WL. 1986. Zooplankton distribution and abundance in the Sacramento–San Joaquin Delta in relation to certain environmental factors. Estuaries 9:326–339. Available from: *http://dx.doi.org/10.2307/1351412*

Orsi JJ, Mecum WL. 1996. Food limitation as the probable cause of a long-term decline in the abundance of *Neomysis mercedis* the opossum shrimp in the Sacramento–San Joaquin Estuary. In: Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): AAAS, Pacific Division. p. 375–401. Available from: *http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.386.5177&rep=rep1&type=pdf*

Orsi JJ, Walter TC. 1991. *Pseudodiaptomus forbesi* and *P. marinus* (Copepoda: Calanoida), the latest copepod immigrants to California's Sacramento–San Joaquin Estuary. Bull Plankton Soc Jpn (Spec Vol):553–562.

Paganini A, Kimmerer WJ, Stillman JH. 2010. Metabolic responses to environmental salinity in the invasive clam *Corbula amurensis*. Aquat Biol. 11:139–147. doi: *http://dx.doi.org/10.3354/ab00304*

Polis GA, Anderson WB, Holt RD. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst [cited 2014 Jan 25];28:289–316. Available from: *http://www.jstor.org/stable/10.2307/2952495*

Polis GA, Strong DR. 1996. Food web complexity and community dynamics. Am Nat [cited 2013 Dec 20];147:813–846. Available from: *http://www.jstor.org/stable/10.2307/2463091*

Potter IC, Chuwen BM, Hoeksema SD, Elliott M. 2010. The concept of an estuary: A definition that incorporates systems which can become closed to the ocean and hypersaline. Estuar Coast Shelf Sci 87:497–500. doi: *http://dx.doi.org/10.1016/j.ecss.2010.01.021*

Poulton VK, Lovvorn JR, Takekawa JY. 2002. Clam density and scaup feeding behavior in San Pablo Bay, California. The Condor 104:518–527. doi: *http://dx.doi.org/10.1650/0010-5422(2002)104[0518:CDASFB]2.0.CO;2*

Puccia CJ, Levins R. 1985. Qualitative modeling of complex systems. Cambridge (UK): Harvard University Press.

Redfield AC. 1958. The biological control of chemical factors in the environment. Am Sci [cited 2014 Feb 26];46:205–221. Available from: *http://www.jstor.org/stable/27827150*

Richman SE, Lovvorn JR. 2004. Relative foraging value to lesser scaup ducks of native and exotic clams from San Francisco Bay. Ecol Appl 14:1217–1231. doi: *http://dx.doi.org/10.1890/03-5032*

Ritter AF, Wasson K, Lonhart SI, Preisler RK, Woolfolk A, Griffith KA, Connors S, Heiman KW. 2008. Ecological signatures of anthropogenically altered tidal exchange in estuarine ecosystems. Estuaries Coasts 31:554–571. doi: *http://dx.doi.org/10.1007/s12237-008-9044-9*

Robertson AI, Crook DA. 1999. Relationships between riverine fish and woody debris: implications for lowland rivers. Mar Freshw Res 50:941–953. doi: *http://dx.doi.org/10.1071/MF99072*

Rollwagen–Bollens GC, Penry DL. 2003. Feeding dynamics of *Acartia* sp. in a large, temperate estuary (San Francisco Bay, CA). Mar Ecol Prog Ser 257:139–158.

Sautour B, Artigas F, Herbland A, Laborde P. 1996. Zooplankton grazing impact in the plume of dilution of the Gironde Estuary (France) prior to the spring bloom. J Plankton Res. 18:835–853. doi: *http://dx.doi.org/10.1093/plankt/18.5.835*

Schaffter RG, Kohlhurst DW. 1997. White sturgeon spawning migrations and location of spawning habitat in the Sacramento River, California. Calif Fish Game. 83:1–20.

Schoellhamer DH. 2000. Influence of salinity, bottom topography, and tides on locations of estuarine turbidity maxima in northern San Francisco Bay. Mehta AJ, McAnally WH, editors. Proc Mar Sci 3:343–357. doi: *http://dx.doi.org/10.1016/S1568-2692(00)80130-8*

Schoellhamer DH. 2002. Variability of suspended-sediment concentration at tidal to annual time scales in San Francisco Bay, USA. Cont Shelf Res. 22:1857–1866. doi: *http://dx.doi.org/10.1016/S0278-4343(02)00042-0*

Siegfried CA, Kopache ME. 1980. Feeding of *Neomysis mercedis* (Holmes). Biol Bull [Internet]. 159:193–205. Available from: *http://www.biolbull.org/content/159/1/193.short*

Simenstad C, Toft J, Higgins H, Cordell J, Orr M, Williams P, Grimaldo L, Hymanson Z, Reed D. 1999. Preliminary results from the Sacramento–San Joaquin Delta breached levee wetland study (BREACH). IEP Newsletter [Internet]. [cited 2013 Dec 11];12:15–21. Available from: *http://www.water.ca.gov/iep/newsletters/1999/IEP_Newsletter-fall-1999.cfm*

Simenstad C, Toft J, Higgins H, Cordell J, Orr M, Williams P, Grimaldo L, Hymanson Z, Reed D. 2000. Sacramento/San Joaquin Delta Breached Levee Wetland Study (BREACH). Seattle (WA): University of Washington.

Sindilariu P–D, Freyhof J, Wolter C. 2006. Habitat use of juvenile fish in the lower Danube and the Danube Delta: implications for ecotone connectivity. Hydrobiologia 571:51–61. doi: *http://dx.doi.org/10.1007/s10750-006-0216-y*

Slater SB, Baxter RD. 2014. Diet, prey selection, and body condition of age-0 Delta Smelt, in the upper San Francisco Estuary. San Franc Estuary Watershed Sci [Internet]. [cited 2015 Mar 3];12(3). Available from: *https://escholarship.org/uc/item/52k878sb* doi: *http://dx.doi.org/10.15447/sfews.2014v12iss3art1*

Sobczak WV, Cloern JE, Jassby AD, Cole BE, Schraga TS, Arnsberg A. 2005. Detritus fuels ecosystem metabolism but not metazoan food webs in San Francisco estuary's freshwater Delta. Estuaries Coasts 28:124–137. doi: *http://dx.doi.org/10.1007/BF02732759*

Sobczak WV, Cloern JE, Jassby AD, Müeller–Solger AB. 2002. Bioavailability of organic matter in a highly disturbed estuary: The role of detrital and algal resources. Proc Natl Acad Sci 99:8101. doi: *http://dx.doi.org/10.1073/pnas.122614399*

Sommer T, Armor C, Baxter R, Breuer R, Brown L, Chotkowski M, Culberson S, Feyrer F, Gingras M, Herbold B, et al. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. Fisheries 32:270–277. doi: *http://dx.doi.org/10.1577/1548-8446(2007)32[270:TCOPFI]2.0.CO;2*

Sommer T, Mejia FH, Nobriga ML, Feyrer F, Grimaldo L. 2011. The spawning migration of delta smelt in the upper San Francisco Estuary. San Franc Estuary Watershed Sci [Internet]. [cited 2011 Nov 15];9(2). Available from: *http://escholarship.ucop.edu/uc/item/86m0g5sz* doi: *http://dx.doi.org/10.15447/sfews.2011v9iss2art2*

Sommer TR, Harrell B, Nobriga ML, Brown R, Moyle P, Kimmerer WJ, Schemel L. 2001. California's Yolo Bypass: evidence that flood control can be compatible with fisheries, wetlands, wildlife and agriculture. Fisheries 26:6–16.

Sousa WTZ, Thomaz SM, Murphy KJ. 2010. Response of native *Egeria najas* Planch and invasive *Hydrilla verticillata* Royle to altered hydroecological regime in a subtropical river. Aquat Bot 92:40–48. Available from: *http://dx.doi.org/10.1016/j.aquabot.2009.10.002*

Sousa WTZ, Thomaz SM, Murphy KJ, Silveira MJ, Mormul RP. 2009. Environmental predictors of the occurrence of exotic *Hydrilla verticillata* (Lf) Royle and native *Egeria najas* Planch in a sub-tropical river floodplain: the Upper River Paraná, Brazil. Hydrobiologia 632:65–78. Available from: *http://link.springer.com/article/10.1007/s10750-009-9828-3* doi: *http://dx.doi.org/10.1007/s10750-009-9828-3*

Sullivan L. 2010. Prey selection of larval and juvenile planktivorous fish in the San Francisco Estuary [Internet]. San Diego (CA): California Sea Grant. Available from: *http://escholarship.org/uc/item/42z0v1bv*

Sverdrup HU. 1953. On conditions for the vernal blooming of phytoplankton. J Cons 18:287–295. doi: *http://dx.doi.org/10.1093/icesjms/18.3.287*

Tan Y, Huang L, Chen Q, Huang X. 2004. Seasonal variation in zooplankton composition and grazing impact on phytoplankton standing stock in the Pearl River Estuary, China. Cont Shelf Res 24:1949–1968. doi: *http://dx.doi.org/10.1016/j.csr.2004.06.018*

Thomas JL. 1967. The diet of juvenile and adult striped bass, *Roccus saxatilis*, in the Sacramento–San Joaquin river system. Calif Fish Game 53(1):49–62. Available from: *http://www.nativefishlab.net/library/textpdf/13576.pdf*

Thompson B, Adelsbach T, Brown C, Hunt J, Kuwabara J, Neale J, Ohlendorf H, Schwarzbach S, Spies R, Taberski K. 2007. Biological effects of anthropogenic contaminants in the San Francisco Estuary. Environ Res 105:156–174. doi: *http://dx.doi.org/10.1016/j.envres.2006.10.005*

Thompson JK. 2005. One estuary, one invasion, two responses: Phytoplankton and benthic community dynamics determine the effect of an estuarine invasive suspension-feeder. Dame RF, Olenin S, editors. Comp Roles Suspens-Feed Ecosyst 47:291–316. doi: *http://dx.doi.org/10.1007/1-4020-3030-4_17*

Thompson JK, Koseff JR, Monismith SG, Lucas LV. 2008. Shallow water processes govern system-wide phytoplankton bloom dynamics: a field study. J Mar Syst 74:153–166. doi: *http://dx.doi.org/10.1016/j.jmarsys.2007.12.006*

Turner JL. 1966. Distribution and food habits of centrarchid fishes in the Sacramento–San Joaquin Delta. Calif Dept Fish Game Fish Bull 136:144–153.

Vadeboncoeur Y, Vander Zanden MJ, Lodge DM. 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. Bioscience 52:44–54. doi: *http://dx.doi.org/10.1641/0006-3568(2002)052[0044:PTLBTR]2.0.CO;2*

Vander Zanden MJ, Vadeboncoeur Y. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83:2152–2161. doi: *http://dx.doi.org/10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO;2*

Wagner CM. 1999. Expression of the estuarine species minimum in littoral fish assemblages of the lower Chesapeake Bay tributaries. Estuaries 22:304–312. doi: *http://dx.doi.org/10.2307/1352986*

Weissburg MJ, Zimmer–Faust RK. 1993. Life and death in moving fluids: Hydrodynamic effects on chemosensory-mediated predation. Ecology 74:1428–1443. doi: *http://dx.doi.org/10.2307/1940072*

Werner I, Hollibaugh JT. 1993. *Potamocorbula amurensis*: Comparison of clearance rates and assimilation efficiencies for phytoplankton and bacterioplankton. Limnol Oceanogr 38:949–964. doi: *http://dx.doi.org/10.4319/lo.1993.38.5.0949*

Whipple A, Grossinger RM, Rankin D, Stanford B, Askevold R. 2012. Sacramento–San Joaquin Delta historical ecology investigation: exploring pattern and process [Internet]. Richmond (CA): San Francisco Estuary Institute, Aquatic Science Center. Available from: *http://www.sfei.org/DeltaHEStudy*

Wilkerson FP, Dugdale RC, Hogue VE, Marchi A. 2006. Phytoplankton blooms and nitrogen productivity in San Francisco Bay. Estuaries Coasts 29:401–416. doi: *http://dx.doi.org/10.1007/BF02784989*

Williams PB, Orr MK. 2002. Physical evolution of restored breached levee salt marshes in the San Francisco Bay estuary. Restor Ecol 10:527–542. doi: *http://dx.doi.org/10.1046/j.1526-100X.2002.02031.x*

Williams PB, Orr MK, Garrity NJ. 2002. Hydraulic geometry: a geomorphic design tool for tidal marsh channel evolution in wetland restoration projects. Restor Ecol 10:577–590. doi: *http://dx.doi.org/10.1046/j.1526-100X.2002.t01-1-02035.x*

Winder M, Jassby AD. 2010. Shifts in zooplankton community structure: Implications for food web processes in the upper San Francisco Estuary. Estuaries Coasts 34:675–690. doi: *http://dx.doi.org/10.1007/s12237-010-9342-x*

Wright SA, Schoellhamer DH. 2004. Trends in the sediment yield of the Sacramento River, California, 1957 – 2001. San Franc Estuary Watershed Sci [Internet]. [cited 2013 Dec 14];2(2). Available from: *http://escholarship.org/uc/item/891144f4* doi: *http://dx.doi.org/10.15447/sfews.2004v2iss2art2*

Yarrow M, Marin VH, Finlayson M, Tironi A, Delgado LE, Fischer F. 2009. The ecology of *Egeria densa* Planchon (*Liliopsida: Alismatales*): a wetland ecosystem engineer? Rev Chil Hist Nat [Internet]. 82:299–313. Available from: *http://rchn.biologiachile.cl/en/contents/2009v82n2/10.php*

York JK, McManus GB, Kimmerer WJ, Slaughter AM, Ignoffo TR. 2013. Trophic links in the plankton in the low salinity zone of a large temperate estuary: Top-down effects of introduced copepods. Estuaries Coasts 37(3):1–13. doi: *http://dx.doi.org/10.1007/s12237-013-9698-9*

## NOTES

Dahlgren R. 2014. E-mail communication to John Durand regarding nutrient constituents and productivity in the north Delta.

Enright C. 2008. Tidal slough geometry filters estuarine drivers, mediates transport processes, and controls variability of ecosystem gradients. Presented at: CALFED Bay–Delta Science Conference; Sacramento, CA.

Enright C. 2010. Hydrodynamics and transport processes on the historical landscape: geomorphic control of functional complexity and implications for restoration. Presented at: CALFED Bay–Delta Delta Science Conference; Sacramento, CA.

Enright C, Culberson S, Burau J. 2006. Comparing natural and modified sloughs in Suisun Marsh: geometry begets variability. Presented at: CALFED Bay–Delta Science Conference; Sacramento, CA.

O'Rear T. 2013. In-person conversation with T. O'Rear on striped bass feeding strategies and gut contents at University of California, Davis, Davis, CA.