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Memorandum

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To: Ellen McBride, Evan Sawyer, National Oceanic and Atmospheric Administration (NOAA)

From: Merri Martz, John Ferguson, Anchor QEA, LLC

cc: Jacob Katz, Cal Trout; Rachel Johnson, NOAA; Steve Edmondson; Bjarni Serup, California Fish and Wildlife; and Joshua Israel, U.S. Bureau of Reclamation

Re: Summary of Ecological and Physical Conditions Characterizing Sacramento River Floodplain Habitats and Importance for Anadromous Fish

This paper summarizes the state of the science about the function and role of floodplains in aquatic ecosystems in general, and specifically their role with respect to anadromous salmonids and sturgeon in the Sacramento Valley and portions of the Sacramento-San Joaquin Delta (Delta). The peer-reviewed articles referenced are a portion of a large body of published literature on the Delta and fish species, but represent key findings on anadromous fish use of floodplains.

Floodplain Contributions to Fish Life-History Diversity and Population Resilience

Globally, floodplain habitats are an integral part of river systems and provide important physical, chemical, and biological functions. The important foundational concept of the "flood pulse" (Junk et al. 1989; Tockner et al. 2000) postulates that the pulse of high flows from rivers into their floodplains is a primary source of productivity for the river ecosystem. Flood pulses can range from short to long durations in predictable or unpredictable cycles, and these pulses allow the exchange of biota and organic and inorganic matter between the river and floodplain. Overall, riverine animal biomass is significantly supported by contributions from primary and secondary production from the floodplain; the aquatic food web in a river receives substantial input from floodplain production compared to organic matter produced within the river (Junk et al. 1989; Tockner et al. 2000).

While Junk et al. (1989) primarily focused on tropical and subtropical river systems that have predictable and long-duration flooding of floodplains, this concept was expanded by Tockner et al. (2000) to temperate rivers and that also identified temperature as another key component affecting productivity and diversity in floodplains. Temperatures in tropical floodplains are relatively constant, but in temperate regions they can vary substantially from season to season. Depending upon when flooding occurs, this seasonality can substantially affect productivity. Floodplain functions are extremely complex, but the seasonal wetting and drying may increase primary productivity and diversity of habitat types compared to systems that experience steady, long-duration flooding.
The relative importance of autochthonous (in-river) versus allochthonous (external to river) organic matter to the overall riverine ecosystem varies widely, but for temperate rivers, the riparian and

floodplain contribution to the ecosystem may be a critical source of organic matter produced outside of the river.

A review of literature on floodplains (Tockner and Stanford 2002) provides evidence that floodplains are important centers of biodiversity and productivity. This is a result of the complex mosaic of aquatic, riparian, wetland, and upland habitats created by frequent disturbance and frequent inputs of nutrient-rich sediments and organic matter. While this is true even in highly modified river systems, a study of minimally modified rivers indicates that under natural conditions, there is very high dynamism that can cause high rates of floodplain habitat turnover on rapid time scales (e.g., Ward et al. [2001] reported that 80% of habitats turned over in a 3-year timespan on the Tagliamento River arising in the Italian Alps), while the overall distribution of habitats remains relatively steady over the long term. A key to floodplain conservation and restoration is that these habitats provide sufficient space for natural geomorphic processes to occur and cause dynamic floodplain turnover, which results in the continual refreshing of the habitat mosaic (Wohl et al. 2021).

Multiple hydrologic sources (e.g., river overflow, groundwater, precipitation, and tributary inflow) play a key role in the overall productivity and geomorphic resilience of floodplains to disturbance. However, the primary drivers of river-wetland floodplain corridors are a complex interaction of geology, geomorphology, and biota, with hydrology being a secondary driver. When these diverse riverine processes are functioning at scale, highly complex river-wetland corridors can make numerous small adjustments to large disturbances while remaining dynamically stable (Wohl et al. 2021).

Floodplains are important habitats to numerous fish species. Sommer et al. (2004) sampled age-0 fish assemblages in the Yolo Bypass and Sacramento River over a 3-year period and showed higher fish species diversity and richness in the Yolo Bypass compared to the river. This was attributed to the greater habitat diversity and hydrologic variation in the floodplain. Even though non-native fish comprised a substantial portion of the catch, multiple native fish species were present and primarily so earlier in the year, and thus were more closely associated with the natural flood regime (February through early May). Mahardja et al. (2019) found that Delta Smelt abundance was higher than previously known in the Yolo Bypass, hatched earlier, and exhibited higher growth rates than in the Sacramento River. This was attributed to high prey density, high turbidity, and higher temperatures in the floodplain. Delta Smelt are not typically present in Yolo Bypass during flood years, and their presence during dry years indicates that habitat accessibility can vary, but high growth rates in years of accessibility can buffer the overall population from effects in other years when suitable habitat quantity may be reduced.

Floodplains are specifically important refuge and feeding areas for anadromous species including salmonids and sturgeon, particularly for juvenile life stages. Sommer et al. (2001) compared growth rates, feeding success, and survival of juvenile Chinook salmon in floodplain (Yolo Bypass) versus riverine (Sacramento River) habitats. Salmon size (fork length) increased substantially in the Yolo Bypass compared to the river in both years, with high numbers of prey in stomach contents and indications of equivalent or slightly higher survival rates compared to the river.

Historical Ecology of the Sacramento River and Delta

Historically, the lower Sacramento River and the Delta was a vast mosaic of channels, tidal and non-tidal wetlands, seasonal wetlands and vernal pools, riparian areas, and upland transitional areas covering nearly 800,000 acres (Whipple et al. 2012). In its unmodified condition, the Sacramento River provided much of the freshwater flow entering the Delta (more than three times the volume of the San Joaquin River and other tributaries to the Delta). The Sacramento River flow is primarily driven by rainfall and displays high flows from December through May, with a peak in March that leads to frequent and long-duration flooding (weeks to months) throughout the flood basins dominated by extensive stands of tule (bullrush; Whipple et al. 2012).

Lakes and numerous seasonal ponds were present throughout the North Delta, although occupying only about 2% of the overall habitat area. Riparian forest occurred parallel to the Sacramento River in varying widths, occupying 10% of the historical flood basins. The North Delta transitioned into the tidally influenced Central Delta that was dominated by emergent marsh of tule, sedges, cattails, reeds, and some shrub wetlands dominated by willows, with nearly 1,600 miles of winding tidal channels. The long-duration flooding and more than 500,000 acres of freshwater emergent and tidal marsh kept the Delta perennially wet when the surrounding landscape was dry throughout the summer and fall (Whipple et al. 2012).

There is limited information on the historical use of floodplain habitats by fish. The earliest known fisheries investigations of Sacramento River floodplains focused on perceived risks of juveniles stranded in floodplain habitats during April and May at the end of the flood season, rather than benefits provided by floodplains to the majority of outmigrants that passed through these same habitats from January through March (Scofield 1913).

Based on the high diversity of fish species currently found in the Yolo Bypass (Sommer et al. 2004), which has a substantially smaller area and lower habitat diversity than the historical North Delta condition, it is likely that the floodplains supported numerous fish species in high abundance.

The evolution of four runs of Chinook salmon reflects the high diversity of habitat types and hydrologic conditions historically present in the Sacramento-San Joaquin watershed that promoted distinct run timing to exploit the highly diverse conditions. This diversity likely supported Chinook salmon, steelhead, and other native fish species abundance through flood and drought years and landscape disturbances. Habitat heterogeneity (in both space and time) creates the trait and phenotypic diversity on which fish population resilience depends (Herbold et al. 2018).

Historical salmon abundance cannot be described with certainty but has been conservatively estimated at 1 to 2 million Chinook salmon spawners annually based on early commercial harvest records (Yoshiyama et al. 1998). Other salmonid species also inhabited Central Valley habitats, although in lower numbers, including winter steelhead, and pink, chum, sockeye, and coho salmon (Yoshiyama et al. 2000). Fall-run Chinook salmon has been the major salmon run in the Central Valley since 1900 and was likely so in earlier times; spawning surveys on some stocks and locations began in the late 1930's and even then, declines in abundance compared to historic estimates due to multiple human activities were evident (Yoshiyama et al. 1998). For the entire Sacramento River basin, fall-run Chinook salmon spawning escapements averaged roughly 300,000 adults annually from 1953 to 1966 and decreased to approximately 200,000 adults between 1967 and 1991 (Yoshiyama et al. 1998). From 2010 to 2018, estimated annual abundance of in-river fall-run Chinook salmon throughout the entire Central Valley averaged 145,202 (calculated from GrandTab escapement database maintained by CDFW, dated 05/07/2019).

Changes to Sacramento-San Joaquin watersheds since the first presence of Europeans are documented by Whipple et al. (2012). Major changes have occurred since Spanish exploration and establishment of missions in the 1770s, during fur trapping and ranching in the early 1800s, and gold mining in the mid-1800s that caused extensive impacts to aquatic habitats. This early period was followed by extensive wetland reclamation and levee building in the Delta from the 1850s to the early 1900s and the construction of major infrastructure to reduce flood damages and provide water supply that occurred from the early 1900s to the 1980s.

Ongoing agriculture, human development, and climate change stressors continue. Currently, more than 95% of the historical natural habitats of the Delta have been eliminated, particularly freshwater emergent wetlands, willow thickets, and seasonal wetlands (SFEI 2014). By contrast, the area of open water has increased by more than 90%. Cloern et al. (2021) provided a similar summary of changes, identifying that historically, there were multiple wetland habitat types (tidal and non-tidal marshes, open water habitats, and floodplains) that supported aquatic food webs, but today these have been disconnected and transformed for agricultural or urban uses, and approximately 98% of the marshes have been converted to other land uses, while open water habitat has increased by 80% since the early 1800s.

In addition to changes in habitat types and area, annual primary production in hydrologically connected habitats is less than 100 kilotons of carbon today, compared to approximately 1,300 kilotons in the historical landscape. Carbon consumption by herbivores and production of detritus has decreased by roughly 90%, resulting in a 90% reduction in the carbon or energy supply to aquatic consumers, from microbes to copepods to fish and birds (Cloern et al. 2021).

Sacramento River hydraulics have also been altered by engineering modifications, vegetation removal, gravel mining, and water storage and sediment retention in upstream reservoirs. This has resulted in significant river channel bed lowering, which decreases the hydrologic connectivity of off-channel habits by lowering river stages for a given flow, resulting in conditions whereby small floods can no longer inundate much of the original floodplain surface (Williams et al. 2009). Even remnant, hydrologically connected habitats, such as Yolo Bypass, have reduced connectivity because the landscape has been altered to drain relatively quickly (Sommer et al. 2020).

Juvenile Fish and the Sacramento River Floodplain

Floodplain Food Webs

Floodplains have important characteristics, such as large areas of shallow and typically low-velocity water with long residence times. These characteristics have important effects on fishes. Poff and Zimmerman's (2010) review of research on altered flow regimes found that reduced floodplain inundation duration resulted in reduced abundance of young fish across a wide range of ecosystems.

In the Central Valley, water residence times are longer in floodplain wetlands than in drainage channels or mainstem river reaches (Jeffres et al. 2020; 2.15 days, 23.5 seconds, and 1.7 seconds, respectively). These hydrologic patterns associated with seasonal, ephemeral flooding provide access for river food webs to floodplain carbon sources and contribute to highly productive heterotrophic energy pathways important to the production of fisheries resources (Jeffres et al. 2020). The seasonal hydrologic patterns in floodplains promote nutrient and organic matter cycling, enhance primary and secondary production, and facilitate higher rates of food web production compared to nearby rivers. Corline et al. (2021) compared zooplankton communities across diverse aquatic habitats inundated during winter (riverine locations within leveed river channels, restored floodplains, rice fields, flood bypasses, and unintentionally inundated agricultural lands) and found similar abundance of zooplankton communities among the habitats and that residence time was the most important factor for zooplankton community assembly. This suggests that flooding of off-channel areas capable of sustaining long residence times could consistently provide abundant, high-quality food web resources for native fish populations (Corline et al. 2021).

These characteristics of floodplain inundation all support high growth rates of fish. Seasonally flooding the Yolo Bypass resulted in significantly higher levels of zooplankton and high Chinook salmon growth rates compared to the adjacent Sacramento River; these results were similar for multiple geographical areas in the Central Valley and in different cover types (non-rice crops and fallow, weedy areas) (Sommer et al 2020). An experiment of hatchery juvenile Chinook salmon rearing in an inundated agricultural wetland versus a perennial drainage canal within the Yolo Bypass showed that salmon in the floodplain fields grew 0.92 millimeters per day, which was five times greater than the rate of growth in the Sacramento River, and zooplankton densities were 53 times more abundant in the floodplain (Jeffres et al. 2020). The field used in the experiment is usually planted to rice, but had been fallow the previous year when naturally recruited herbaceous vegetation had been allowed to grow. Carbon in floodplains has a much greater source component from detritus as inundation of floodplains facilitates the decomposition of terrestrial vegetation, which allows floodplain soils to leach labile carbon into the water column, whereas carbon sources in the mainstem river are primarily from in-river phytoplankton (Jeffres et al. 2020).

Sommer et al. (2001) found that juvenile salmon had significantly more prey items (particularly dipterans, which are a preferred prey item) in their stomachs in the Yolo Bypass than in the Sacramento River; although water temperatures were higher in the Yolo Bypass, the increased prey biomass and rate of consumption outweighed the increased metabolic effects of higher temperatures. Juvenile Chinook salmon in the Cosumnes River floodplain grew more rapidly on vegetated, ephemerally inundated habitats compared to perennial ponds or riverine habitats; food was abundant, and the fish grew rapidly even though the water temperature averaged 21°C for a week and daily maximum temperatures reached 25°C (Jeffres et al. 2008). This underscores the benefits of food resources even under higher-than-optimal temperatures (Williams 2012).

The hydrologic characteristics of floodplains also contribute to food webs early in the migration season of fishes that supports diverse life histories. Benigno and Sommer (2008) sampled invertebrate drift and potential sources of the invertebrates in floodplains during early winter (late December to early January). Drift was dominated by chironomids that over-summer in floodplain sediments and then rapidly emerge within 2 weeks of the floodplain sediments being inundated, which provides an important food source for fish migrating in this period.

Even though floodplain flood frequency and duration vary widely from year to year, floodplain food webs can support fish species across a wide range of conditions. Goertler et al. (2017) evaluated the diets of juvenile Chinook salmon in the Yolo Bypass during drought years and flood years. During flood years, the diet was dominated by aquatic-riparian insects, and during drought years, the diet was dominated by zooplankton. The number of inundation days was the most representative explanatory variable when compared to modeled inundation acreage and discharge, suggesting that temporal rather than spatial expansion of floodplain habitat may provide the greatest benefit to life-history diversity of juvenile salmon in Yolo Bypass and Cache Slough.

A specific type of managed floodplains is rice field inundation. Corline et al. (2017) studied zooplankton production in rice fields inundated during winter and found zooplankton densities to be 150 times higher than in the adjacent Sacramento River throughout the 6-week study. Katz et al. (2017) reported mean growth rates of 0.68 to 0.70 millimeters per day for juvenile Chinook salmon in winter-inundated rice fields and that Chinook salmon stomach contents were primarily cladoceran zooplankton. Managed inundation of Yolo Bypass rice fields in winter and early spring appeared to mimic the long-duration inundation of historical Sacramento Valley floodplains, re-exposing salmon to an approximated version of the hydrologic regime under which they evolved and to which they are adapted (Holmes et al. 2021).

Floodplains contribute to the riverine food webs downstream as biota and organic matter are transported out of the floodplain as it drains after a flood event. Schemel et al. (2004) found a rapid increase in phytoplankton production after a flood pulse into the Yolo Bypass and a high abundance of phytoplankton in discharge from the Yolo Bypass drainage channel as it drained; high levels of chlorophyll *a* were also measured further down river. While such discharges are brief, they may provide an important source of phytoplankton to downstream areas with currently low phytoplankton biomass. Years with multiple floodplain pulses may further enhance primary production and transport from the floodplain. The periodic connection and disconnection of the Cosumnes River floodplain with the channel was vital to the functioning of the floodplain as a source of concentrated suspended algal biomass to subsidize downstream aquatic ecosystems (Ahearn et al. 2006).

Access, Survival, and Risks in Sacramento River Floodplains

For fish to benefit from the productivity of floodplains described in the previous sections, they need access to floodplain habitats with sufficient frequency and duration. The Yolo Bypass typically floods in nearly 2 out of 3 years, with a flood duration of several days (4 to 10 days) or even extending to 1 or 2 months in higher flood events (Takata et al. 2017; Jeffres et al. 2020). The duration and magnitude of flooding is positively correlated with the abundance of juvenile Chinook salmon in the floodplain, because more juveniles can access the floodplain when it is connected over a longer period. Takata et al. (2017) found that juvenile Chinook salmon rear progressively longer in the Yolo Bypass during longer duration flood events, which results in larger size at emigration. Sommer et al. (2005) assessed habitat use and stranding risk for juvenile salmonids within the Yolo Bypass based on recapture of tagged fish. Juvenile Chinook salmon were found to be using all habitat types sampled (riparian, agricultural field, and natural vegetated habitats) and in all regions of the floodplain. Mean residence time varied from 30 to 56 days; fish were significantly larger when emigrating out of the floodplain than when they were released after tagging. Also, recapture rate was higher in the floodplain than in the Sacramento River in a wet year and similar or lower in moderate years, indicating that floodplain survival is not substantially lower than the river and that floodplain survival may be improved in higher flow years.

Access to floodplain habitats supports life-history diversity, an important component of stock biocomplexity and for maintaining salmon population productivity through time (Hilborn et al. 2003). All three salmon phenotypes (fry, parr, and smolts) are found in the Yolo Bypass, indicating that floodplain habitats provide rearing and migrating opportunities to a diversity of juvenile salmon life stages; however, information on residence times is limited. Johnston et al. (2018) evaluated the travel time and survival of juvenile Chinook salmon through the Yolo Bypass compared to other routes in the North Delta during dry years. Study fish were large and outfitted with acoustic transmitters. Travel time through Yolo Bypass was slightly slower and more variable than the Sacramento River, and there was no significant difference in mean survival to Chipps Island; both years of the study were below normal or dry. While acoustic tagging studies provide information on the behavior and survival of actively migrating salmon, floodplains are thought to provide disproportionate benefits as nursery and rearing habitat to salmon that are too small to acoustically tag.

The role of life-history diversity in sustaining populations through a range of conditions has been shown in other Central Valley systems. Sturrock et al. (2019) analyzed juvenile fall-run Chinook salmon emigration, life-history diversity, and survival in comparison to flows in the Stanislaus River. Overall, years with higher flow resulted in more juveniles being produced and more adult returns, but importantly, all phenotypes were represented in adult returns, showcasing the importance of maintaining all life-history types to sustain the overall population. This was observed even though fry emigration in the river has been suppressed by lower and less variable winter flows that reduce migratory cues, result in slower travel times to downstream habitats, and may increase exposure to predation. Larger smolts have also been suppressed by higher temperatures later in the season following flow releases to aid smolt migration and parr rearing in the river. The constrained migratory window and reduced access to downstream floodplain habitats for later migrants due to low flows has implications for the overall survival of the population.

There are risks associated with anadromous fish accessing seasonally inundated floodplains. These include stranding and exposure to metals and other pollutants. The overall risk of stranding based on area is limited, because the area of isolated ponds is relatively small compared to total floodplain area. Assemblages of smaller-sized fish in isolated perennial ponds within the Yolo Bypass were observed to be dominated by non-native species (Feyrer et al. 2004). This likely reflects the initial distribution of fish into a pond during flood inundation, followed by the sequential loss of species that cannot tolerate the higher temperatures and low dissolved oxygen conditions during summer months or were removed via predation, as well as fish that voluntarily emigrated before the pond was isolated.

Adult fish can also become stranded in floodplains as waters recede. Salmon use olfactory navigation cues to follow source water and migrate to specific spawning grounds and water operations influence the routing of Upper Sacramento River-origin water such that salmon deviate from the mainstem Sacramento River migration corridor and become stranded in agricultural fields behind flood bypass weirs (Windell et al. 2017).

The Yolo Bypass does not provide suitable spawning habitat for adult salmonids or sturgeon except in its tributary, Putah Creek, but some Chinook salmon and both white and green sturgeon adults enter the Yolo Bypass through the Cache Slough Complex during their spawning migrations (Johnston et al. 2020; Beccio 2016). There can be greater tidal flows ebbing from the Cache Slough Complex than flows in the Sacramento River during low-flow periods that may cue adult fish to enter Cache Slough instead of proceeding in-river. White sturgeon spawn from February to early June. The estimated probability of White Sturgeon exiting the floodplain was 0.99. Most White sturgeon exited the floodplain from April to June, but also returned to the floodplain in September or October. This indicates that White sturgeon may use the floodplain habitat and many exit through the perennial drainage channel. Fall-run Chinook salmon spawn from October to November. The estimated probability of fall-run Chinook salmon exiting the floodplain was only 0.74. Some of the Chinook salmon tagged by Johnston et al. (2020) spawned in Putah Creek, but others did not exit the floodplain and may have been stranded.

Stranding can occur on winter- and spring-run Chinook salmon as well. In some years, flows through bypasses likely result in false migration cues and large numbers of adults traveling up the Colusa Basin Drain for 40 to 70 miles before being blocked at weirs preventing successful migration. In 2013, more than 600 stranded adult winter- and spring-run Chinook salmon were observed, and 312 were rescued and relocated to the mainstem Sacramento River or the Livingston Stone National Fish Hatchery (Killam et al. 2014, Beccio 2016). The loss of adults prior to spawning can be demographically costly to the population (Windell et al. 2017). Initial information about stranding at the Fremont Weir has led to modifications of the fish passage structure that should improve passage (DWR 2020) by allowing adult salmon to avoid stranding, re-enter the Sacramento River, and continue migrating upriver.

The Fremont Weir and weirs on the Sutter Bypass pose significant barriers to green and white sturgeon when the Yolo Bypass stops overtopping. Creating fish passage at this site is a major feature in the Yolo Bypass Fish Passage and Habitat Restoration Program (USBR 2021) and other local planning efforts in the Sutter Bypass. Information about stranding at the Fremont Weir has led to modifications of the fish passage structure that should improve passage (DWR 2020) by allowing adult salmon to re-enter the Sacramento River and continue migrating upriver. Recent and historical records of adult sturgeon and salmon stranding at the Fremont Weir (Beccio 2016) demonstrate that many fish can be stranded, although a population-level effect has been difficult to demonstrate. However, Thomas et al. (2013) modeled a recent stranding event and showed that the magnitude of green sturgeon stranding could have significant impacts on population growth rates and that adult fish passage at Fremont Weir improves the viability of the green sturgeon population.

While floodplains may provide a variety of habitat types and food resources that promote growth and contribute to phenotypic diversity in salmon, these habitats have both legacy contaminants and ongoing use of contaminants that could be harmful to salmon and sturgeon and could warrant consideration as potential impacts. A large risk to juvenile salmonids in floodplains is the potential for bioaccumulation of methylmercury, particularly because of the history of mercury and gold mining in the Coast Range and Sacramento-San Joaquin watershed. Mercury is a neurotoxin and methylmercury is a potent form that forms in anaerobic conditions in aquatic environments and can bioaccumulate in fish through dietary uptake. Methylmercury can affect behavior, growth, reproduction, and survival of fish (Crump and Trudeau 2009). Cache Creek was an area of extensive mercury mining and the long residence time of water in the Yolo Bypass and higher temperatures may contribute to high production of methylmercury. An evaluation of growth of juvenile Chinook salmon and uptake of methylmercury by Henery et al. (2010) identified increased growth and increased uptake of methylmercury by juvenile Chinook salmon in the floodplain compared to the Sacramento River. However, there was a linear bioaccumulation in drier years dominated by Cache Creek flows and then a leveling of bioaccumulation in wetter years with flood flows coming from the Sacramento River. Several factors may be involved that require further study as to whether the relatively short residence time of juvenile salmon in the floodplain affects the long-term physiology and survival of the fish. Agricultural fields (e.g., rice fields) may be even more likely to contribute to bioaccumulation of mercury. For example, Ackerman and Eagles-Smith (2009) evaluated mercury uptake by mosquitofish and Mississippi silversides in the Yolo Bypass, and total mercury accumulation was much greater in rice fields compared to permanent wetlands. This may be attributed to the shallower water and wetting and drying of the rice fields compared to the deeper permanent wetlands.

Sturgeon are also susceptible to bioaccumulation of contaminants. Sampling of white sturgeon tissue from 1986-1990 indicated that selenium levels are elevated in both adult and juvenile fish at levels approaching chronic and acute effects in other fish (Urquhart et al. 1991; White and Hammond, 1987). Selenium is found in high levels in their common prey items, including native and introduced clams. Similar to white sturgeon, green sturgeon growth, fecundity, and egg size are likely negatively affected by contaminants that persist for a long time in the environment, such as selenium and mercury (Linville 2006). Early life-history stages may also be impacted from maternal effects of selenium exposure.

Numerous invasive species are present in Sacramento Valley floodplains and the Delta that can have direct (e.g., predation or competition) or indirect (e.g., effects on food webs) impacts to anadromous fishes. This includes plant, phytoplankton, invertebrate, and fish species. Non-native invertebrates may be having a major influence on phytoplankton production in the Delta and estuary from herbivory, and non-native fish species can be competitors or predators of native fish species. More information on the effects of invasive species on native anadromous species is needed.

Net Benefit

As discussed in the previous sections, floodplains generate high rates of primary productivity that supports juvenile salmon growth and life-history diversity, and the primary productivity is also transported into the river downstream and estuary. The overall net benefit to salmon and sturgeon appears to be positive, and further restoration and enhancement of floodplains will help offset some negative effects such as predation by non-native species. However, the potential negative effects of the bioaccumulation of methylmercury and perhaps other chemicals, as well as invasive species, warrant additional investigation.

The benefits to salmon from occupying floodplain habitats may also extend out into the ocean and to adult returns under certain conditions. The Yolo Bypass and other floodplain and emergent wetland habitats have been shown to provide increased growth rates and resulted in similar or higher survival rates for juvenile Chinook salmon (Sommer et al. 2001; Johnston et al. 2018). Greater survival within a population has been correlated to size (mean length) when migrating through freshwater habitats for spring-run Chinook salmon in the Columbia River basin (Zabel and Achord 2004). This may be attributed to earlier emigration and avoidance of predators and may confer increased survival benefits through the life cycle to adult returns. Larger size at emigration to the ocean has been linked to greater ocean survival. Woodson et al. (2013) evaluated growth rate and survival during the early ocean residence period for fall-run Chinook salmon from the Sacramento-San Joaquin system and found that larger size at ocean entry translated to better survival in years when food may be limiting in the ocean, which could bolster adult returns in years of poor ocean conditions. However, in years when there were abundant food sources in the ocean, size at ocean entry did not make a significant difference.

The biological productivity of the coastal ocean and the Gulf of Farallones rises sharply in the spring when changes in the coastal winds shift currents to a predominantly southward flow, which induces upwelling of nutrient-rich water from the coastal shelf and slope (Lindley et al. 2009). As the timing of this spring transition varies from year to year, natural variation in the timing of ocean entry among and within salmon stocks can be thought of as a bet-hedging strategy that spreads the risk of mortality among individuals arriving at different times and as a result, minimizes the possibility of a complete mismatch between juvenile salmon arrival to the ocean and the availability of their prey (Satterthwaite et al. 2014). As floodplains provide life-history diversity and stock biocomplexity, and maintain salmon population productivity, they help support this bet-hedging strategy that salmon rely on to spread risks and maintain populations through time and environmental variability.

Juvenile salmon use a diversity of habitats to rear along their outmigration route. For example, Phyllis et al. (2018) evaluated strontium isotopes in the otoliths of winter-run Chinook salmon spawners that returned to the Sacramento River and identified that 44% to 65% of the returning adults sampled rear in non-natal areas, including a major portion in the Delta. This indicates that Delta rearing supports a major component of returning adults and may improve smolt-to-adult survival. Unfortunately, strontium isotopes are not different between the mainstem Sacramento River and the Yolo and Sutter bypasses, which may also be important non-natal rearing habitats. Recent work by Bell-Tilcock et al. (In press), shows that the Yolo Bypass has a unique carbon and sulfur isotopic signature recorded in salmon archival tissues like otoliths and eye lenses. Because the layers in otoliths and eye lenses are sequentially formed, the carbon and sulfur values that are incorporated into these tissues are a permanent record of diet and floodplain use throughout a fish’s life. This research opens avenues for quantifying the population-level benefits of juvenile floodplain rearing to adult survival.

Bellido-Leiva et al. (2021) developed a model for winter-run Chinook salmon that connects rearing habitat availability and quality with existing hydrologic conditions (i.e., flow and temperature regimes), which was used to explain the impact of each individual habitat on juvenile development and outmigration success. The model included alternative rearing habitats (e.g., floodplains, river side channels, and tributaries), defined rules of habitat access and use based on hydrologic instream conditions and incorporated a juvenile growth module that combined bioenergetics modeling with empirical growth rates. Based on the model, floodplain habitat contributed to a quarter of salmon out-migrant biomass despite representing less than 18% of the available habitat and less than 10% of total rearing days, and off-channel growth was one of the most sensitive parameters in the model.

In summary, accessing highly productive floodplain habitats by different life-history stages and different stocks provides net benefits to individual growth and the overall productivity. These benefits support the resilience of salmon populations to environmental conditions by diversifying the timing of juvenile salmon and steelhead in-river migrations and ocean entry. This helps spread the risk throughout differing freshwater and ocean conditions via a portfolio effect that buffers populations from adverse events or years that might otherwise reduce the population. Risks associated with floodplains include stranding and legacy contaminants and current use of contaminants, especially the potential for bioaccumulation of methylmercury and selenium. Stranding is being addressed through passage modifications at upstream weirs. Stranding and contaminants both warrant further investigation, along with additional data gaps listed below.

Data Gaps

While this summary of the state of the science shows clear benefits to fish species from floodplain habitats, key data gaps remain. Addressing these gaps would further inform the design and implementation of floodplain restoration and conservation actions that benefit Sacramento-San Joaquin fish populations. These include the following:

- Quantify changes in the survival of juvenile fish that use floodplain habitats relative to those that rear in-river for use in population models to estimate life-cycle benefits from accessing floodplains.
- Quantify if managed floodplain rearing increases or decreases juvenile salmon productivity and life-history diversity.
- Measure adult and juvenile stranding on floodplains among water years and operations and estimating whether the level of stranding has a significant effect on population productivity.
- Relate increased growth rate and enhanced body condition resulting from floodplain rearing to returning adult population size.
- Evaluate whether growth or survival benefits at one life stage (i.e., juvenile) compensate for negative effects at another life stage (i.e., adult stranding).

- Quantify the trade-offs between mortality on the floodplain and survival at sea on the overall population size.
- Evaluate whether floodplains can be managed to both enhance benefits and mitigate impacts.
- Evaluate to what extent the bioaccumulation of mercury and other contaminants on floodplains affects salmon or sturgeon survival, reproductive success, and ultimately, population-level effects.
- Evaluate predation rates on juvenile salmon by non-native species.
- Evaluate the effect of invasive species on floodplain food webs and whether this affects salmon and sturgeon growth and survival.
- Evaluate whether fish passage criteria for low flows are sufficient for sturgeon passage through notches, weirs, and other openings.

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