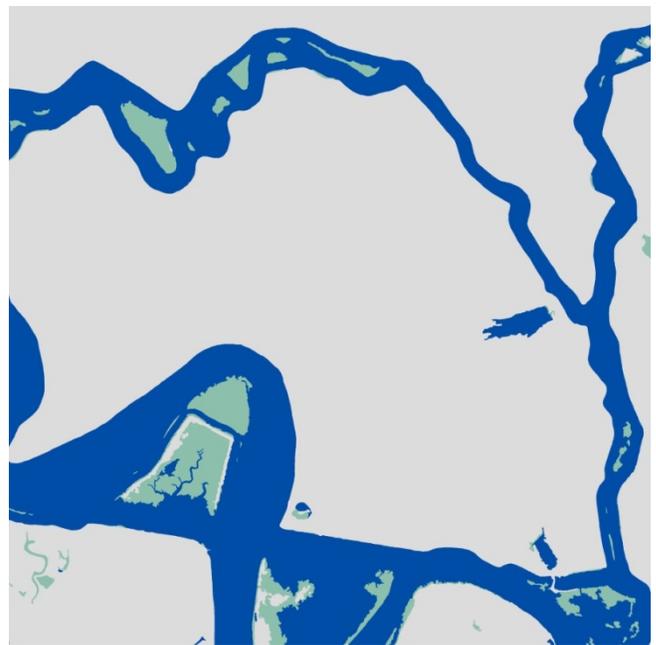


Ecological implications of modeled hydrodynamic changes in the upper San Francisco Estuary

Phase II Technical Memorandum

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Summary

The physical and ecological environment of the upper San Francisco Estuary has been profoundly altered since the early 1800s. Recent efforts have utilized maps of the upper estuary's historical habitat types to infer associated changes in desired ecosystem processes and functions. The work presented in this memo builds on these previous efforts, but utilizes a new tool for evaluating change over time: a 3D hydrodynamic model of the pre-development estuary. This model was constructed by Resource Management Associates (RMA) using a new digital elevation model of the pre-development upper estuary generated by SFEI and UC Davis (UCD) and "natural" boundary flows calculated by the California Department of Water Resources (CDWR).

Once completed and calibrated, the pre-development model was paired with a similar model of the contemporary system in order to analyze hydrodynamic changes in the upper estuary. These analyses are presented in a technical memorandum published by RMA (2015). This memorandum takes these analyses and considers the ecological implications of modeled changes (see the "Results" section). Hydrodynamic analyses include analyzing changes in tidal prism, isohaline positions, low-salinity zone habitat, channel velocity, and source water distribution. Key findings include:

- (1) **a decrease in temporal salinity variability:** the variability in X2 position across wet and critically dry years has been reduced, which would be expected to decrease site-scale heterogeneity in tidal marsh plant communities, with potential implications for the diversity and metapopulation dynamics of marsh animals;
- (2) **an increase in X2 position due to changes in estuarine geometry:** changes in the geometry of the upper estuary have increased the position of X2 by an average of 3.23 km, which means substantially more water is now required to maintain X2 at any one position. Impacts of geometry-driven changes in X2 on wildlife populations are hard to predict given uncertainties in the mechanisms driving correlations between X2 and species abundance, but are potentially sizeable;
- (3) **loss of low-velocity refugia in blind channels:** in the pre-development simulations, average channel velocities are up to 520% higher in the mainstem channel than at the head of the adjacent blind channel. Since the majority of the upper estuary's blind channels have been diked and filled, loss of these habitats is expected to have significantly decreased low-velocity refugia for aquatic organisms (such as outmigrating chinook salmon) and has likely decreased the heterogeneity of aquatic habitat with respect to velocity at the landscape-scale;
- (4) **changes in source water distribution:** preliminary model results suggest San Joaquin source water "signal" has been severely truncated, while Sacramento "signal" has been widely diffused, which could contribute to a decrease in the ability of migratory organisms (especially adult salmon) to navigate the Delta using source-water specific chemical cues (though improved model calibration in the upper reaches of the estuary is needed to draw firm conclusions).

These and other findings are summarized in more detail in Table 1. In addition to describing the ecological implications of modeled hydrodynamic changes, this memorandum summarizes major ongoing questions about estuarine hydrodynamics that might be explored using these models, including changes in water residence time, temperature, transport pathways, and the connectivity of aquatic and semi-aquatic habitats (see the "Background" section). Understanding changes in these and other factors would greatly improve our understanding of the desirable ecosystem functions provided by the historical system and, as a result, improve our ability to recover these functions now and into the future.

Table 1. Summary of modeled hydrodynamic changes in the upper estuary since the pre-development period and a summary of some of the ecological implications. See the “Model implementation section” for a full discussion of this work.

Analysis	Modeled hydrodynamic changes	Summarized potential ecological implications
Tidal prism	<ul style="list-style-type: none"> • Tidal prism at Carquinez Strait has decreased by 2.5% since pre-development period. • Ebb-dominance of tidal flows at Carquinez has increased since pre-development period. 	<ul style="list-style-type: none"> • Ecological implications of relatively small decrease are unclear. • All else being equal, a reduction in tidal prism is expected to decrease water velocities and erosion rates in the estuary, promoting the contraction of tidal channel networks. The contraction of tidal channel networks would be accompanied by a reduction in the ecological functions they may provide (e.g. large food supplies from marsh subsidies and high densities of phytoplankton, low-velocity refuge for fish, etc.). • Increased ebb-dominance expected to have increase tidal advection of free-floating materials (and biota) from the upper estuary to the lower estuary (and decrease transport into upper estuary).
Source water fingerprinting	<ul style="list-style-type: none"> • Preliminary model results suggest San Joaquin source water “signal” has been severely truncated, while Sacramento “signal” has been widely diffused, but improved calibration in upper Delta reaches is needed to draw firm conclusions. 	<ul style="list-style-type: none"> • If preliminary results reflect actual conditions, it is possible there has been a decrease in the ability of migratory organisms to navigate the Delta using source-water specific chemical cues, especially when combined with other stressors. Again, more work is needed to calibrate the model in the upper reaches of the estuary for this analysis.
Isohaline position	<ul style="list-style-type: none"> • Seasonal variability in X2 has been altered since the historical period, though the direction of change differs across years—total range higher now in wet year simulation, but lower in dry year simulations. • Interannual variability (measured as total range across the full 3-year simulation period, which included both wet and critically dry years) was greater in the pre-development system. • Changes in geometry alone are responsible, on average, for a 3.23 km increase in X2. 	<ul style="list-style-type: none"> • A decrease in interannual salinity variability is expected to be accompanied by a decrease in the maintenance of site-scale heterogeneity in tidal marsh plant communities, with potential implications for diversity and metapopulation dynamics of marsh animals. • Geometry changes mean higher net Delta outflows are now required to force the salinity field to any particular location within the estuary, with potentially significant implications for water supply (e.g., maintaining X2 at Roe Island with the estuary’s current geometry requires flows that are 4,500 cfs higher than maintaining it there with the pre-development geometry, a difference equal to ~9% of CA’s total freshwater withdrawals). • Though it varies from species to species, correlations between X2 and species abundance suggest that negative effects of geometry changes on the abundance of estuarine biota are <i>potentially</i> sizeable (e.g., a 3.23 km increase in X2 correlates with a 31-36% decrease in longfin smelt abundance index). However, uncertainties about the mechanisms behind the X2-abundance relationships limit our ability to infer how geometry changes have impacted biota.
Low salinity zone habitat characteristics	<ul style="list-style-type: none"> • When X2 is between Carquinez and the Confluence, the LSZ area is now 2-3x smaller; when X2 is upstream of Port Chicago, average depth of LSZ now substantially greater; when X2 is below Big Break, volume of LSZ is similar in pre-development and contemporary systems. • Higher sustained spring flows might have situated the LSZ within Carquinez Strait more frequently in the pre-development system. • There is now much less tidal-scale variability in the depth and area of the LSZ. 	<ul style="list-style-type: none"> • Contemporary research has found that the physical extent of habitat at suitable salinities is not a likely mechanism behind the observed relationship between flow and wildlife population sizes. However, these findings may not apply to the pre-development Delta; it is possible that density dependence of estuarine species has decreased over time with declines in population size. • Lower average depths in the pre-development period could mean that a higher proportion of the low-salinity aquatic habitat was net-autotrophic, which would translate to higher phytoplankton primary productivity available for primary consumers in the pre-development period (though invasive clams complicate the relationship between depth and net primary productivity available for other aquatic organisms). • Decreased daily fluctuations in the depth and area of the LSZ today reflect a decrease in marsh-plain inundation in the LSZ. Marsh-derived primary productivity available to consumers in the LSZ has likely decreased since the pre-development period.
Channel velocity	<ul style="list-style-type: none"> • For the pre-development system, modeled maximum cross-sectionally averaged channel velocities are up to 520% higher in the mainstem channel than at the head of the adjacent blind channel. 	<ul style="list-style-type: none"> • Loss of blind channels has likely meant the loss of low-velocity refugia for aquatic organisms (such as outmigrating chinook salmon), and a likely decrease in the heterogeneity of aquatic habitats with respect to velocity at the landscape-scale.

Introduction

Understanding how the pre-development upper San Francisco Estuary supported native wildlife is challenging because our current understanding of local wildlife ecology is largely based on the profoundly altered modern landscape. This difficulty is compounded by the dynamic nature of the upper estuary's aquatic habitats, which naturally experience tremendous temporal variability, largely due to the region's Mediterranean climate. One approach to understanding how the system historically supported native wildlife is through a lens of landscape ecology (Whipple et al. 2012; SFEI-ASC 2014). This memorandum documents the first efforts to understand the landscape ecology of the upper estuary, comprising the Sacramento-San Joaquin River Delta and Suisun Bay, using a 3D hydrodynamic model of the pre-development system. By studying the pre-development landscape, we hope to gain insight into the deficiencies of the contemporary landscape and to help develop solutions for remedying these deficiencies.

Although some might note an apparent contradiction of terms, the themes of *landscape* ecology are useful for understanding *aquatic* environments (Wiens 2002). In aquatic systems, as in terrestrial ones, different areas are characterized by different habitat qualities, the boundaries between these areas affect the flows and connectivity between them, and important ecological patterns and processes operate at different scales of time and space. It is noted, however, that aquatic landscapes (including the estuarine-riverine landscape of the Delta) are somewhat unique since the medium in which they are embedded—water—exerts such a strong, variable, and directional force on the system. Water flow makes the patch structure of these landscapes quite dynamic since aquatic patches change (in size, shape, and composition) as flows vary.

This dynamic nature of aquatic landscapes makes hydrodynamic models, which can be used to represent, track, visualize, and quantify various qualities of the aquatic environment, particularly useful tools for studying the landscape ecology of the system. Up until now, our efforts to understand landscape-scale change in the upper estuary have primarily focused on the two-dimensional changes in the spatial extent and distribution of habitat types, including aquatic habitat types such as rivers, tidal sloughs, and ponds, and wetlands (or semi-aquatic habitats) such as floodplains, tidal marshes, and vernal pools (SFEI-ASC 2014). This approach has proved useful for understanding how the landscape worked historically to support native Delta wildlife, but it ultimately has limited utility for understanding how the Delta's complicated hydrodynamics drove ecological processes and supported ecological functions in the pre-development landscape. This technical memorandum discusses ways in which hydrodynamic models of the pre-development and contemporary upper estuary can help us to close this gap in our understanding.

As a new tool, the 3-D hydrodynamic model of the pre-development upper estuary should help the scientific community answer fundamental questions about how the estuary has changed that we have not been able to answer using only primary historical sources (e.g., maps, photographs, and texts). This is a fairly ambitious and novel undertaking. We know of only one other study (Thomas et al. 2002) that has developed a detailed 3-D hydrodynamic model of a historical landscape, and no other projects to

develop 3-D hydrodynamic models of a landscape prior to industrial anthropogenic modifications. This work is also unique for its impressive scale; the model covers approximately 3,600 km², an area larger than the state of Rhode Island. Finally, the availability of spatially explicit information on pre-development vegetation communities and habitat types (Goals Project 1999, Whipple et al. 2012) to complement the pre-development hydrodynamic model presents a unique opportunity to assess changes in a wide range of physical and ecological processes.

This project has been a collaborative effort between researchers at multiple institutions, including the San Francisco Estuary Institute (SFEI), UC Davis Center for Watershed Science (UCD), Resource Management Associates (RMA), California Department of Water Resources (DWR), and Metropolitan Water District of Southern California (MWD). Funding for SFEI's contribution is from MWD. This manuscript draws heavily from the Phase 2 Technical Memorandum developed by RMA (2015), which presents the model results that are the subject of discussion in the second section of this manuscript.

How to read this report

This memorandum is composed of two main sections. The first, "Background: Hydrodynamics and the landscape ecology of the pre-development Delta" presents some questions that the hydrodynamic models might help answer in order to understand how the historical system functioned to support native wildlife (and ultimately how these functions might be regained in the future). This section is based on a review of the available literature and ongoing discussions with regional scientists. It is organized around some of the central themes of landscape ecology.

The second section, "Results: Ecological implications of the hydrodynamic model analyses," takes results from analyses conducted with the models, which were chosen, at least in part, to answer some of the questions outlined in the first section, and discusses the specific ecological implications of these analyses. This second section is summarized in Table 1 above. It should be noted that neither of these sections is comprehensive. Given the complexity of ecological systems (especially estuarine ones, and particularly the upper part of San Francisco Estuary), we have attempted only to compile a selection of ways in which the models and their preliminary results might be used to understand the ecological implications of hydrodynamic changes.

A note on coupling hydrodynamic and ecological models

Many of the questions about the estuary's ecology the hydrodynamic models could help us answer might be addressed through the pairing of hydrodynamic and ecological models. In a recent paper, Ganju et al. (2015) review the history of coupling these two kinds of models and describe some of the associated challenges. Much of what they discuss is highly relevant to our goal of using the pre-development hydrodynamic model to better understand the ecology of San Francisco Estuary.

The authors note that the need to couple hydrodynamic and ecological models to address research and managements questions is clear given the critical feedbacks biotic and physical processes. They stress the complexity of ecological systems, writing that "ecological systems are characterized by high levels of individual variation, weak explanatory relationships, strong dependence on previous events, and

numerous potential future states that are difficult to predict.” As a result, when it comes to numerical modeling, the equations that govern estuarine hydrodynamics are “well constrained and tractable,” but ecological models are more limited by the lack of fundamental deterministic equations. They also note that the ability to model many ecological processes is still notably limited by observational data availability and the relative difficulty of collecting field measurements of key ecological variables. Despite these challenges, the authors remain optimistic, noting how recent advances suggest that hydrodynamic, ecological, and paired hydrodynamic-ecological estuarine models will continue to improve in realism, precision, and accuracy.

Background: Hydrodynamics and the landscape ecology of the pre-development system

Habitat availability and heterogeneity

A central theme of landscape ecology is that landscapes are spatially heterogeneous places and that the composition, configuration, and arrangement of pieces in landscape mosaics influence what goes on within and among individual pieces (Turner 1989, Wiens et al. 1993, Wiens et al. in press). Landscapes can be thought of as mosaics of relatively discrete “patches” that each differ in their physical and biological attributes. To the organisms occupying a landscape, these differences may reflect differences in patch quality and the relative costs or benefits of being in a particular patch (Wiens 1997). Although this framework was originally developed for terrestrial landscapes, it also applies to aquatic and semi-aquatic landscapes like the upper estuary (Wiens 2002).

Abiotic qualities of aquatic and semi-aquatic environments such as salinity, temperature, turbidity, residence time, inundation frequency, local hydraulics, and chemical composition all vary across time and space in the upper estuary. These environmental gradients can directly affect ecological processes and influence (or even outright define) the extent, quality, and availability of habitat. Spatial and temporal gradients directly affect key ecological processes and can ultimately translate into strong effects on biodiversity, productivity, and population stability (Frenette et al. 2006 and references therein). Environmental variables interact at multiple spatial and temporal scales to define the patch structure of aquatic and semi-aquatic environments and to create habitat heterogeneity. There are many examples of how, in the pre-development system, aquatic habitats were heterogeneous at multiple scales, providing support to aquatic organisms at the individual, species, and community levels (Whipple et al. 2012, SFEI-ASC 2014). Many of the outstanding questions about how the upper estuary functioned prior to major anthropogenic modifications deal with the extent and distribution of habitats for native wildlife and how the physical qualities of the landscape influenced the availability of these habitats.

With this in mind, the themes outlined below all deal with the overarching questions of how specific environmental gradients have been altered, how these changes have possibly affected habitat heterogeneity in the upper estuary, and what it all might mean for the estuary’s native wildlife. In general, it is only the goal of this section to *raise* questions that can be examined using the models, not necessarily to answer them (though we do summarize what is known and present any existing hypotheses about the how environmental gradients have been altered). Some answers to the various questions are presented in the second section of this report (“Results: Ecological implications of the hydrodynamic model analyses”).

How has the **salinity** of the estuary been altered?

One of the defining principles of estuarine ecology is that biological communities vary along the estuarine salinity gradient that forms from the mixing of oceanic saltwater downstream and riverine

freshwater upstream (Cloern et al. 2016). As an estuary's salinity gradient varies, so too does the distribution and abundance of the estuary's biota (Cloern et al. 2016). In this section, we primarily focus on the role salinity plays in structuring tidal marsh communities, and consider specific aspects of estuarine salinity that might be explored using the pre-development and contemporary hydrodynamic models. At the end of the section we spend a bit of time discussing the relationship between freshwater flows (and X2) to aquatic estuarine organisms, which is of particular research and management interest.

The estuary's salinity gradient plays a critical role in structuring the distribution of tidal marsh plant species at the landscape scale (e.g., Culbertson 2001, Watson and Byrne 2009). Salinity influences vegetation directly by limiting plant growth, and indirectly by influencing competition, parasitism, and other biotic interactions (Culbertson 2001). Because salinity is the most naturally variable environmental condition affecting marsh plant distributions, salinity and changes in salinity are thought to be responsible for most of the changes in the abundance and distribution of tidal marsh vegetation over time (Watson and Byrne 2009). As noted by Watson and Byrne (2009), salinity naturally varies over the course of a season, inter-annually due to year-to-year variability in precipitation, due to longer-term climate variability and climate change, and due to changes in estuarine morphology. Because each of these factors can be examined using the pre-development and contemporary hydrodynamic models, the models have potential to shed light on how historical changes in estuarine hydrodynamics might have affected the distribution and composition of tidal marsh plant communities.

To understand implications of changes in the salinity of the estuary since the pre-development period, future work should attempt to model soil or "pore water" salinity, which is generally the best known predictor of the presence or absence of individual marsh plant species (Watson and Byrne 2009). Specifically, the soil salinity of the rooting zone is known to underlie regional distribution patterns in the estuary's tidal marshes (Culbertson 2001). Surface water is probably the dominant factor influencing soil salinity in lower tidal marshes with higher inundation frequencies, but its influence on soil salinity begins to decrease as marsh elevation and inundation frequency decreases (de Leeuw et al. 1991). Soil salinity is influenced not only by surface water salinity, which has a dominant influence at lower intertidal sites with higher inundation frequencies, but also by factors such as inundation frequency and duration, precipitation, plant water uptake, and evapotranspiration (Parker et al. 2012). Additionally, soil salinity is modified by biological processes through feedback mechanisms, such as the density of the plant canopy, which influences solar insolation, the rate of evapotranspiration, and ultimately the concentration of salts at the soil surface (Parker et al. 2012 and references therein). Soil salinity has been successfully modeled in other tidal marsh systems (Wang et al. 2007).

One important aspect of the estuary's salinity gradient is its seasonal and annual variability. A prevailing conceptual model of ecosystem processes in the estuary holds that variability in flow/salinity is a key physical-chemical process contributing to ecosystem resilience (Lund et al. 2007 in Enright and Culbertson 2009). A corollary of this conceptual model is that native species evolved under variable conditions and may therefore lose competitive advantage by temporal homogenization of the flow/salinity regime (Enright and Culbertson 2009). Increasing (or perhaps "restoring") temporal variability in salinity is one possible method for limiting the negative effects of invasive species, including overbite clam, Brazilian waterweed, and the Asiatic clam, which all tend to prefer stable salinities or

relatively constant freshwater flows (Lund et al. 2007). Although historical salinity data (post-1921) show that the state and federal water projects have dampened seasonal and annual salinity variability by storing winter runoff and releasing it to meet demands during the dry season (e.g. Enright and Culbertson 2009, Hutton et al. 2016), there has been no consensus on the relative magnitude of salinity variability during the pre-development period. It has been hypothesized that the hydrology of the pre-development system, which featured extensive flood basins that stored floodwaters during the wet season and then slowly drained into the dry season, may have reduced or buffered seasonal variability in salinity (e.g. Enright and Culbertson 2009, Whipple et al. 2012). Using the models to analyze seasonal and annual variability in salinity across multiple water year types would help to answer these questions.

As one example of its importance, interannual variability in salinity appears to strongly influence the composition of tidal marsh plant communities, a process that is perhaps best evidenced by historical shifts in marsh species distributions associated both with droughts and extreme wet years. Droughts during the 1970s, for example, are known to have triggered a decrease in the abundance of bulrush (*Schoenoplectus* spp.) in marshes bordering Carquinez Straight and a subsequent colonization of these areas by the halophyte *Sarcocornia pacifica* (Atwater et al. 1979). In Suisun Bay, droughts coincided with the rapid upstream movement of *Spartina foliosa* (Collins and Foin 1992). Changes in plant distribution attributed to drought often reverse in the years after extreme conditions abate, but not necessarily entirely (Josh Collins, personal communication). Meanwhile, extreme wet years are known to promote the establishment of persistent stands of *Bolboschoenus maritimus* (generally a brackish marsh species) in the low-to-high marsh transition zone of salt marshes (Parker et al. 2012) and to increase the seed production, local distribution, and population size of certain species, including *Grindelia stricta* and *Atriplex triangularis*. *Grindelia* populations doubled at China Camp marsh following El Niño conditions in 1997-1998, and individuals that established away from tidal channels persisted for a few growing seasons before dying out (Parker et al. 2012). In this way, interannual variability in salinity has functioned in the recent past to create vegetative and structural diversity in estuarine wetlands.

Insofar as seasonal and interannual variability in marsh salinity can drive changes in the distribution and diversity of tidal marsh plants, the same should be true of tidal marsh animals. A greater diversity of plant species could provide animals with a wider range of microhabitats, a greater variety of food resources, greater structural diversity, and, as a result of the latter, a reduced risk of predation (Sustaita et al. 2011 and references therein). Complex landscapes are expected to promote genotypic variability, which is important for the long-term adaptive capacity of marsh animal populations. In the San Francisco Estuary, Suisun Marsh is the center of plant species diversity (Watson and Byrne 2009) and features a number of different marsh plant assemblages, a factor often attributed to the variable salinities that are characteristic of the embayment. It has been suggested that this floristic habitat diversity could drive metapopulation dynamics and contribute to the relatively high genetic diversity found in the population of salt marsh harvest mouse (*Reithrodontomys raviventris halicoetes*; a federally endangered species) found in Suisun Marsh (Sustaita et al. 2011). Similarly, in the estuary, morphological and genetic divergence of Song Sparrows is correlated with salinity, which means it is possible that variation in salinity (and others factors like vegetation and available food resources with which salinity is correlated) affects the selective landscape to which sparrow morphology responds

(Chan and Arcese 2003). At a simpler level, there are number of known relationships between salinity and how animals utilize marshes. California red-legged frogs (*Rana draytonii*), for example, breed in marshes when water salinity is low (tadpole abundance is highest when water salinity is less than 6.5 ppt; Jennings 1999). Mean salinity is also an important predictor of Salt Marsh Common Yellowthroat (*Geothlypis trichas sinuosa*) abundance (Stralberg et al. 2010), and the species is known to move in and out of marshes as salinities rise and fall (Josh Collins, personal communication). We expect seasonal and interannual variability to be especially relevant for species like the Common Yellowthroat, which are thought to respond to environmental variables over relatively short time scales (see Stralberg et al. 2010).

Simenstad et al. (2000) speculate that the ecological consequences of temporal variability in salinity are ultimately dependent to a large degree on landscape structure. Continuous marsh patches and corridors along the estuarine gradient would be expected to increase the viability of movement and habitat availability for both aquatic and terrestrial estuarine species that need to migrate as the salinity field shifts. Conversely, significant gaps in natural landscape structure (i.e. areas where tidal channels and marshes have been diked and filled) are expected to be detrimental. The hydrodynamic models could be used to quantify the distribution of available marsh and channel habitats across the salinity gradient at different flows in both the pre-development and contemporary Delta. Comparing the results could help to identify where there are notable “gaps” in availability of habitat as the salt field shifts. Such an analysis would be more nuanced than a simple two dimensional analysis of the distribution of marsh and tidal channel habitat across the longitudinal axis of the estuary.

Though this section has focused on the implications of changes in salinity on tidal marsh communities, the effects of salinity are also pronounced for aquatic organisms. This has perhaps been best studied with regards to the position of the 2 psu bottom salinity isohaline, known as X2 (RMA 2015). Though the primary mechanisms driving the relationship are the subject of ongoing research, the position of X2 is known to correlate with the abundance of many aquatic organisms (Jassby et al. 1995, Kimmerer 2002, Kimmerer et al. 2009). Specifically, there is a negative relationship between X2 and population survival/abundance for many estuarine species, including Bay shrimp, longfin smelt, striped bass, Pacific herring, starry flounder, Sacramento splittail, and Pacific sanddab. Though the abundance of these species correlates with this measurement of estuarine salinity, it is important to remember that the relationships are not necessarily caused by changes in salinity. Isolating the effect of salinity is challenging since there are so many covariates (see Kimmerer 2002). Without a better understanding of the mechanisms behind the X2-species relationships, it will be somewhat difficult to infer what X2 “means” in the context of the pre-development system and to interpret the ecological implications of any changes in isohaline position. As a starting place, we reviewed each of the likely mechanisms described by Kimmerer (2002) and developed a hypothesis for the effect size of each mechanism in the pre-development system relative to existing conditions (Table 2). Essentially, we accepted each mechanism as “true” and then, based on our understanding of the pre-development system, determined whether the mechanism would have been more or less pronounced in the historical system. In practice, we conceptualized whether the slope of the line relating flow to each mechanism likely increased or decreased since the historical period and recorded the assumptions that led us to each

Table 2. Likely mechanisms for effects of flow on estuarine biota (derived from **Kimmerer 2002**; first 3 columns) with our hypotheses for the strength of the mechanism in the pre-development estuary relative to today. In the final column we also note whether we think each mechanism (or at least a component of the mechanism) can be easily evaluated using the hydrodynamic models.

Mechanism index #	Mechanism type	Mechanism	Hypothesized relative effect size of mechanism in pre-development system	Can any portion of this mechanism be this be easily evaluated using the hydrodynamic models?
1	Bottom-up	Nutrient loading increases with flow, stimulating primary production, which is passed up the food web.	Probably greater in the predevelopment system: <ul style="list-style-type: none"> assuming nutrient levels were lower in the during the predevelopment period (Robinson et al. 2016) and that the predevelopment system was more frequently nutrient limited 	Not yet (would need to couple an ecological model, but see Robinson et al. 2016)
2	Bottom-up	Stratification increases with freshwater flow due to compression of the salinity gradient, stimulating primary production, which is passed up the food web.	Probably less in pre-development system: <ul style="list-style-type: none"> assuming the proportion of total primary productivity derived from phytoplankton was relatively small in pre-development system (Robinson et al. 2016), thus decreasing the rate at which increases in phytoplankton-derived primary production increase total primary production 	Yes (the hydrodynamic models should be able to compare the extent/degree of stratification across a range of flows)
3	Bottom-up	Loading of organic matter increases with flow, stimulating bacterial production, which is passed up the food web.	Probably greater in pre-development system: <ul style="list-style-type: none"> assuming organic matter production was higher in the pre-development system and that the positive slope of the flow-organic matter relationship was greater in the pre-development system (given the pre-development system's extensive vegetated floodplains; see Robinson et al. 2016) 	Perhaps (the hydrodynamic models could potentially compare organic matter loading rates from in-estuary sources--such as marshes and riparian habitats--using particle tracking models [or another technique] and some simplifying assumptions about the rate of organic matter accumulation in these systems)
4	Bottom-up	Osmotic stress shifts benthic community from salt-tolerant to freshwater when flow is high, resulting in suppression of predators or grazers.	Possibly less in pre-development system: <ul style="list-style-type: none"> assuming lower densities of grazers (given absence of invasive clams), which would increase the negative slope of the flow-grazing relationship (making the slope less negative) 	Perhaps (but would require major simplifying assumptions about the grazing rates at different salinities in pre-development and contemporary systems)
5	Direct	High flow provides clearer cues to guide migration.	Probably less in pre-development system with respect to <i>salmon upmigration</i> : <ul style="list-style-type: none"> assuming minimum flow thresholds for impairment of migratory cues were lower (due to absence of reverse flows and a more "coherent" channel network), thus decreasing positive slope of the flow-migration rate relationship 	Perhaps (see "Source water fingerprinting" section for how the models might be used to understand migration cues)
6	Indirect	Loading of sediment increases with increasing flow, increasing turbidity, reducing rates of capture by visual predators, increasing survival of larvae and juveniles.	Probably greater in pre-development system: <ul style="list-style-type: none"> assuming that positive slope of the flow-sediment loading relationship was greater in the pre-development system (Robinson et al. 2016) Probably less in pre-development system: <ul style="list-style-type: none"> assuming that other mechanisms for predator avoidance (e.g. holding in shallow habitats) were greater in the pre-development system, decreasing the positive slope of the flow-survival relationship 	Not yet (would require major simplifying assumptions and coupling with an ecological model)
7	Direct or Indirect	Freshwater flow dilutes contaminants resulting in higher survival with high flow either directly or through food web. Available evidence suggests loading of contaminants increases with increasing rainfall and freshwater flow.	Probably less in pre-development system: <ul style="list-style-type: none"> assuming that contaminant sources and loading rates were negligible in pre-development system at all flows 	Not yet (would require major simplifying assumptions and coupling with an ecological model)
8	Direct	High flow transports biota more rapidly to rearing areas, e.g., low-salinity zone, where daily growth rate is higher or mortality is lower than elsewhere	Unknown	Yes (the hydrodynamic models should be able to compare the transport of biota extent/degree of stratification across a range of flows)
9	Direct	Influence of export pumping decreases as the fraction of freshwater pumped decreases, or as habitat moves seaward away from pumps.	Less in pre-development system: <ul style="list-style-type: none"> given the absence of pumps 	N/A
10	Indirect	Physical area of, or access to, suitable spawning or rearing habitat increases with increasing flow or seaward X2.	Probably less in pre-development system with respect to <i>low-salinity habitats</i> : <ul style="list-style-type: none"> assuming that the positive slope of the flow-LSZ habitat area was lower in the pre-development system (because there was less variability in the physical area of LSZ habitat for across the full range of flows) Probably greater in the pre-development system with respect to <i>floodplain habitats</i> : <ul style="list-style-type: none"> assuming that positive slope of the flow-floodplain habitat relationship was greater in the pre-development system (because there was substantially more floodplain habitat; SFEI-ASC 2014) 	Yes (the hydrodynamic models can be used to calculate the area and volume of the LSZ in the pre-development system)
11	Direct	Asymmetric residual (e.g., gravitational) circulation increases with flow, and interacts with vertical position to reduce seaward losses or increase landward movement to rearing areas.	Unknown	Yes (the hydrodynamic models should be able to compare this hydrodynamic process in the pre-development and contemporary systems)

conclusion. Note that there is a great deal of uncertainty in many of these hypotheses. Also note that this analysis does make any assumptions about whether any one mechanism is more or less “important” or likely to explain flow-species relationships than another in either the pre-development of contemporary systems.

How has the temperature of the estuary been altered?

Water temperature has an “all-pervasive” influence on aquatic organisms and affects estuarine habitat suitability through a variety of mechanisms (Coutant 1976). At the most basic level, most aquatic organisms have a characteristic thermal range, and temperature can have a direct or indirect lethal effect when it falls outside of this range. Temperature acts as a controlling factor, influencing the metabolism, growth, and activity of estuarine biota; it can also serve as a “directing agent” when organisms travel along temperature gradients or respond to temperature cues (Coutant 1976).

Examples of these influences from the upper estuary are numerous. Water temperature regulates the rates of phytoplankton photosynthesis and respiration—thus affecting aquatic net primary productivity—as well as the growth rate of zooplankton (Cloern 2007). Temperature also affects detrital primary productivity pathways, since it greatly influences the bioavailability of organic matter through its effect on microbial decomposition rates (Robinson et al. 2016). Fish species of concern in the Delta, including delta smelt, chinook salmon, and Sacramento splittail, are all sensitive to water temperature at some point in their life cycle (Wagner 2012 and references therein). Summertime water temperatures in the upper estuary—which average 21-24°C in July (Nobriga et al. 2008)—already regularly threaten delta smelt survival. Smelt abundance is severely reduced in areas when water temperatures near or exceed their 25 °C lethal limit (Nobriga et al. 2008; Swanson et al. 2000). Juvenile chinook salmon reared at 21-24°C have lower growth rates, impaired smoltification indices, and increased predation vulnerability compared with juveniles reared at lower temperatures (Marine and Cech 2004). Up to a point, however, warmer temperatures—such as those associated with off channel habitats along the Sacramento—may promote higher juvenile salmon growth rates and thus improve their survival (Limm and Marchetti 2009). Laboratory studies suggest that juvenile salmon growth rates increase with temperature up to approximately 19°C.

It is difficult to hypothesize how large scale temperature gradients have been altered in the Delta due to competing influencing factors. Habitat losses in the Delta—such as the clearing of riparian forests and diking of freshwater emergent wetlands—are expected to have significantly reduced vegetative shading of the aquatic environments in the upper estuary (a change that would be expected to increase water temperatures over time). The magnitude of this effect is difficult to quantify, but is presumably significant. In the contemporary system, restored emergent marshes dramatically lower surface water temperatures relative to areas of aquatic vegetation with no plant canopy shading the water surface (Miller and Fuji 2010). Upstream losses of riparian vegetation have also potentially increased the temperature of Delta inflows. An increase instream temperatures after forest clearing is well documented in other systems, an effect not only attributed to an increase in solar radiation, but also to increased wind speed and exposure to air advected from clearings (Moore et al. 2005).

Research conducted in Suisun Marsh suggests that tidal marsh plain inundation, the extent of which has been significantly reduced since the pre-development period—also has a dramatic effect on water temperature (Enright et al. 2013). When water spills onto the marsh plain during high tides, the surface area of the total water volume exposed to the air increases, which magnifies the effect of climatic and meteorological drivers on water temperature (e.g., air temperature, humidity, solar insolation, and wind). As a result, water temperature variability is much greater over both tidal and fortnightly timescales in natural sloughs with connectivity to the marsh plain than in modified sloughs where this connectivity has been severed by artificial levees. Enright et al. (2013) found that water exiting First Mallard Slough (which has a natural morphology) was cooled by 6 °C over the course of night-time summer spring tide events. This cooling effect was only half as pronounced in Sheldrake Slough (which has a modified morphology). Because of the phase shift in the tidal-diurnal cycle (335 years long), these summer time spring tide events can also occur during the day, which would likely elevate water temperatures (Robinson et al. 2016).

For reasons that are similar to the effects of tidal marsh plain inundation, the Delta's extensive flood basins, which frequently held water at relatively shallow depths for months at a time and have no real functional equivalent in the contemporary system, also probably affected temperature (Whipple et al. 2012, SFEI-ASC 2014). Trappers working along the Mokelumne River during the summer of 1833 complained that the shallow water in the flood basin was “very warm and we cannot get to the river where it might be a little colder” (Whipple 2012 and references therein). This quote, though anecdotal, illustrates the potential effects of the interaction between the Delta's morphology and hydrology on spatial heterogeneity in temperature.

In general, the diverse assortment of aquatic habitat types—which included tidal and fluvial mainstem channels, tidal dead-end sloughs, intermittent streams, intermittent and perennial ponds and lakes, and various floodplain habitats—likely contributed to spatial and temporal heterogeneity in the estuary's thermal environments (see Limm and Marchetti 2009). As with other abiotic physical gradients, it is likely that this heterogeneity has decreased since the pre-development period with alterations to the estuary's hydrology and geometry (Moyle et al. 2010). The hydrodynamic models should be a useful tool for testing this hypothesis and understanding how the landscape changes described above have affected temperature dynamics in the upper estuary.

How have water residence times in the estuary been altered?

Residence time is a transport time scale that measures water-mass retention within a defined area (Monsen et al. 2002). It measures how long a water parcel, starting from a specified location in a waterbody, remains in the waterbody before exiting. Along with other transport time scales, residence time is a useful concept and measurement for understanding spatial and temporal variability in environmental factors in aquatic systems.

As partially reviewed by Monsen et al. (2002), many ecological processes—including the occurrence of harmful algal blooms, distribution of pelagic bacteria, export of copepod life stages, partitioning of primary production between macroalgae and phytoplankton, and variability of dissolved nutrient concentrations—are strongly influenced by residence time in estuaries. As suggested by these particular

examples, residence time is particularly important for a variety of food web processes. High residence times allow for accumulation of phytoplankton biomass, which is currently the dominant food supply to the planktonic food web in the Delta (Sobczak et al. 2002). According to Jassby (2008), the main source of interannual phytoplankton variability in the Delta during 1996–2005, including the upward trend, appears to have been freshwater flow variability and its effect on particle residence time. Increased residence times would also be expected to increase the metabolism of particulate organic matter (such as plant detritus outwelled from tidal marshes) by microorganisms and the bioavailability of this carbon within the Delta. It has been hypothesized that marsh-based productivity might have been more important in the pre-development system (Robinson et al. 2016) and areas with high residence time might have been key for processing this carbon source.

Changes in the Delta's geometry have probably affected the residence time of its aquatic habitats. One of the most dramatic changes in geometry is the loss of the Delta's blind dendritic channels and increased connectivity between the remaining flow-through channels. It is hypothesized that the pre-development Delta's blind channels each featured a pronounced residence time gradient scaled to spring-neap variability in tidal excursion length within these channels (Enright 2008). Put another way, we expect that water at the heads of the Delta's blind channels only exchanged with water from the mainstem channel during spring tides, and that residence time in these areas was relatively high as a result. In the modern system, previous modelling results (RMA 2005) have shown that residence time is substantially longer in the Sacramento Deep Water Ship Channel than most other portions of the Delta, especially during periods of low inflow, a quality some have hypothesized is related to the relatively high densities of delta smelt found there. Finally, although likely difficult to model, the pre-development marshes also likely featured myriad aquatic microhabitats (<1 cm deep) that remained on the emergent marsh surface after ebb-tides that had even higher residence times. In other systems, these environments are important for the early life stages of multiple organisms (e.g., Kneib 1997a). With the dramatic loss of blind channels and tidal marsh habitats, as well as the loss of intermittently connected ponds and lakes, we expect that there is a lower availability of high-residence time habitats in the contemporary Delta, with potential implications for the amount and bioavailability of primary production in the Delta.

It is also likely that *system-wide* residence time in the Delta has been altered. Some change has occurred only over the last few decades: Jassby (2008) describes appreciable increase (9 days) in the mean residence time of the Delta as a whole (measured as the time it takes for particles released in the Sacramento River to pass into Suisun Bay) between 1996 and 2004, a change attributed to freshwater flow variability (higher flows are associated with shorter system residence times). The implications of this change are potentially significant; Jassby notes that a one week increase in the system's residence time would translate to a four-fold increase in biomass production (assuming a conservative value for the exponential phytoplankton net increase rate). Although uncertainties about changes in related variables (such as turbidity and temperature) would make direct to draw conclusions about differences between the pre-development and contemporary systems based on changes in residence time alone, the results of a system-wide residence time analysis would still be useful. Changes in flows since the predevelopment period have also affected system residence time, but the direction of this change

probably varies by season (the pre-development system probably generally had higher flows in the winter through early summer, but lower flows in the late summer through fall; see RMA 2015). That said, the loss of the Delta's extensive network of flood basins, blind channels, and marshes has probably decreased the system's residence time over time. These pre-development landscape features also may have decoupled the negative relationship between flows and system-wide residence time that is observed today (at a certain point, high flows activated the Delta's floodplains, which probably had much higher residence times than the mainstem channel). The hydrodynamic models should be used to test these hypotheses.

How have novel aquatic habitat types affected habitat heterogeneity?

The contemporary Delta features an assortment of aquatic habitat types that did not exist in the pre-development system. Interestingly, however, some of these novel habitat types at least superficially resemble prominent habitat types of the pre-development system. Examples include the contemporary Delta's flooded islands and the pre-development Delta's lakes (both are non-channelized open water habitats); as well as the contemporary Delta's Sacramento Deepwater Ship Channel and the pre-development Delta's dendritic channel networks (both function as relatively long blind tidal channels). Since current restoration and management strategies for the Delta emphasize the restoration of specific ecological functions required to sustain native wildlife, it is important to understand how the functional attributes of the Delta's novel habitat types compare to those of the pre-development habitats they resemble. Below we briefly describe one example of novel aquatic habitats (flooded islands), the pre-development habitats they resemble (lakes and ponds), and how examining their respective hydrodynamic attributes with the 3D models might prove useful.

Existing historical data suggests that lakes in the pre-development Delta varied in size, depth, shape, landscape position, and hydrologic regime, but that most all had convoluted, vegetated edges that increased the capacity of exchange at the border of the aquatic environment (Whipple et al. 2012). These lakes and ponds were certainly important habitat for many native fish (Whipple et al. 2012), and it has been noted that many native species—including Sacramento perch, Sacramento blackfish, amongst others—exhibit physiological and behavioral adaptations that seem divorced from the present landscape but seem uniquely adapted to a pre-development landscape that featured many isolated, warm, shallow lakes and ponds (Moyle 2002 in Whipple et al. 2012). Lakes and ponds also featured a number of aquatic plant species (Whipple et al 2012), including the yellow pond lily (*Nuphar polysepala*), which is now largely extirpated from the Delta. We are not aware of any work explaining the local decline of this species, but suspect the hydrodynamic models could help identify changes in the distribution of physical conditions required for its growth and potential opportunities for its reintroduction.

Flooded islands, which resemble pre-development lakes in their size and shape, now account for most of the Delta's non-channelized open water habitat. Since additional islands are expected to flood in the future, it is important to understand how they relate to the lakes and ponds of the pre-development system, especially in regards to the important habitat attributes described above (salinity, temperature, and residence time). Though the effects of an increase in the amount of flooded islands habitat on native fish are potentially favorable, there is a great deal of uncertainty (Moyle 2008). Despite being superficially similar, existing flooded island habitats in the Delta vary in their production of

phytoplankton biomass (Lucas et al. 2002) and in the level of support they ultimately provide for native fish (Lund et al. 2012). A useful next step might be to follow the general approach of Lucas et al. (2002), use the hydrodynamic models to assess the variability within and between the pre-development lakes and ponds, and then compare this variability to that of the flooded islands. The goal of such an analysis would be to inform discussions around how to alter or manage flooded islands to maximize the benefit they provide to native wildlife.

Landscape connectivity

In studies of riverine landscapes, connectivity is defined as the flow of energy, matter, and organisms between elements of a landscape via the aqueous medium (Ward et al. 2002). Connectivity provides the connections, space, and physical and biological gradients needed for species to move in response to changing conditions (Beller et al. 2015). It also allows organisms to escape unfavorable conditions, take advantage of redistributed or newly available resources, recolonize areas after a disturbance, and exchange genes between populations.

The appropriate degree of connectivity varies with context (Beller et al. 2015). It is dependent on the organism/process and on spatiotemporal scale (see examples in Wiens 2002). Human activities often reduce connectivity of aquatic habitats (e.g. through the construction of dams), which presents a threat to persistence and viability of certain populations and species, but there are also situations where artificially increasing connectivity may result in deleterious outcomes (see Crook et al. 2015 for a good review of the subject). “Over-connectivity” can degrade the integrity and identity of discrete landscape elements, alter the physical environment to which species are adapted, and facilitate transmission of stressors between different parts of the landscape. Given the nuanced and potentially complicated outcomes of increased connectivity, it has been recommended that a thorough understanding of natural patterns of connectivity and how these patterns are affected by human activity is necessary to ensure the long-term viability of aquatic organisms (Fullerton et al. 2010 as cited in Crook et al. 2015). The hydrodynamic models of the pre-development and contemporary systems of the upper estuary are uniquely suited to help develop such an understanding.

In this section, we consider the importance of two different kinds of connectivity in the upper estuary: (1) the connectivity within aquatic habitats (water-water connectivity) and (2) the connectivity between water and land (land-water connectivity). We describe what is known or hypothesized about these two kinds of connectivity in the pre-development system, how they have changed over time, and the possible ecological implications. In doing so, we hope to raise questions that can be explored using the hydrodynamic models.

How has connectivity of aquatic habitats been altered?

Many have noted that changes in the Delta’s geometry—including channel cuts, the elimination of blind channels, and channel widening, straightening, and dredging—have likely increased the connectivity of the Delta’s aquatic habitats and homogenized environmental conditions over time (e.g. Lund et al. 2007, Enright 2008, Whipple et al. 2012, SFEI-ASC 2014). Homogenous conditions affect native wildlife by, for example, reducing the range of unique/suitable aquatic habitats, decreasing the “coherence” of the aquatic landscape, increasing the “distance to different” conditions, and decreasing the competitive

advantage of native species that are adapted to variable conditions. Though these conclusions are based on first principles of hydrology and ecology, as well as a sound understanding of both the pre-development and contemporary systems, the effects of “over-connection” in the Delta have never been quantified or explored in detail. To what degree have key environmental gradients actually been homogenized? Are different environmental variables (e.g. salinity, temperature, residence time, velocity) equally affected by over-connection? Have certain regions of the Delta been more or less impacted? Is homogenization mostly driven by loss of local gradients (such as those associated with blind channels), or have large-scale gradients also been affected? The pre-development and contemporary hydrodynamic models can help us answer these questions, and doing so will help to determine mechanisms by which heterogeneity might be restored moving forward (and perhaps tested with a hydrodynamic model of future conditions).

Much can be learned about changes in the connectivity and potential homogenization of aquatic habitats by modeling, mapping, and otherwise quantifying the spatial and temporal variability of the major environmental variables described in the “Habitat availability and heterogeneity” section, specifically salinity, temperature, and residence time. Additionally, however, the hydrodynamic models should be used to explore the connectivity of the aquatic habitats through the lens of population ecology. Via effects on the dispersal and retention of biota, hydrodynamics can play a critical role in the population dynamics of aquatic organisms. This is perhaps especially true for organisms—such as many benthic invertebrates—that are sessile as adults, but have planktonic larval phases. It also is applicable to hydrochoric plants (those dispersed through water). The relative connectivity of different sites in the estuary is expected to affect the connectivity of these organisms across space and time, influencing metapopulation source-sink dynamics and population genetics in the process. Understanding how hydrodynamics have changed in the upper estuary since the pre-development period thus has the potential to improve our knowledge of aquatic ecology, including our management of both threatened and invasive species.

To this end, hydrodynamic models have been successfully used to predict the dispersal of planktonic larvae in numerous systems (e.g., Lundquist et al. 2009, Smyth et al. 2016). Most studies couple 3-D hydrodynamic models with particle tracking, which allows researchers to identify the paths of dispersal that connect isolated populations and to assess how spatiotemporal variability in the intensity of dispersal along these paths influences population connectivity (Haase et al. 2012). Again, it is generally hypothesized that the contemporary Delta’s aquatic habitats are “over-connected” relative to the pre-development system. We suggest that evaluating the dispersal of planktonic life stages of aquatic organisms using the hydrodynamic models —possibly through particle tracking models—is a useful framework with which to evaluate this hypothesis.

Another way to consider changes in the geometry of the Delta and the connectivity of its aquatic habitat is from a standpoint of ecological network structure. Streams can be thought of as “dendritic ecological networks” where connectivity is a function of network topology (the way different branches and nodes are arranged; Campbell Grant et al. 2007). Network topology can affect ecological processes at both the population and community levels (e.g., by differentially mediating the movement of species among branches; Campbell Grant et al. 2007). Where the connectivity of different parts of the network has

increased due to changes in topology (e.g., through the channel cuts in the Delta), disturbances might be more easily transmitted through the network as a whole, resulting in more tightly correlated extinction risks for organisms in different parts of the system (Jones et al. 2000 as cited in Campbell Grant et al. 2007). A Delta-specific example of this might be found in the negative impacts of invasive organisms (such as *Egeria densa* and *Corbicula*) on native wildlife—it is conceivable that increased hydrologic connectivity has facilitated the invasion of these invasive species through the network as a whole. This might be thought of as an example of “over-connectivity” decreasing the resilience of native wildlife via a reduction in redundant systems (Beller et al. 2015).

In their discussion of alluvial rivers, Ward et al. (2002) note that fluvial dynamics, including the expansion and contraction of surface waters, are the primary driving force affecting hydrologic connectivity. Examples of this concept can be found in the pre-development system, especially along the fluvial reaches of the Sacramento and San Joaquin Rivers: small increases in water level would have increase the connectivity of the mainstem channel with side channels and crevasse splays (see Whipple et al. 2012), but larger floods would have driven connectivity of the flood basins and oxbow lakes. Less obviously, perhaps, Ward et al.’s concept can also be applied to the tidal environment. As a stark example, changes in water level are expected to have altered the connectivity of the pre-development Delta’s dendritic tidal sloughs: during low tides, distinct dendritic channel networks occupying the same island would only have been connected via the mainstem channel. At extreme high tides, this connectivity would have been altered, with the channels more closely connected through their tips across the inundated marsh surface (Figure 1).

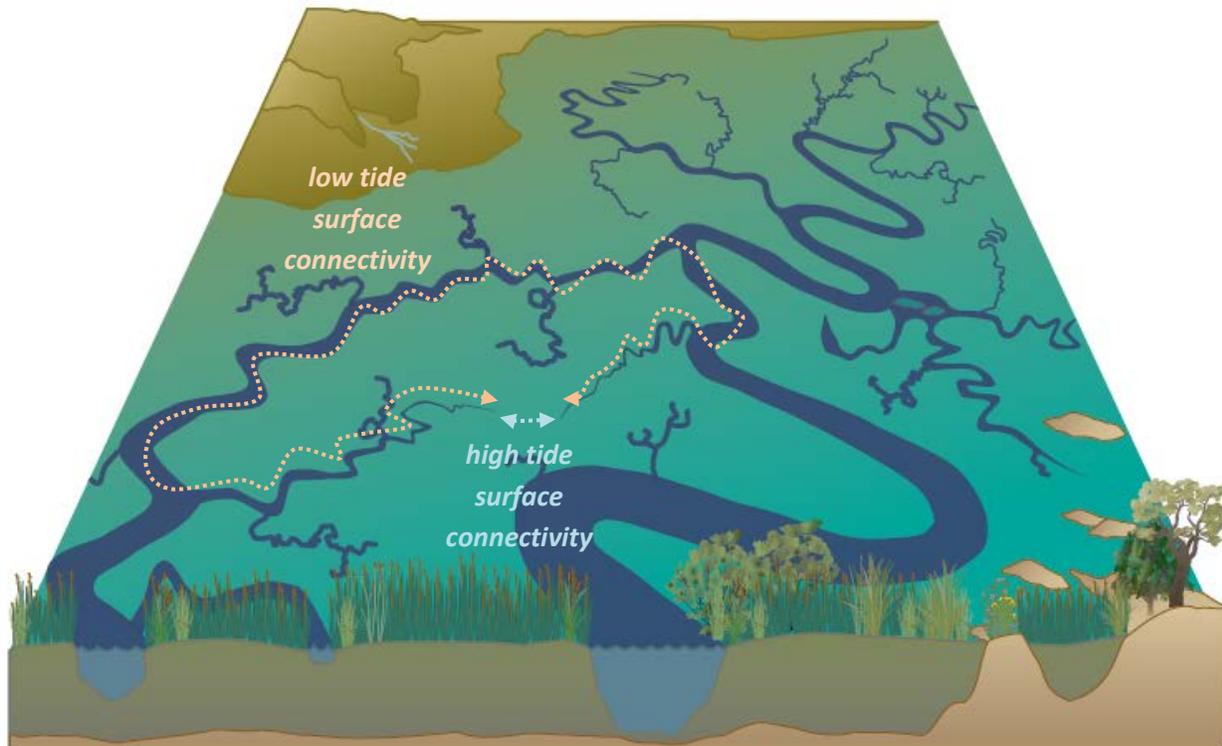


Figure 1. Hydrologic connectivity of tidal habitats in the pre-development system (in this case distinct tidal sloughs) would have varied significantly with tide height. During low tide, water in the tips of dendritic sloughs only exhibited surface connectivity via the mainstem channel; during extreme high tides the tips would have been connected via flows over the marsh plain, a much shorter pathway. In this way, connectivity could vary by as much as two orders of magnitude over the full range of tide heights. Base image from Whipple et al. 2012.

The scale of islands in the Delta meant that connectivity (measured as distance between the tips of the dendritic sloughs) could vary by as much as two orders of magnitude over the full range of tide heights (likely over the spring-neap cycle). On Bethel Island, for example, the heads on Dutch Slough and Sand Mound Slough were more than 50 kilometers apart at low tide via the mainstem Sacramento, but less than 0.5 kilometers apart via flows over the marsh surface. Intermittent connectivity between distinct blind channel networks over the marsh plain is an example of “out-of-network connectivity” that effectively reduces some of the restrictions imposed by the structure of the larger channel network (see Grant et al. 2007). This sort of connectivity (with some “weak links”) may enhance the dynamic stability of the network as a whole (Csermely 2004 in Campbell Grant et al. 2007). Since the sloughs are now permanently connected via cross-channel cuts (Whipple et al. 2012, SFEI-ASC 2012), this variability in connectivity has been eliminated in the contemporary system. At successively smaller scales, meander cuts have likely increased the connectivity and decreased heterogeneity between reach systems, and channel armoring has likely increased the connectivity of and decreased the heterogeneity within reach systems (at the scale of pool/riffle scale). The increase in connectivity likely homogenizes aquatic environmental gradients (see Enright 2008) and would be expected to decrease the range of unique/available aquatic habitats as a result.

How has the connectivity of land and water been altered?

The loss of land-water connectivity in the upper estuary since the pre-development period is profound. In the Delta, the area subject to seasonal fluvial inundation has decreased by approximately 85% (from 117,000 ha to less than 19,000 ha), while the areas subject to tidal inundation has decreased by nearly 98% (from 148,000 ha to 3,300 ha; SFEI-ASC 2014). This change has been driven by changes in the Delta’s geometry and hydrology, particularly the historical reclamation of tidal marshes and fluvial floodplains for agricultural and residential purposes (Whipple et al. 2012). In the Delta alone, more than 1,770 km of artificial levees sever the connectivity between water and land.

The ecological implications of the loss of land-water connectivity are equally profound. Though detailing all the ways in which floodplain and tidal marsh inundation affect ecological processes is outside the scope of this manuscript (refer to Junk et al. [1989] for a review of fluvial floodplains and Palaima [2012] for a review of tidal marshes in San Francisco Estuary), below we highlight how land-water connectivity was likely critical to primary production in the upper estuary.

Briefly, however, it is worth mentioning that, though other efforts have already quantified pre-development land-water connectivity as a function of *area* (Whipple et al. 2012), the connectivity has not yet been quantified as a function of area *and* time. This could be accomplished with the hydrodynamic models relatively simply by multiplying the area of inundated areas by the duration of this inundation (whether over daily, fortnightly, seasonal, annual, or larger time-scales). This metric (in units such as hectare-hours of marsh plain inundation, for example) more directly quantifies land-water connectivity than a simple measurement of area. Due to changes in landscape structure, it is possible that losses in hectare-hours of land-water connectivity are not directly proportional to the loss in total area of this connectivity.

Land-water connectivity is expected to influence a variety of abiotic variables, which, as described in the “Habitat availability and heterogeneity” section above, each have their own effects on ecological processes in the estuary. A good example of this comes from contemporary studies of Suisun Marsh, which show how marsh plain inundation affects water temperature (Enright et al. 2013). As mentioned above, when water spills onto the marsh plain during high tides, the surface area of the total water volume exposed to the air increases, which magnifies the effect of climatic and meteorological drivers on water temperature (e.g., air temperature, humidity, solar insolation, and wind). As a result, water temperature variability is much greater over both tidal and fortnightly timescales in natural sloughs with connectivity to the marsh plain than in modified sloughs where this connectivity has been severed by artificial levees. Though the authors were able to quantify the effect of marsh-plain inundation in a two slough systems, they note that “sophisticated modeling” would be required to properly characterize the effect of changes in land-water connectivity on water temperature dynamics at the full scale of the upper estuary.

Perhaps some of the most fundamental effects of the loss of land-water connectivity are those related to primary production and food-web processes. Today, the Delta is a low-productivity ecosystem, with the majority of its primary production contributed by the photosynthesis of phytoplankton in open water habitats. However, new hypotheses are emerging that suggest that this low primary productivity is not a fundamental attribute of the Delta, but instead largely a consequence of landscape change (Robinson et al. 2016). Specifically, it is hypothesized that the Delta has been transformed from an ecosystem largely dependent on marsh-derived production, to one dependent on production by aquatic plants and algae (despite, according to preliminary calculations a 5-6x *increase* in phytoplankton production since the pre-development period; Robinson et al. 2016). Since it would have been critical to the availability of marsh-derived production in the aquatic environment, a loss of land-water connectivity is major factor implicated in these changes.

Hydrologic connectivity between the marsh plain (intertidal) and open water (subtidal) habitats drives the exchange of materials between these environments. In Suisun Marsh, for example, there is evidence of a chlorophyll a subsidy as high tides drain off the marsh plain and back into the tidal slough network (Enright et al. 2013). Despite its relatively small area, emergent vegetation contributes significantly to the diets of multiple primary consumer groups (including amphipods, insects, zooplankton, and fish) in the northwest Delta (Robinson et al. 2016). Invertebrates that feed directly on the marsh plants (grazers) and detritus (detritivores) are also sometimes available to fish that feed on or near the marsh surface. Delta smelt, for instance, are known to utilize the marshes of Liberty Island and supplement a zooplankton-based diet with larval insects in the spring and amphipods in the winter; marsh habitats are thus hypothesized to provide smelt with high-energy resources that could improve their growth rates (Whitley and Bollens 2014). A large component of net primary productivity derived from marshes, however, would have entered the aquatic food web through a heterotrophic “microbial loop, the process whereby particulate and dissolved organic matter is utilized by bacteria and fungi, which are in turn consumed by flagellates and ciliates. In addition to any outwelling of organic matter and productivity from marshes and floodplains (Odum 2000), land-water connectivity also would have allowed nekton to access the food resources directly at their source (Kneib 1997b). Juvenile salmon

reared in the Delta's seasonal floodplains habitats, for instance, grow significantly larger than those reared within the river's main channel (Sommer et al. 2001; Jeffres et al. 2008). This difference is generally attributed, at least in part, to the higher invertebrate prey availability on floodplains (Gladden and Smock 1990; Sommer et al. 2001).

Given the fundamental importance of primary production—it sets the potential capacity of ecosystems to support animal populations—ways in which the hydrodynamic models can help to understand how productivity has changed over time should be explored. It is likely that the hydrodynamic models will be critical for understanding and describing changes in land-water connectivity in the Delta and the effects of the spatial and temporal variations in the availability of different types of organic matter in the estuary (Robinson et al. 2016). A major area of potential study includes the “influence” and fate of marsh and floodplain subsidies to the aquatic environment. The hydrodynamic models should help to tease apart the scale-dependent effects of habitat loss on food resources, which are not currently well understood (SFEI-ASC 2014).

Results: Ecological implications of the hydrodynamic model analyses

Upper estuary tidal prism

Background

Tidal prism is the volume of water entering and exiting an estuary between high and low tides (our analyses specifically examine the tidal prism of the upper estuary, upstream of Carquinez Strait). The measurement correlates with an estuary's available tidal energy, which in turn influences tidal range and the extent of both tidal and intertidal habitats. Although some have hypothesized that the Delta's tidal prism has decreased over the last 200 years (Rose et al. 1895, Gilbert 1917), competing factors make it difficult to determine how tidal prism might have changed. Factors we expect to have decreased tidal prism since the pre-development period include the widespread reclamation of tidal marshes, diking of low-order tidal channels, and deposition of hydraulic mining debris; those expected to have increased tidal prism include extensive channel dredging, channel widening, flooding of subsided islands, reduced river inflows, in-Delta water exports, and sea-level rise. It is also possible that the Delta's tidal prism is ultimately controlled by the cross-sectional area of Carquinez Strait, which, since it is carved into bedrock (Martin 2004 and references therein), is not thought to have significantly changed over time. The work conducted by the project team represents the first effort to quantify the pre-development Delta's tidal prism using a 3-D hydrodynamic model and to determine if the parameter has changed over time.

Results and implications

Model results described by RMA (2015) suggest that the upper estuary's tidal prism has decreased 2.5% since the predevelopment period, from $205 \times 10^6 \text{ m}^3$ to $200 \times 10^6 \text{ m}^3$. Additional analyses would be needed to explain the factors contributing to this change. There is not enough information, for example, to conclude that the relatively small percent change in tidal prism is due to control enforced by the geometry of Carquinez Strait.

The ecological implications of the relatively small modeled changes in tidal prism are not yet obvious. All else being equal, a decrease in tidal prism would be expected to decrease water velocities and erosion rates within the estuary, promoting the contraction of tidal channel networks and a decrease their hydraulic duty (Allen 1997, Kirwan and Murray 2007). Since these channels are thought to provide a range of ecological functions (e.g. coherent gradients in abiotic conditions and habitats, large food supplies from marsh subsidies and high densities of phytoplankton, low-velocity habitat for juvenile fish holding and rearing; SFEI-ASC 2014), any reduction in the extent would come with a decrease in the provision of these functions. This said, the intense direct modification (destruction) of the Delta's marshes and tidal channel networks makes it difficult to assess any long-term effect of an altered tidal prism on these features. Otherwise, decreases in tidal prism would also be expected to be accompanied by decreases in tidal range and extent. Future work should also examine changes in these parameters,

which have a more direct relationship with the size and distribution of tidal habitats, including tidal wetlands (which also historically provided myriad ecological functions; SFEI-ASC 2014). If the relationship between these parameters and tidal prism is non-linear, a slight decrease in tidal prism could have outsized effects. At the broadest level, it is promising that tidal prism has not substantially decreased since the pre-development period, since the value correlates with the tidal energy that is available for restoring tidal habitats in the upper estuary (see Enright 2014).

Finally, the tidal prism calculations show that peak flood tide flows (associated with mean higher high water) have decreased since the pre-development period, while peak ebb tide flows (associated with mean lower low water) have increased since the historical period. Both modeled systems are ebb-dominant at Carquinez; the dominance is just weaker in the pre-development system. The increase in ebb dominance would theoretically be accompanied by a decrease in tidal advection of materials and organisms from the lower estuary into the upper estuary (though the magnitude of this effect is hard to extrapolate from the modeled velocity values alone). These results are discussed more in the channel velocity section below.

Source water fingerprinting

Background

RMA (2015) used the pre-development and contemporary hydrodynamic models to carry out source water fingerprinting analyses, which tags major riverine inflows with a tracer to visualize general flow patterns and assess the influence of various sources of freshwater entering the Delta. When interpreting these results, it should be noted that calibration of the contemporary model focused on achieving realistic flow and stage values in the Central Delta (which are most critical to the isohaline position analyses) and that there are some known issues with the calibration in the upper reaches of the Delta. Though the calibration is generally characterized as “accurate” or “acceptable” for nearly all of the upper San Joaquin River stations, there is “poor agreement” between modeled and measured stages for three of the five Old River stations (at Frank’s Tract, Rock Slough, and the Delta Mendota Canal). In the North Delta, there are higher modeled flows through Georgiana and Sutter sloughs (distributaries of the Sacramento River) than are actually observed, though the calibration at stations on the Sacramento River itself is considered “accurate” or “acceptable.” Considering this, the source water fingerprinting results and implications drawn from them should be considered preliminary. Improved calibration in upper Delta reaches is needed to draw firm or detailed conclusions.

The distribution and relative concentrations of water from various sources in the Delta are expected to have an influence on any organisms that use stream-specific chemical signals to navigate their environment. One well-studied example of this behavior is natal homing in salmon, the process by which populations of adult salmon migrate from the open ocean to the specific stream of their birth in order to reproduce. Although the mechanisms driving natal homing are multifaceted (Lohmann et al. 2008), olfactory cues are known to be particularly important during salmon’s freshwater migration phase: juvenile salmon “imprint” on the chemical signals of their home stream and then later, as adults, can use

olfactory memory of their home stream waters to navigate upstream to their natal site (e.g., Wisby and Hasler 1951, Dittman and Quinn 1996).

Although not generally implicated as a major factor in the historical decline of Central Valley chinook salmon populations, it is conceivable that altered patterns of stream flow (and the subsequent distribution and concentration of source water and chemical cues) have affected the ability of adults to reliably and efficiently navigate through the Delta during upstream migration. Concerns about impaired navigational ability due changes in hydrodynamics were raised as early as 1970, when Department of Fish and Wildlife scientists suggested that reverse flows in the San Joaquin River—driven by the operation of water export pumps in the south Delta—could have prevented San Joaquin salmon populations from locating home stream waters and contributed to population declines during the early 1960s (Hallock et al. 1970). There is also evidence linking decreased San Joaquin River flows and increased exports in the Delta to an increase in the rate at which San Joaquin adults stray to other river systems (Mesick 2001, Marston et al. 2012). Numerous authors have thus hypothesized that change in the distribution of natal water compromise the ability of salmon to navigate the Delta (EPA 2011, Marston et al. 2012). Though researchers have correlated stray rates with flow parameters, to date no known studies have directly examined how source water distribution (with its explicit spatial dimension) affects the migration of adult chinook salmon in the Delta. Notably, most recent studies addressing the effects of hydrodynamics on salmon migration in the Central Valley are focused on juvenile outmigration.

Results and implications

Of the four chinook salmon runs in the Central Valley, the spring run has experienced the most dramatic decline since the pre-development period. Once numbering between 0.5 and 1.5 million adults per year, nearly all of the large spring-run populations have since been extirpated (Yoshiyama et al. 1998, Moyle 2002). Historically, spring-run fish were probably most abundant in the San Joaquin system, where snowmelt from the southern Sierras provided sufficient streamflow during the spring and early summer (Yoshiyama et al. 1998). The modeled pre-development and contemporary source water distributions during a spring simulation period (May 2008) suggest dramatic differences in the spatial extent of San Joaquin River influence.

The hydrodynamic model results (RMA 2015) suggest that in the pre-development system, water from the San Joaquin River had a relative abundance exceeding 5% downstream through Carquinez Strait and beyond; in the contemporary simulations, the same relative concentration threshold only extends as far downstream as Franks Tract (the signal is “lost” well before the confluence; Figure 2). This difference means migrating spring run adult salmon would have to travel more than 60 additional kilometers in the modern system before encountering the San Joaquin river water at the minimum modeled relative concentration (5%). It is conceivable that this difference, with its potential negative effects on navigation efficiency and migration success, contributed to the extirpation of the San Joaquin spring run by the late 1950s. It should be noted that this interpretation assumes that source water distribution was altered (at least in part) by the mid-20th century, which is possible given the timing of

dam construction, major alterations to San Joaquin inflows, and the initiation of Delta water exports (landscape modifications we expect to have driven changes in source water distribution).

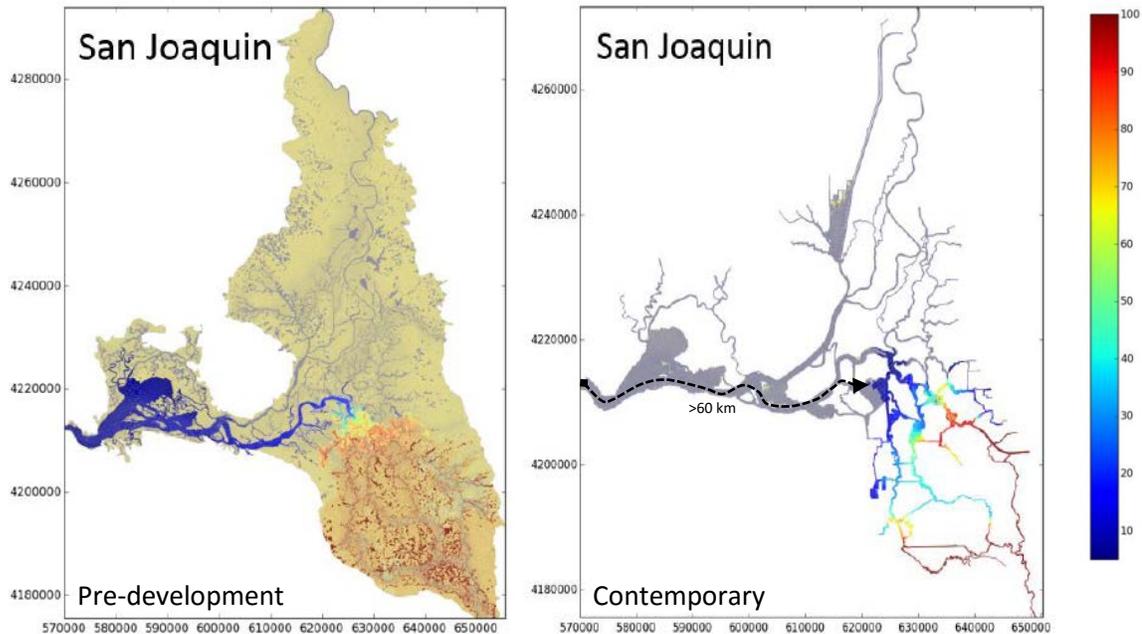


Figure 2. Relative concentration of San Joaquin water in the pre-development (left) and contemporary (right) simulations, 1 March, 2008 (from RMA 2015). Cells with less than 5% relative concentration are colored gray. The dotted line in the contemporary simulation image measures the minimum additional distance (relative to the pre-development system) that organisms travelling upstream from the Bay need to travel before encountering San Joaquin River water with a relative concentration of 5%.

Although the Sacramento spring run was generally less prolific than the San Joaquin's, Sacramento spring run chinook (added to the federal endangered species list in 1999) were still abundant during the historical period (Yoshiyama et al. 1996) and the hydrodynamic models allow us to assess how Sacramento River source water distribution has been altered for these fish. Although the Sacramento River signal extends downstream to Carquinez Straight in in both the pre-development and contemporary spring simulations, the model results suggest major differences in how far Sacramento River water is "diverted" into the San Joaquin system (Figure 3). In the pre-development simulation, Sacramento River water has a 5% relative concentration along the San Joaquin only as far upstream as Medford Island (approximately 50 km from the confluence and 30 km from the mainstem Sacramento via Threemile Slough). In the contemporary system, this same relative concentration extends up the San Joaquin system as far as the Undine Road bridge on Middle River (approximately 90 km from the confluence and 70 km from the mainstem Sacramento via Threemile Slough), or approximately 40 km further than in the pre-development system. This difference could contribute to straying and migration failure in adult Sacramento spring run chinook. Again, however, these results should be considered preliminary, as more work is needed to calibrate the model in the upper reaches of the estuary to draw firm conclusions about changes in source water distribution.

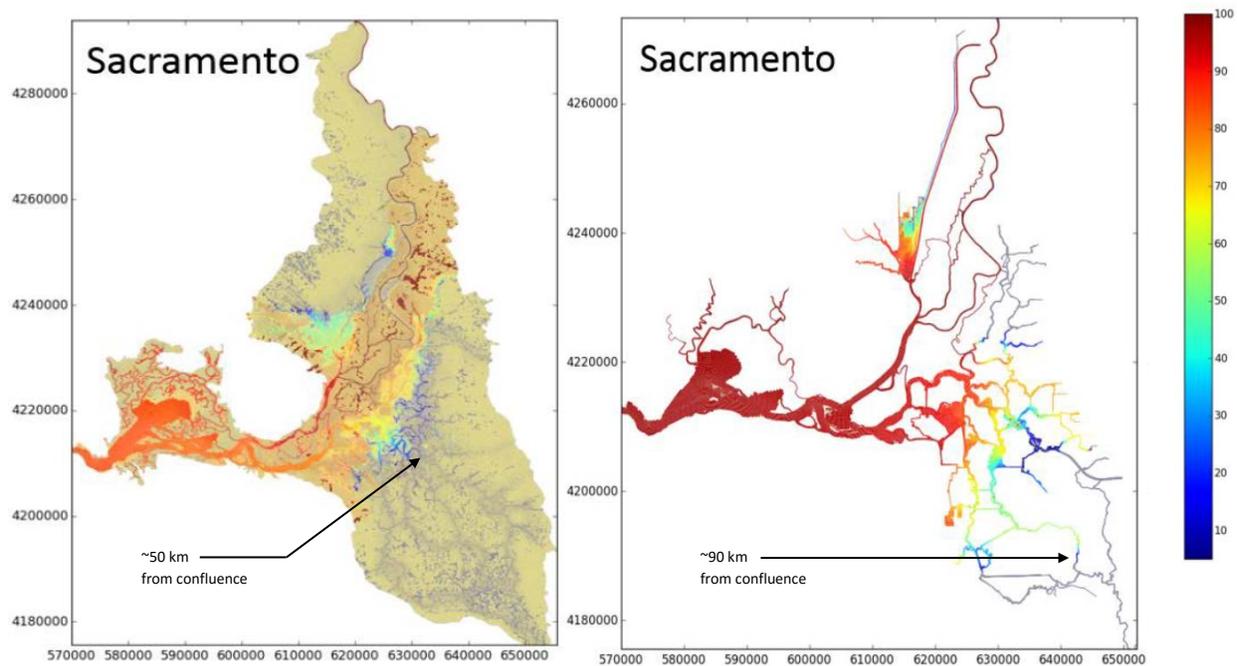


Figure 3. Relative concentration of Sacramento River water in the pre-development (left) and contemporary (right) simulations, 1 March, 2008 (from RMA 2015). Cells with less than 5% relative concentration are colored gray. The arrows in both images indicate the maximum distance Sacramento River water with a relative concentration of 5% is found from the confluence up the San Joaquin River.

The potential problems for migrating salmon posed by changes in the distribution of source water in the Delta are not the same across tributaries. While the San Joaquin River’s signature appears to have been “truncated,” the Sacramento’s has been “diffused.” Although distinct in certain regards, both kinds of changes have the potential to decrease the “coherence” of the aquatic environment for the migratory salmon and other organisms (including green sturgeon, a listed species that migrates to the Sacramento River for spawning and is thought to exhibit strong natal homing; Nelson et al. 2013). Many species have evolved particular behavioral responses to particular environmental gradients and signals. Altering these environmental cues has the potential to disrupt the outcome and efficacy of their evolved responses.

It is worth noting that, even if altered source water distributions were not a primary or direct contributing factor to the historical decline of chinook salmon, there are reasons to expect that any negative effects of navigation inefficiencies driven by changes in source water distribution are amplified in the contemporary system. First, the costs of inefficient navigation are likely greater now than in the pre-development system because migrating adults in the contemporary Delta are presumably more frequently exposed to other detrimental environmental conditions that directly inhibit migration (e.g. high water temperatures, low dissolved oxygen concentrations, and low flows). Second, due to the role of “collective navigation” in salmon migration (whereby rates of successful homing increase with population abundance; Berdahl et al. 2014), the navigational ability of individual fish is likely impaired today due to decreases in the total number of fish.

It is currently unclear how the relative concentrations modeled during these efforts relate to the concentration of home stream water that successfully elicits a homing response in chinook salmon. Research on this topic seems limited. Laboratory study of sockeye salmon (*Onorhynchus nerka*) and masu salmon (*O. masou*) suggests that the minimum concentration of source water (in this case from the culture ponds in which they were reared) needed to induce response in the olfactory nerve was between 0.1 and 1.0% (Sato et al. 2000). It is worth noting, however, that the authors did not report on the concentration of the source water's constituent chemicals, which could influence the concentration of source water that ultimately elicits a response. Put another way, 1% of source water might be the detection threshold in some systems, but this could differ in other systems with different concentrations of active constituent chemicals. It is also unknown how detection thresholds might differ between and within species (the study cited above did not test chinook salmon). Ultimately, more research would be needed to identify meaningful concentration thresholds for exploring any impacts of changes in hydrodynamics on the ability of adult salmon to navigate through the Delta.

Recent work to track migrating adult salmon with electronic tags suggests that many individuals take a disproportionately long time to navigate through the Delta, swimming back and forth between different parts of the system. A fair number of these fish never ultimately make it through the Delta (C. Michel, National Marine Fisheries Science, Southwest Fisheries Science Center, unpublished data). Future work could attempt to compare source water concentration and distribution with actual observations of fish migratory behavior. Analyses of source water distribution should be combined with analyses of flow direction, since migrating adult salmon navigate primarily via positive rheotaxis.

Finally, other environmental factors that have likely been affected by changes in the distribution and relative concentration of source waters include water temperature and turbidity. Since water temperature and turbidity are expected to vary from one tributary to the next, changing the distribution and relative influence of the Delta's water sources would be expected to affect large scale gradients in these environmental variables. Both, broadly speaking, are important variables for Delta fish species of special concern.

Isohaline position

Background

See Section #1 ("*How has the salinity of the estuary been altered since the predevelopment period?*") for background on the ecological importance of estuarine salinity and isohaline positions.

To analyze changes in the salinity regime of the upper estuary, the project team conducted a statistical analysis of isohaline positions, with a focus on the position of the 2 psu bottom salinity isohaline, known as X2 (RMA 2015). In addition to developing time series of X2 across multiple years for both the pre-development and contemporary systems (with their respective differences in the timing and magnitude of freshwater flows), the project team also isolated the effects of changes in the geometry of the upper estuary on the position of X2 by developing regressions relating to X2 to net Delta outflow for each both systems (RMA 2015).

Using the isohaline position model results generated by RMA, we conducted a series of simple secondary analyses to address the ecological implications of modeled changes. First, we reviewed the time-series of X2 for the pre-development period and extracted the annual minimum and maximum values to explore changes in seasonal and interannual variability in salinity. Next, we explored the implications of changes in X2 attributable to the historical modification of the upper estuary’s geometry using equations that relate X2 to (1) effective net-Delta outflow and (2) estuarine species abundances. The results and interpretation of these analyses are presented below.

Results and implications

In Section 1, we described the importance of seasonal and interannual salinity variability, a variable we examined by reviewing the modeled minimum and maximum X2 values across years for both the pre-development and contemporary systems. The hydrodynamic models suggest that seasonal variability in X2 has been altered since the historical period, though the direction of change differs across years (Table 3). For the 2006 simulation period (classified as a wet year), the range in X2 values (one measure of seasonal variability in salinity) was 22% lower in the pre-development system than the contemporary system. Although minimum X2 positions during the spring were similar in both systems, reduced outflows in the fall led to a higher maximum (landward) X2 value in the contemporary system. For both the 2007 and 2008 simulation periods (classified as “dry” and “critical” waster years, respectively), the range in X2 values was much higher in the pre-development system than the contemporary system (58% higher for 2007 and approximately* 32% higher for 2008). In both years, this difference is driven by both the pre-development system’s lower minimum X2 values in the spring and higher maximum X2 values in the fall.

Table 3. Modeled annual minimum and maximum X2 values for the pre-development and contemporary systems, with total range. Minimum and maximum values for the pre-development and contemporary systems across the full three year simulation period are in bold.

		2006		2007		2008	
		pre-dev.	contemp.	pre-dev.	contemp.	pre-dev.	contemp.
X2	minimum	37	36	49	58	53	57
	maximum	82	94	109	96	108	98*
	range	45	58	61	38	55	43

The model results presented here do not equivocally support or refute the hypothesis that seasonal variability in outflow and salinity is larger now than during the pre-development period, which is based on the understanding that flows buffered by storage in the pre-development Delta’s extensive wetlands and floodplains. Based on the model results, this may have been true during wet years, such as the 2006 simulation, when upstream movement of the salinity field was limited during the summer/fall (relative to the 2007 and 2008 simulations), but during drier years (such as 2007 and 2008) the simulations

* Note that the absolute maximum X2 value for the contemporary system in 2008 was not captured by the simulation period (which only extended through October)--we used an estimated maximum value of 98 km when calculating that year’s range, a value taken from the time-series developed by Hutton et al. (2015).

suggest that the pre-development Delta experienced a larger total salinity range. Total estimated pre-development net channel depletions during the summer/fall appear to be similar across years (see RMA 2015, Figure 35), so it is unlikely that an in-Delta flood storage effect accounts for the relatively high NDO and low X2 peaks indicated by the 2006 pre-development model run.

As measured by the modeled range of X2 values across the full 3-year simulation period (which included both wet and critically dry years), interannual salinity variability was 20% greater in the pre-development system than in the contemporary system. This difference is driven by a higher pre-development dry-season X2 maximum (as opposed to a lower pre-development wet-season X2 minimum, which was not observed). As explained in Section 1, greater interannual salinity variability would broadly be expected to increase the vegetative heterogeneity of the estuary’s tidal marshes. It is important to note that the simple analyses of total range X2 do not address the duration of salinity extremes. More nuanced analyses of salinity temporal variability—including analyses that track salinity at specific points (a Eulerian approach) and not just isohaline position—should be considered to better understand the ecological implications of hydrodynamic changes.

It has also been hypothesized that changes in estuarine geometry may be the most important long-term driver of salinity regime change since European settlement of the region (Enright and Culberson 2009). By controlling for differences in net Delta outflow, the hydrodynamic models suggest that changes in the geometry of the upper estuary are responsible for an average increase in X2 position of 3.23 km (RMA 2015). One practical implication of this difference is that, compared with the pre-development system, higher net Delta outflows are now required to force the salinity field to any particular location within the estuary. To approximate the magnitude of this difference in outflows, we utilized the flow-salinity relationships developed by Hutton et al. (2015), as calibrated for the pre-development and contemporary model by RMA (2015) and summarized below:

Flow-salinity relationship (Hutton et al. 2015):

$$X2 = \beta * G^\gamma$$

G = antecedent Delta outflow in units of cms
 β = scaling coefficient
 γ = fitting parameter describing the responsiveness of the salt intrusion length to flow

Flow-salinity relationship calibration (RMA 2015):

	Pre-development system	Contemporary system
β	277	281
γ	-0.237	-0.230

The results of these calculations are presented in Table 4. They suggest that the contemporary system requires additional outflows of 930 cfs to maintain X2 at a very low value (X2 = 90) and up to 45,200 cfs to maintain X2 at a very high value (X2 = 40). These flows are not trivial—they are equal to approximately 2% and 94% of California’s total freshwater withdrawals (31.1 billion gallons per day; Maupin et al. 2014), respectively. The analysis suggests that to maintain X2 at Roe Island (an intermediate position of X2 = 65), the contemporary geometry requires outflows that are ~4,500 cfs higher than would be required with the pre-development geometry, a difference equal to ~9% of CA’s total freshwater withdrawals. Please note that this analysis relies on a number of potentially significant simplifying assumptions, and is meant only to broadly contextualize the modeled differences in X2

position. A more refined analysis is needed to better understand the implications of changes in Delta geometry on the relationship between outflow and isohaline positions.

Table 4. What do changes in the geometry of the upper estuary mean for water supply? In the table below, we use the flow-salinity relationship and calibration described above to calculate the outflows required to maintain a range of X2 values in both the pre-development and contemporary systems. X2 is the distance upstream from the Golden Gate of two parts per thousand bottom salinity; G is antecedent Delta outflow calculated for the pre-development (Pre-dev.) and contemporary (Contemp.) systems. The difference between these two values approximates the additional water required to maintain X2 at any particular location because of changes in the geometry of the upper estuary, and is reported in three different units in the right-hand columns: cubic feet per second (CFS), millions of acre feet per year (MAF/year), and as a percentage of California’s total freshwater withdrawals in 2010 (31.1 billion gallons per day; Maupin et al. 2014).

X2 (km)	G (cms)		G (cfs)		Difference (cfs)	Difference (MAF/yr)	Difference (% CA freshwater withdrawals)
	Pre-dev.	Contemp.	Pre-dev.	Contemp.			
35	6,177	8,575	217,966	302,574	84,608	61.3	175.8
40	3,516	4,798	124,079	169,314	45,235	32.8	94.0
45	2,139	2,875	75,485	101,459	25,973	18.8	54.0
50	1,371	1,819	48,394	64,172	15,778	11.4	32.8
55	917	1,202	32,370	42,401	10,031	7.3	20.8
60	635	823	22,423	29,045	6,622	4.8	13.8
65	453	581	15,996	20,509	4,512	3.3	9.4
70	332	421	11,701	14,860	3,159	2.3	6.6
75	248	312	8,746	11,009	2,263	1.6	4.7
80	189	236	6,661	8,315	1,654	1.2	3.4
85	146	181	5,157	6,388	1,231	0.9	2.6
90	115	141	4,052	4,983	930	0.7	1.9
95	91	112	3,226	3,939	713	0.5	1.5
100	74	89	2,598	3,152	554	0.4	1.2

Another way to assess the significance of a decrease in X2 driven by changes in the Delta’s geometry is to use known correlations between X2 and indices of species abundance (Kimmerer et al. 2009). These relationships were developed for the contemporary system, so using them to extrapolate ecological conditions in the pre-development system is problematic. Instead, we present these results to contextualize what the average difference in X2 position caused by geometry changes might mean under modern conditions. For each significant X2-species abundance index regression reported by Kimmerer et al. (2009), we calculated the percent change in species abundance index correlated with a 3.23 km increase in X2 (Box 1). Relatively strong responses are indicated for longfin smelt (31-36% decrease in species abundance index per 3.23 km increase in X2), starry flounder (20% decrease), and Sacramento splittail (19% decrease). Appreciable decreases (> 10%) are also indicated for bay shrimp, American shad, and striped bass. Species for which the regressions indicate an increase in species abundance index include Delta smelt (1959-1981 time period) and shiner surfperch. Taken as a whole, the calculations presented here suggest that direction and magnitude of changes in species abundance

correlated with a 3.23 km upstream shift in X2 (the difference attributable to changes in the geometry of the upper estuary) vary from taxa to taxa, but can be sizeable and are predominantly negative. However, when considering the implications of these calculations, it is important to remember that the mechanisms behind X2-species abundance correlations are not all known and likely vary from species to species (see discussion on pages 9-10). Since the abundance of some or all of the species examined may not be causally related to X2 (and instead might be related to one of salinity's many covariates), we cannot ultimately assume that shifts in X2 driven by altered geometry will affect the abundance of estuarine biota. The analyses presented should therefore be considered mere approximations of the upper range of possible effects on species abundance of changes in X2 position driven by changes in estuarine geometry. The results should also be tempered by the fact that the calculations only evaluated 10 species.

Table 5. What does a 3.23 km difference in X2 mean for wildlife? This table presents the information used to estimate the percent change in various species abundance indices associated with a 3.23 km increase in the value of X2 (the average modeled X2 difference between the pre-development and modern simulations given equivalent net Delta outflows). To accomplish this, we used the significant X2-species abundance relationships reported by Kimmerer et al. 2009, which each took the form $y = mx+b$, where $y = \log_{10}(\text{species abundance index})$ and $x = X_2$. We determined the percent change in species abundance by solving each linear regression for two values of X2 with a difference of 3.23, calculating the anti-log of the resulting y values to obtain two species abundance index values, and then calculating the percent difference between these two numbers (see Box 1). For each linear regression, percent change in the real value of species abundance index is constant when the difference in starting X2 values is held at 3.23 km, meaning there was no need to present the calculations for a series of X2 values (as was done in Table 4).

<i>from Kimmerer et al. 2009, Table 2</i>						
Species	Source	N	p	b (intercept)	m (slope)	Percent change in species abundance index with 3.23 km increase in X ₂
Bay shrimp	Bay OT	26	<0.0001	3.7	-0.02	-13.82
Starry flounder	Bay OT	27	0.0006	4.7	-0.03	-20.00
American shad	MWT	38	0.004	4.0	-0.013	-9.22
American shad	Bay MW	25	0.004	4.9	-0.018	-12.53
Delta smelt (1959–1981)	TNS	20	0.018	-0.3	0.022	17.78
Longfin smelt	MWT	38	<0.0001	7.0	-0.05	-31.06
Longfin smelt	Bay MW	26	0.0001	8.0	-0.06	-36.00
Longfin smelt	Bay OT	27	<0.0001	8.1	-0.06	-36.00
Sacramento splittail	MWT	38	0.0002	3.0	-0.028	-18.80
Striped bass	TNS	32	<0.0001	4.6	-0.025	-16.97
Striped bass	TNS	44	<0.0001	2.5	-0.019	-13.18
Striped bass	MWT	38	<0.0001	4.1	-0.011	-7.86
Striped bass	Bay MW	26	0.0006	5.8	-0.027	-18.19
Striped bass	Bay OT	27	0.0001	5.2	-0.016	-11.22
Bay goby	Bay MW	27	0.004	4.4	0	0.00
Pacific sanddab	Bay MW	27	0.0005	4.5	-0.007	-5.07
Shiner surfperch	Bay MW	27	0.003	4.1	0.003	2.26

Box 1. Example calculations to determine the percent change in species abundance index with 3.23 km increase in X_2 for longfin smelt (MWT data source), based on X_2 -Species abundance regression reported by Kimmerer et al. 2009.

Regression from Kimmerer et al. 2009:

$$\log_{10}(\text{longfin smelt abundance index}) = -0.05(X_2)+7$$

Solve for $X_2 = 60.00$:

$$\log_{10}(\text{longfin smelt abundance index}) = -0.05(60)+7$$

$$\log_{10}(\text{longfin smelt abundance index}) = 4.00$$

$$\text{longfin smelt abundance index} = 10,000$$

Solve for $X_2 = 63.23$:

$$\log_{10}(\text{longfin smelt abundance index}) = -0.05(63.23)+7$$

$$\log_{10}(\text{longfin smelt abundance index}) = 3.84$$

$$\text{longfin smelt abundance index} = 6,894.46$$

Percent change in species abundance index:

$$(6,894.46 - 10,000) / 6894.46 * 100 = -31.06\%$$

[note that percent change value is constant when the difference in starting X_2 values is held at 3.23]

Channel velocity

Background

Water velocity is a key physical variable affecting aquatic habitats, but historical descriptions of water velocity in the Delta are sparse (Whipple et al. 2012, pgs. 135-136, 236). The limited available written descriptions of water velocity from the pre-development system are almost exclusively general descriptions of surface velocity, but water velocity in channels varies vertically within the water column, as well as laterally, longitudinally, and temporally over multiple scales (Kimmerer 2004). Given the lack of historical data, the pre-development hydrodynamic model will be critical for understanding changes in water velocities in the Delta and the implications for the estuary's biota.

Examples illustrating the importance of water velocity are numerous. For plants, water velocity has an effect on the distribution of floating and submerged aquatic vegetation (annual maximum water velocity has been found to limit submerged vegetation cover in the Delta above 0.49 m/s; Hestir 2010). Water velocity also is one of the "fundamental hydrologic properties" contributing to the structure of algae assemblages in rivers (Leland et al. 2011). If the size of a planktonic organism population is to increase, its reproductive rate must exceed the advective rate of water, a factor related to net velocity (Ketchum 1954). It is sometimes noted that successful zooplankton reproduction becomes rare above the apparently critical velocity of 0.4 m/s (Rzoska 1978 as cited in Sommer et al. 2004). Moving to higher trophic levels, the upstream migration of the mysid shrimp *Neomysis mercedis*—a major prey item for

Delta fish—is known to be limited by net flow velocities (it does not occupy channels with velocities greater than 0.12 m/s). Water current strength is also cited as a principal variable controlling the abundance and composition of benthic organisms (Nichols and Pamatmat 1988 as cited in Kimmerer 2004), as well as a relevant factor for fish. One requirement, for example, for the successful reproduction of some species is sufficient water velocities to keep the eggs and larvae suspended in the water column (0.1 m/s for American shad eggs; Herbold and Moyle 1989 and references therein). Not surprisingly, mean water velocities also influence the downstream migration rate of fish, with greater water velocities correlating with faster rates of travel for juvenile Chinook salmon (Horn and Blake 2004). Juvenile salmon are able to actively recognize and position themselves in high velocity areas when migrating downstream, which may aid in outmigration (Schreck et al. 1995 as cited in Horn and Blake 2004). During the day, when the outmigrating juveniles hold in place (likely to minimize the risk posed by visual predators), they appear to seek low-velocity refuge areas, a behavior that probably serves to minimize the energetic demand of maintaining their position (Burau et al. 2007). Young salmon also appear to seek out low-velocity areas when rearing on the Yolo Bypass (Sommer et al. 2005). Lastly, insofar as water velocity affects the distribution and visibility (through its effects on water turbulence) of prey items, water velocity would also broadly be expected to influence the food availability and foraging activity of birds and other predators (e.g. Schwemmer et al. 2009).

The direction of tidal asymmetry in Delta channels, which is determined by water velocities (see RMA 2015 for background information), also has ecological implications. At a broad level, whether tidal current maxima occur most often on ebb tides or flood tides is expected to influence the transport of water and its constituents (including biota). Flood dominant velocities tend to transport material upstream, while ebb dominant velocities tend to do the opposite (see Enright et al. 2013). Small tidal asymmetries can lead to large differences in material transport; as noted by Morgan-King and Schoellhamer (2013), sediment transport scales with shear stress to the 1.5 power, and shear stress scales to velocity squared, so sediment transport roughly scales to velocity cubed. The same authors determined that flood-dominant velocities are a main cause of estuarine turbidity maxima observed in the blind, dendritic channels of the Cache Slough complex. Similar processes could influence concentration of nutrients and estuarine biota.

Results and implications

The pre-development model suggests that dendritic channels in the pre-development Delta contributed to spatial heterogeneity in water velocity. Model results show strong longitudinal gradients in water velocity along blind, dendritic sloughs. This is well-illustrated by the results from Elk Slough, a former blind channel draining Webb Tract in the Central Delta (not to be confused with the Sacramento River tributary of the same name). Over the course of the analysis period, the maximum modeled cross-sectionally averaged velocity in the mainstem San Joaquin channel just downstream of the slough's mouth was 0.79 m/s (Figure 4). However, just inside the mouth of Elk Slough, this velocity was 0.43 m/s, a reduction of nearly 50%. At the head of the slough, the velocity was only 0.15 m/s, meaning modeled cross-sectionally averaged maximum velocity is more than 520% higher in the mainstem channel than at the head of the blind channel. Similar relationships were observed for other modeled historical blind sloughs.

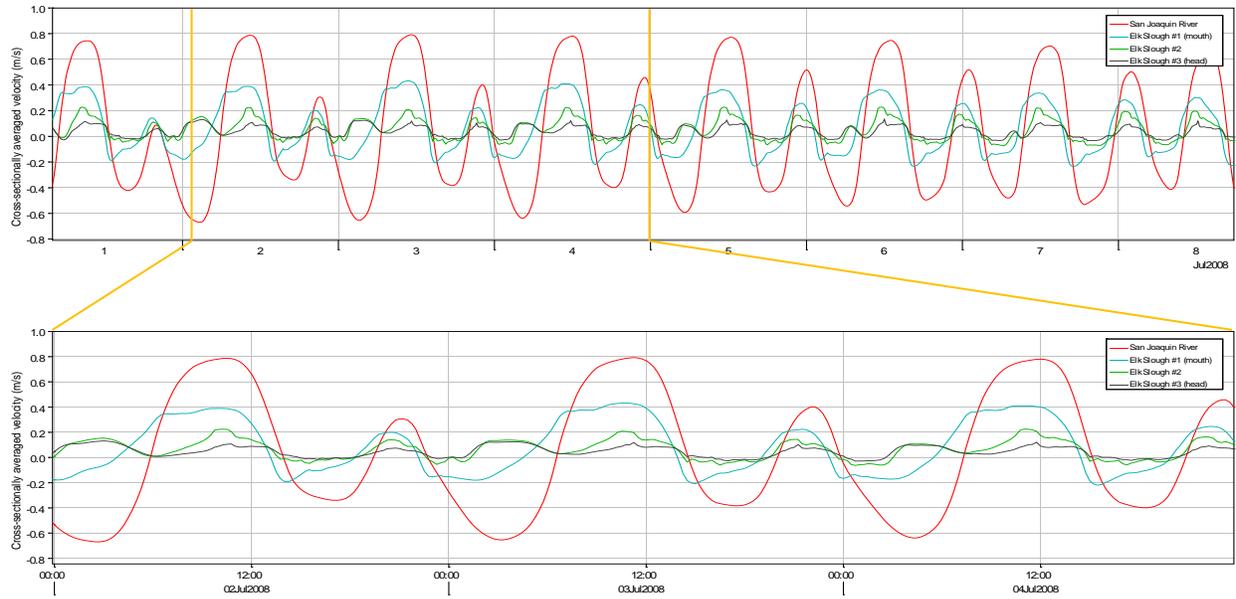


Figure 4. Modeled pre-development cross-sectionally averaged velocities from multiple points along Elk Slough (former Webb Tract blind tidal channel off of the San Joaquin River). Maximum velocities are substantially lower in the blind channel than in the mainstem river. See map for location of transects.

Extrapolating out from Elk Slough, one can imagine how the tremendous loss of blind tidal channels (the total length of which has decreased 75-90% since the pre-development period; SFEI-ASC 2014) has affected the availability and distribution of low-velocity habitats in the Delta and impacted native wildlife. Research into the movements of outmigration juvenile salmon along the Sacramento River's Clarksburg Bend show that the young fish move down the higher-velocity, outer portion of the bend during night, and hold in the lower-velocity, inner portion of the bend during the day (Burau et al. 2007). Fish appear to seek out low-velocity areas by moving upstream along the inner bend once they are ready to hold, stopping once they find a suitable area. The authors note that Clarksburg Bend is one of the few locations in the contemporary Delta where significant bathymetric variability exists (due to the Bend's extremely tight curve radius) and that most channels presumably provide relatively little low-velocity habitat. The pre-development model suggests this kind of habitat could historically have been found wherever a blind slough met a mainstem distributary channel. Due to the sheer number of these channel networks, which were spaced at fairly regular intervals—outmigrating salmon would have been much more likely to encounter low-velocity habitat along any given stretch of their migration route. The sloughs might also have been more conducive to prolonged periods of residency and rearing, a behavior observed in low-velocity areas of the Yolo Bypass (Sommer et al. 2005) and blind tidal channel networks in other systems (Hering et al. 2010 and references therein). Speaking generally, a greater range in water velocities—especially along such a coherent gradient across a relatively small distance—means that there is a greater range of habitats (as defined by velocity) available to aquatic organisms and greater potential for mobile organisms to fine-tune their position with respect to velocity.

Future work should attempt to classify (and quantify/visualize) the total area of open-water by measurements of velocity (net-velocity, maximum velocity, average velocity, etc.) to better understand large-scale changes in the upper estuary. It should also explore the velocity dynamics of pre-development blind channels over longer time-series that capture at least a full spring-neap cycle.

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