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A Conceptual Model for Floodplains in the Sacramento–San Joaquin Delta

Jeffrey J. Opperman[1]

ABSTRACT

Floodplains are among the most biologically pro-ductive and diverse ecosystems on Earth and they provide significant benefits to society such as attenu-ation of floodwaters, groundwater recharge, filtra-tion of nutrients and sediments, carbon sequestra-tion, fisheries productivity and recreation. However, floodplains are also among the most converted and threatened ecosystems. Floodplain habitats in the Sacramento–San Joaquin Delta (the Delta), and throughout California's Central Valley, have been greatly reduced from their historic extent and key processes that create and maintain floodplains, such as flood flows and meander migration, have been greatly altered. These widespread alterations to habi-tats and processes have lead to declines in many species' populations in the Delta and Central Valley, creating challenges for both environmental and water management. To address these challenges numerous entities and programs are now focused on restoring floodplains and other Delta habitats. This paper pro-vides a conceptual model for floodplains that char-acterizes the key features and identifies the critical processes, drivers, and linkages that allow floodplains to produce a variety of functional outputs important to management. These outputs include: (1) the flood-plain habitat mosaic, including riparian vegetation and its associated wildlife; (2) spawning and rearing habitat for native fish; and (3) food-web productivity that can support native fish on the floodplain as well as be exported to downstream ecosystems. The model emphasizes that the production of these outputs requires hydrological connectivity between river and floodplain across a broad range of flow conditions. For example, long-duration flooding in the spring promotes native fish spawning and food-web produc-tivity that benefits native species.
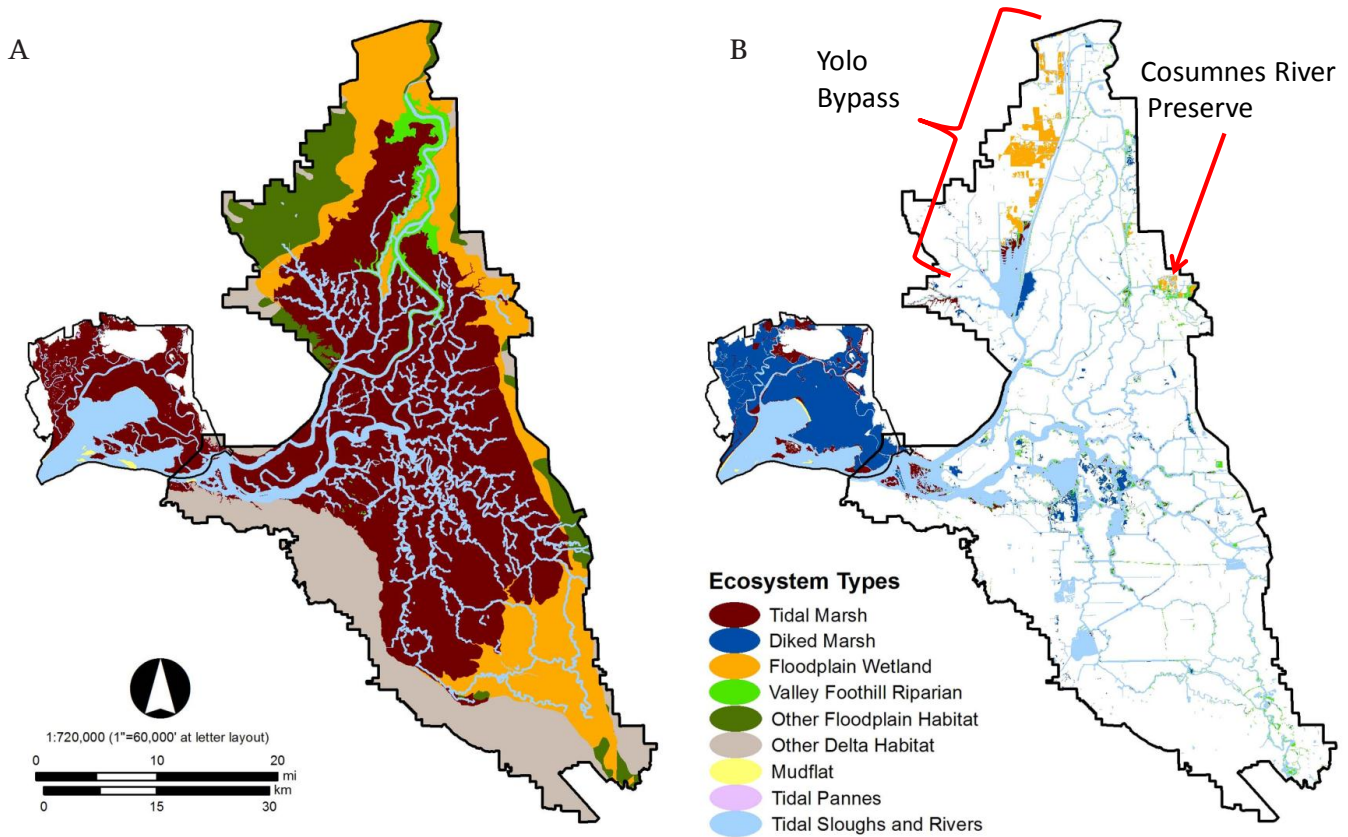
KEY WORDS

Floodplain, riparian forest, floodplain food web, Chinook salmon, Sacramento splittail, Delta Regional Ecosystem Restoration Implementation Plan (DRERIP).

INTRODUCTION

The Sacramento–San Joaquin Delta, within California's Central Valley (Figure 1), encompasses a broad suite of habitat types including open water, tidal marsh, agricultural fields, and river-floodplain ecosystems (TBI 1998). The Delta's ecosystem has declined, with numerous species listed as threatened or endangered, and faces numerous ongoing threats (Sommer and others 1997; Lund and others 2007;

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Ecosystem Types

- Tidal Marsh
- Diked Marsh
- Floodplain Wetland
- Valley Foothill Riparian
- Other Floodplain Habitat
- Other Delta Habitat
- Mudflat
- Tidal Pannes
- Tidal Sloughs and Rivers

Data sources:
Historic Ecosystems: Suisun=SFEI 1998 EcoAtlas; Delta=The Bay Institute 1998, Atwater 1982
Modern Ecosystems: Suisun=SFEI 1998 EcoAtlas, DWR 2006 Blacklock; Delta=CDFG 2005 Veg Map
Produced by WWR, September 2012

Figure 1 The distribution of habitat types, including floodplains, within the (A) historic and (B) modern Sacramento–San Joaquin Delta. Two sites that are discussed frequently in this paper, the Yolo Bypass and the Cosumnes River Preserve, are identified in B. Sources: TBI (1998); WWR (2008).

BDCP 2010). Because of the Delta's importance for agriculture and as the hub of the California water system, reversing this decline poses a considerable challenge for natural resource managers. To maintain healthy ecosystems and reduce conflicts with other land and water management objectives within the Delta, state and federal agencies and various other interests seek to sustain and restore its key habitats, populations, and processes (BDCP 2010).

Here, I describe a conceptual model that characterizes the current habitats and processes of lowland river-floodplain ecosystems of the Delta and upstream contributing rivers. I focus on the key processes and features required to maintain a set of outputs from floodplains that have management significance, including native fish populations, biologically avail-

able carbon and other aquatic food resources, and riparian vegetation and riparian-associated fauna. This paper summarizes the floodplain conceptual model developed for the Delta Regional Ecosystem Restoration Implementation Plan (DRERIP), which was one of a series of conceptual models for habitats and processes within the Delta commissioned by DRERIP (see other articles in this special issue of *San Francisco Estuary and Watershed Science*). The full model includes greater detail and is available online (Opperman 2008).

Globally, floodplains are among the most important—and most threatened and degraded—ecosystem types (Tockner and Stanford 2002). Floodplains support high biological diversity and productivity, and provide significant ecosystem services of economic

and societal value. For example, Costanza and others (1997) provided coarse estimates of the economic values provided by the world's ecosystem types and floodplains ranked second only to estuaries in terms of their value per hectare (ha). Despite occupying less than 1% of the earth's terrestrial surface, floodplains provide almost 25% of all non-marine ecosystem services. These services include flood attenuation (Akanbi and others 1999), groundwater recharge (Jercich 1997), recreation and open space (Lant and Tobin 2005), sequestration of carbon, nutrients and sediment (Noe and Hupp 2005), and production of fish (Baran and others 2007), wildlife, timber and other economically valuable plants (Duvail and Hamerlynck 2007). Periodic connectivity and exchanges during flood events directly affect the health of river and floodplain ecosystem and in many river systems a large proportion of total riverine productivity is derived from floodplain habitats (Bayley 1991). Despite these benefits, floodplains have been widely converted (e.g., to agriculture) throughout the developed world and are being converted or degraded rapidly in the developing world (Tockner and Stanford 2002).

Central Valley Floodplains

Before the expansion of the European population in California, the Central Valley contained approximately one million hectares of floodplain habitats, including riparian forests and savannas, oxbow lakes and other water bodies, and vast expanses of tule marsh (Katibah 1984; TBI 1998). These habitats supported large, culturally important populations of fish, waterfowl, and ungulates. Diverse economic activities lead to conversion of these habitat types and it is estimated that currently less than 10% of original floodplain habitats remain (Katibah 1984; Barbour and Billings 1988) (Figure 1). In the late 19th century, hydraulic gold mining in the Sierra Nevada delivered approximately one billion cubic meters of sediment into Central Valley rivers and floodplains, leading to channel aggradation and exacerbating flooding for early settlers (James and Singer 2008). Concurrently, riparian forests were cleared for settlements and firewood, and settlers built an uncoordinated set of levees and drained the lands behind them, resulting

in extensive conversion of tule marshes to agriculture (Kelley 1989). The levee system evolved into a coordinated federal project featuring levees flanking the Sacramento and San Joaquin rivers and their large tributaries. These levees prevent floodplain inundation of most of the historic floodplain in all except the very largest flood events and facilitated conversion of most of the valley's floodplain into agriculture (TBI 1998). Hydrological connectivity between rivers and floodplains has declined further because of flow regulation from large upstream multipurpose dams, including Friant on the San Joaquin, Shasta on the Sacramento, Folsom on the American, and Oroville on the Feather (TBI 1998). Dams reduce flood peaks in most years because of flood-control operations and water storage. Because these reservoirs refill during the spring, the magnitude of the spring snowmelt flood pulse—historically a predictable annual hydrological event—has decreased considerably (TBI 1998; Yarnell and others 2010). Due to this flow regulation even remnant floodplain habitats within the levees are inundated much less frequently than historically (Williams and others 2009) (Figure 2). Geomorphic processes, such as meander migration, have also lessened considerably as a result of protection amendments, including stabilization "rip-rap" materials (Larsen and others 2006a; Florsheim and Mount 2008).
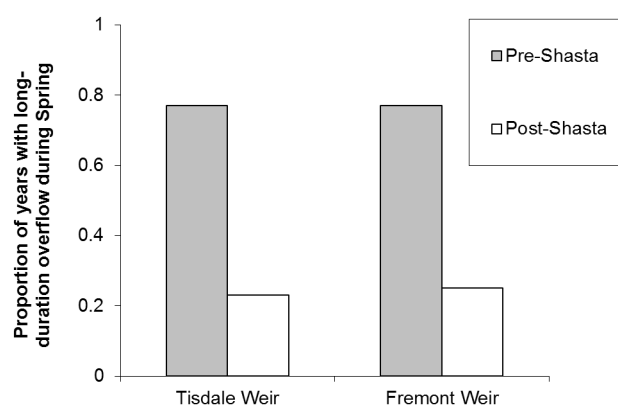

Figure 2 Proportion of years with overflow events of 7 days or longer during the spring (March 15 to May 15) of Tisdale Weir into Sutter Bypass and Fremont Weir into Yolo Bypass, before Shasta Dam was constructed on the Sacramento River and after Shasta Dam. See Williams and others 2009.

This conceptual model emphasizes that dynamic geomorphic processes and periodic inundation are essential features of healthy, functioning floodplains. In addition to direct conversion of floodplains to agriculture and housing, the loss of these key floodplain processes has contributed to a dramatic decline in species that depend on floodplain habitats in California's Delta and Central Valley (Sommer and others 1997; Hunter and others 1999). Numerous native species once common to the river and floodplain ecosystem have been listed under both state and federal Endangered Species Acts (Table 1). In addition to signaling the decline of important ecosystems, these listings have lead to numerous conflicts with land and water management (Lund and others 2007).

Objectives and Structure of the Floodplain Conceptual Model

State and federal resource agencies along with stakeholders ranging from environmental organizations to irrigation and water-supply managers are now seeking solutions that will promote healthy and resilient ecosystems in the Delta and Central Valley. This floodplain conceptual model characterizes the key features—and identifies the critical processes, drivers, and linkages—that allow floodplains to produce a variety of outputs important to management.

Along with other complementary DRERIP models (e.g., those for riparian vegetation and fish species), this model provides a framework to compare and evaluate various management and restoration alter-

Table 1 Species that use Delta floodplain habitats with state or federal status (E = endangered; T = threatened; C = candidate for listing; SSC = California species of special concern). Source: BDCP 2010.

Species	Latin name	Federal status	State status
Greater sandhill crane	*Grus canadensis tabida*	—	T
Least Bell's vireo	*Vireo bellii pusillus*	E	E
Swainson's hawk	*Buteo swainson*	—	T
Tricolored blackbird	*Agelaius tricolor*	—	SSC
Western yellow-billed cuckoo	*Coccyzus americanus* ssp. *occidentalis*	C	E
Willow flycatcher	*Empidonax traillii*		
Yellow-breasted chat	*Icteria virens*	—	SSC
Chinook salmon, fall run	*Oncorhynchus tshawytscha*	—	SSC
Chinook salmon, spring run	*Oncorhynchus tshawytscha*	T	T
Chinook salmon, winter run	*Oncorhynchus tshawytscha*	E	E
Sacramento splittail	*Pogonichthys macrolepidotus*	—	SSC
California red-legged frog	*Rana Aurora Daytonii*	T	SSC
Giant garter snake	*Thamnophis gigas*	T	T
Western pond turtle	*Actinemys marmorata*	—	SSC
Valley elderberry longhorn beetle	*Desmocerus californicus dimorphus*	T	—
Riparian brush rabbit	*Sylvilagus bachmani riparius*	E	E
Riparian woodrat	*Neotoma fuscipes riparia*	E	SSC

natives. Although this model is populated with specific Central Valley examples, it articulates a set of concepts that can be applied or adapted to a range of other lowland floodplain systems.

The habitats described in this model occur within the jurisdictionally defined Delta, which includes floodplain areas of the Yolo Bypass and Cosumnes River Preserve (Figure 1), and along the lowland rivers just upstream of the Delta. Floodplain inundation (e.g, of the Yolo Bypass) effectively expands the total wetted area of the Delta (Jassby and Cloern 2000) and floodplains also produce outputs—such as fish and algae— that can be exported to downstream Delta and estuary habitats (Sommer and others 2004; Ahearn and others 2006). In this model, the general term "floodplain" is used to encompass a broad range of habitat features that interact within the river-floodplain system, including habitats such as riparian forest and wetland and riverine features that include main and side channels, oxbow lakes, and bars.

The conceptual model has three primary components organized as interacting sub-models. Several of the models share a common set of symbols (Figure 3). The first model, "Creating the Template," captures the processes and linkages that collectively produce the habitat mosaic, which is the physical template of a given floodplain including topography, soils and vegetative communities. This model describes how these primary biophysical components, features

treated as more or less static in the other models, are dynamically created and maintained. The second model, "Inundating the Template," depicts how a given floodplain site, with features established by Model 1, is inundated by river flows and other sources of water to create specific hydrological conditions within the inundated floodplain that are important to the species or processes described in Model 3. The third model "Management Outputs," illustrates how the inundated habitat characteristics, developed in Model 2, influence the production of biota— including algae, zooplankton, and native fish—that directly interest Delta restoration planners. Thus Model 3 focuses on several of the outputs of interest to management, while Model 1 focuses on the habitat mosaic, an important management output on its own.

These models describe broad-scale processes and biophysical interactions and therefore do not provide in-depth attention to a specific process and response (e.g., finer-scale hydraulic and sedimentary mechanisms that operate during floodplain inundation). Table 2 provides examples of quantitative studies or tools that can be used to understand or predict finer-scaled processes and mechanisms that operate at the scale of each model. Within the narrative the first mention of a model element is bolded.
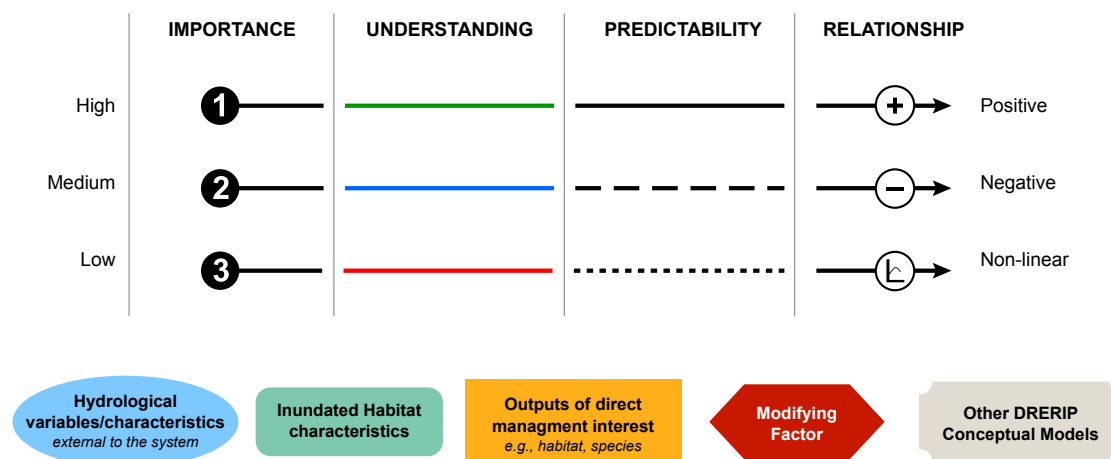

Figure 3 Graphic elements that are common to the conceptual models

Table 2 Quantitative tools or studies that provide examples of—or that can be used to explore or predict—processes and mechanisms that operate at the scale of each sub-model of this conceptual model

Model 1	
Hydrological patterns	Dams and Central Valley hydrology (Singer 2007)
	Indicators of Hydrologic Alteration (IHA) software; (Richter and others 1996; Mathews and Richter 2007) *http://www.conservationgateway. org/ConservationPractices/Freshwater/EnvironmentalFlows/ MethodsandTools/IndicatorsofHydrologicAlteration/Pages/indicators-hydrologic-alt.aspx*
Geomorphic processes	Meander migration (Larsen and others 2006a, 2006b; Constantine and others 2009);
	Development of floodplain topography and sediment transport (Florsheim and Mount 2002; Florsheim and others 2006; Singer and Aalto 2009)
	Meander cutoffs and formation of off-channel waterbodies (Kondolf and Stillwater Sciences 2007)
Recruitment of riparian vegetation	Recruitment box model (Mahoney and Rood 1998);
	Seed release and flow regime in Central Valley (Stella and others 2006)
Development of floodplain mosaic	(Greco and Plant 2003)
	Sacramento River Ecological Flows Tool; (ESSA Technologies Ltd. 2007) *http://www.dfg.ca.gov/ERP/signature_sacriverecoflows.asp*
Model 2	
Water surface profiles; inundation of floodplain	HEC-RAS; *http://www.hec.usace.army.mil/software/hec-ras/*
Inundation of flood surfaces by specific flow types	Long-duration spring floods (Williams and others 2009)
	3-year recurrence interval flood (Greco and others 2008)
Model 3	
Algal productivity	(Schemel and others 2004; Ahearn and others 2006)
Invertebrate productivity	(Sommer and others 2001, 2004; Grosholz and Gallo 2006)
Growth of juvenile salmon on floodplains	(Sommer and others 2001; Limm and Marchetti 2009; Jeffres and others 2008)

MODEL 1: CREATING THE TEMPLATE

Healthy, functional floodplains are often composed of a mosaic of diverse habitat features, and this mosaic promotes floodplain biodiversity (Salo and others 1986; Ward and others 2002). The mosaic is created through dynamic river-floodplain interactions, including geomorphic processes that erode and deposit sediment (Ward 1998), which produce the physical template for ecosystem development (the focus of this model) and processes that occur during subsequent inundations (the focus of Models 2 and 3).

Model Scale, Objectives, Structure, and Outcomes

Model 1 describes biophysical floodplain processes occurring throughout the lower Central Valley and riverine portions of the Delta (i.e., where fluvial, not tidal, processes predominate). The model can be used across a broad range of spatial scales, from a site to a reach or larger. Here, 'floodplain site' refers to the floodplain of interest to the user, which can range across these spatial scales (e.g., from the scale of the Cosumnes Preserve [hundreds of hectares] to the Yolo Bypass [24,000 ha]) (Figure 1). Model 1 encompasses processes that occur over temporal scales ranging from single flood events (e.g., bank erosion) to

decades or centuries (development of mature flood-plain forest on an alluvially deposited surface).

The model's objective is to describe the basic processes that create and maintain floodplain ecosystems and how management actions either stress or restore these processes (Figure 4). Because of the coarse level of this model, I do not use the information-coded arrows (from Figure 3), and include only a few negative signs to indicate that levees and rip-rap reduce river-floodplain interaction and that flow regulation reduces the frequency and/or magnitude of geomorphically effective flows.

Model Summary

The model has five inputs external to the spatial scale of the model; the first four (**surface hydrology, sediment, large wood and vegetative reproductive elements**) operate primarily during an inundation event while the fifth, groundwater, operates during ecosystem development between flood events.

1. **Surface hydrology** encompasses the various sources that provide water flows to a given river-floodplain system. Flow from the main river is the most important part of surface hydrology for performing geomorphic work. Other sources of surface hydrology, such as direct precipitation,
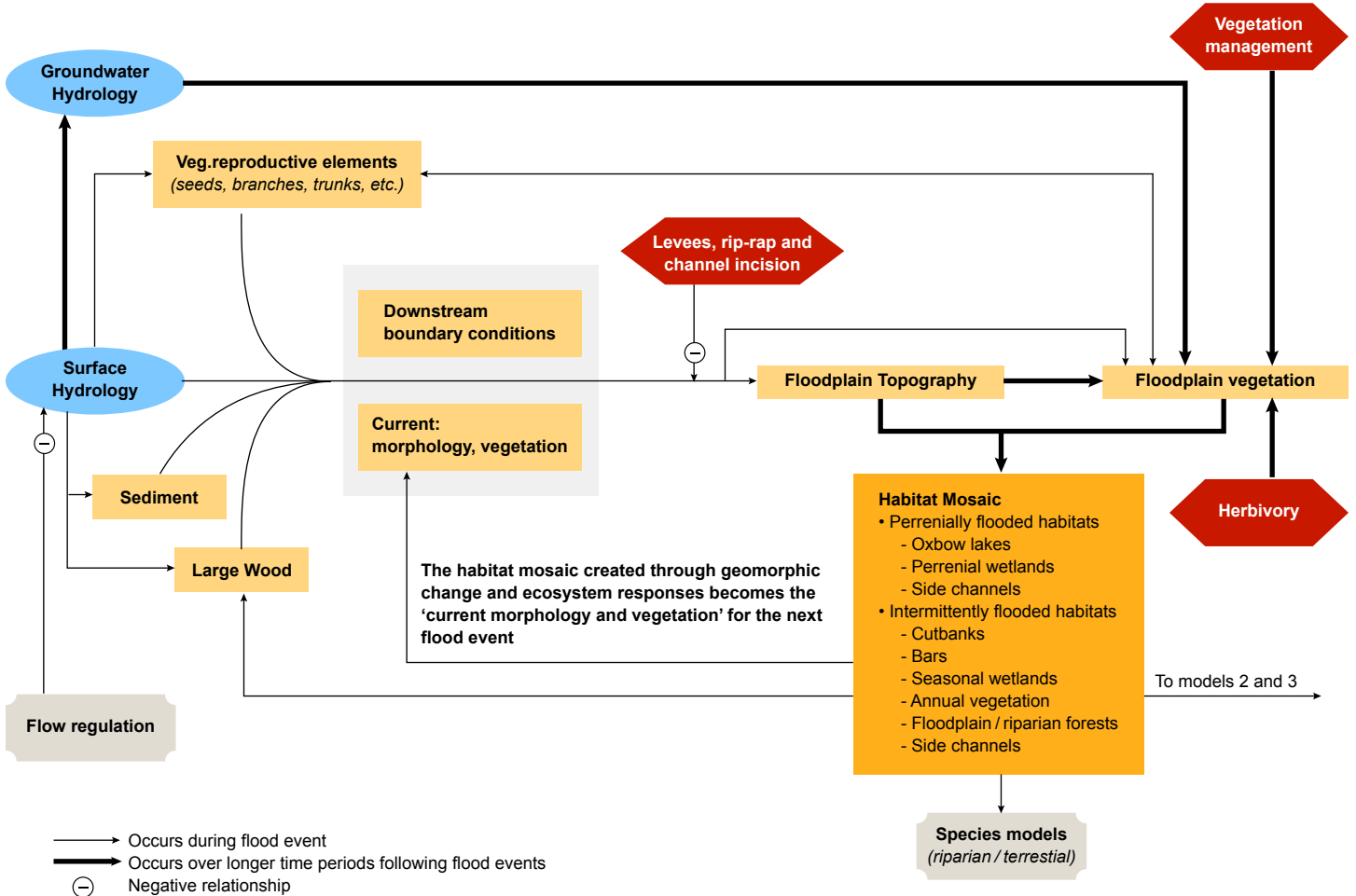

Figure 4 Model 1 ("creating the template") emphasizes the processes that create and maintain features of the habitat mosaic. Thin lines indicate processes operating at the time step of a flood event, such as flood-driven geomorphic processes, while the thick lines indicate processes that occur over longer time periods, such as the development of floodplain vegetation. The habitat mosaic at any time period becomes the current morphology and vegetation with which subsequent floods interact. This sequential feedback is denoted by the line connecting the box habitat mosaic with the box current morphology, vegetation and downstream boundary conditions.

likely have minor influences on the geomorphic processes, although antecedent inundation of the floodplain by these sources can influence patterns of subsequent riverine inundation and sediment deposition (Mit 1997; Wohl 2000). For floodplain sites in the lowland Central Valley and Delta, the surface hydrology for a given floodplain is a sum of discharges from regulated and unregulated portions of the upstream watershed and is therefore a function of precipitation, runoff, and dam operations.

2. **Sediment** inputs are a sum of the sediment loads derived from regulated and unregulated portions of the Central Valley watershed.

3. Although **large wood** is undoubtedly much less common in Central Valley floodplains than in the past, because of a legacy of forest clearing and snagging in addition to ongoing trapping behind dams, it has been shown to be a primary structural element in other floodplain rivers (Abbe and Montgomery 1996; Gurnell and others 2005). The pool of large wood available to a given floodplain site is the sum of both external inputs and local inputs from the floodplain forest.

4. The pool of **vegetative reproductive elements** available to a given floodplain is also a product of upstream inputs and local sources. Vegetative reproductive elements include seeds and vegetative elements that are capable of generating new individuals. Trees of the family *Salicacae*, such as willows and cottonwoods, can regenerate from branches or even entire trees that are deposited on the floodplain during floods (Opperman and others 2008). Trees such as narrow-leaved willow (*Salix exigua*) can also regenerate on-site through clonal growth from root suckering (Douhovnikoff and others 2005).

5. **Groundwater hydrology** influences the hydroperiod of floodplain wetlands and the depth to groundwater influences the structure and composition of vegetative communities (Shafroth and others 2000). Groundwater hydrology can be influenced by the adjacent primary river but is also influenced by local factors such as sediment characteristics and groundwater pumping (Stromberg and others 1996).

The central portion of the model is the interaction of flood hydrology, sediment and large wood with the existing floodplain topography and vegetation. In the model, these three primary inputs interact with the floodplain's **current morphology**, **vegetation**, and **downstream boundary conditions**. Current morphology includes the spatial arrangement and relative elevation of floodplain surfaces and the geomorphic character of those surfaces (e.g., grain size, erodibility). Downstream boundary conditions, including sea level, grade controls, and topographic features that create backwater effects, also influence the hydrologic and geomorphic processes operating at a given floodplain site. In summary, river hydrology, in concert with sediment and large wood, shapes floodplain topography and vegetation through various geomorphic processes. These geomorphic processes operate through a filter of current morphology, vegetation, and downstream boundary conditions.

Constructed levees, **rip-rap and channel incision** are depicted as modifying factors that influence the type, rate, and extent of geomorphic process; these factors can effectively prevent geomorphic processes from occurring on the floodplain site during all but the highest magnitude flood events. **Flow regulation** is also depicted as a modifying factor because it reduces the frequency and magnitude of high flow events that allow floodwaters, sediment and large wood to interact with floodplain topography and vegetation.

Geomorphic Processes

Collectively, geomorphic processes operate upon the current morphology and vegetation, creating a new arrangement of floodplain topography and surfaces and vegetation. Geomorphologists originally emphasized two primary processes for building floodplain surfaces—deposition on point bars (lateral accretion) and deposition during overbank flows (vertical accretion)—and posited that lateral accretion predominated. For example, Wolman and Leopold (1957) suggested that 90% of floodplain development resulted from lateral accretion and within-channel deposits. More recent reviews question the dominance of lateral

accretion, noting that a limited range of rivers provided the basis for early theories of floodplain development. Now a diverse array of floodplain developmental processes are recognized (Nanson and Croke 1992; Knighton 1998).

The type of geomorphic process (e.g., bank erosion vs. crevasse splay formation) and the spatial extent of the area influenced by the geomorphic process depend on complex interactions among all the model elements described above. In general, higher magnitude floods (e.g., a recurrence interval >25 years) result in processes, such as channel avulsion, that affect a larger area. Lower magnitude events (e.g., bankfull events) contribute to bank erosion and meander migration (Trush and others 2000; Opperman and others 2010). Over time various flows that perform geomorphic work result in heterogeneous topography, hydroperiod, and soil and sediment characteristics (e.g., substrate size and organic content).

Large wood significantly affects floodplain geomorphic processes and topographic heterogeneity (Florsheim and Mount 2002). Major wood jams in the channel can induce bank erosion, splay formation and channel avulsion and raise river stage upstream (Abbe and Montgomery 1996; Gurnell and others 2005). Wood may have been an important element influencing channel avulsion in the historic Central Valley lowland river system.

Ecosystem Development

Ecosystems develop upon this physical template with species, communities and successional trajectories influenced by the physical heterogeneity (topography, soils, and hydroperiod). In addition to this heterogeneity, dynamic hydrologic and geomorphic processes frequently alter the physical template, community composition and structure of a given site during the process of ecosystem development, resetting communities to earlier successional stages (Ward and others 2002; Greco and Plant 2003).

Riparian vegetation dynamics are linked to inter- and intra-annual variability of the hydrograph and the dynamic hydrologic and geomorphic processes of the floodplain environment (Decamps and others 1988; Trush and others 2000). Many riparian species in the Central Valley appear to have evolved to release their seed during the period when snowmelt historically caused spring floods (Stella and others 2006). These spring floods distributed seeds onto freshly deposited alluvial surfaces which provided suitable conditions for willow and cottonwood regeneration (e.g., mineral soil with low levels of litter and shade competition). These relationships have been summarized in conceptual models such as the recruitment box model (Mahoney and Rood 1998) and in the DRERIP riparian vegetation model (Fremier and others 2008).

In addition to geomorphically effective high flows, other hydrological patterns also influence the distribution of plant communities. The hydro-period of a patch of floodplain fundamentally influences the distribution and development of floodplain plant communities (Mitsch and Gosselink 2000). Patches with frequent and long durations of inundation are dominated by wetland plant communities and/or annual herbaceous plant communities. Woody riparian plants generally grow in areas that do not have prolonged inundation during the growing season (Trowbridge and others 2005). Riparian vegetation establishment is thus strongly influenced by the microtopography created by geomorphic processes such as sand splays. In the Cosumnes River, riparian vegetation established with greater density on sand splays than the surrounding floodplain, because the sand splays had higher elevation, better drainage, and a shorter hydroperiod (Florsheim and Mount 2002).

Similarly, the depth to the water table can affect the distribution and development of floodplain vegetative communities. Deep water tables can lead to stress or mortality of riparian trees (Scott and others 1993; Shafroth and others 2000). The water table can be influenced by the stage of the river or local effects such as groundwater pumping. Beavers and ungulate herbivores can strongly influence riparian vegetation (Case and Kauffman 1997; Andersen and Cooper 2000; Opperman and Merenlender 2000), as can rodents that consume seeds and seedlings (Griggs and Golet 2002).

Habitat Mosaic

The processes described above collectively create a shifting habitat mosaic on the floodplain (Figure 5). Many of the features of the habitat mosaic are direct management objectives, such as a riparian forest with a certain species composition and structure. Further,

Figure 5 A floodplain habitat mosaic along the Sacramento River, including side channels, oxbow lakes, wetlands, bars, and riparian vegetation of varying age and structure

this mosaic provides the habitat features required by a number of species that are management objectives, including threatened and endangered species and other species of concern (Table 1) and numerous other species including wading birds, waterfowl, and songbirds (Golet and others 2008).

Management Influences

Management activities can influence several of the drivers, linkages and outcomes of Model 1. Flow regulation, levees and rip-rap all reduce the frequency, magnitude and spatial extent of dynamic hydrologic and geomorphic processes. Management can adjust all three of these modifying factors. Examples include flow releases to promote floodplain inundation; the removal, breaching or setting back of levees to increase connectivity between river and floodplain; and rip-rap removal to increase the geomorphic interactions between river flows and channel banks and floodplain features.

Vegetation management and other human activities such as fires influence the vegetative structure and habitat characteristics of riparian forests. For example, riparian restoration, including active planting, irrigation, and protection from herbivory, can influence riparian forest composition (Opperman and Merenlender 2000). Though active riparian restoration approaches can lead to development of riparian forests, experience at the Cosumnes River Preserve indicates that dynamic hydrologic and geomorphic processes are more effective at lower cost to regenerate riparian forests (Swenson and others 2003).

Topographic manipulation, such as excavation and grading, can mimic some of the outcomes of dynamic geomorphic process. Although topographic manipulation can be quite expensive, it may be one of the few options for promoting inundation of floodplain surfaces where the adjacent rivers have become incised (Williams and others 2009).

MODEL 2: INUNDATING THE TEMPLATE

Model 2 depicts how a given floodplain, with topography and vegetation created within Model 1, is inundated by river flows and other sources of water to create specific conditions within the inundated
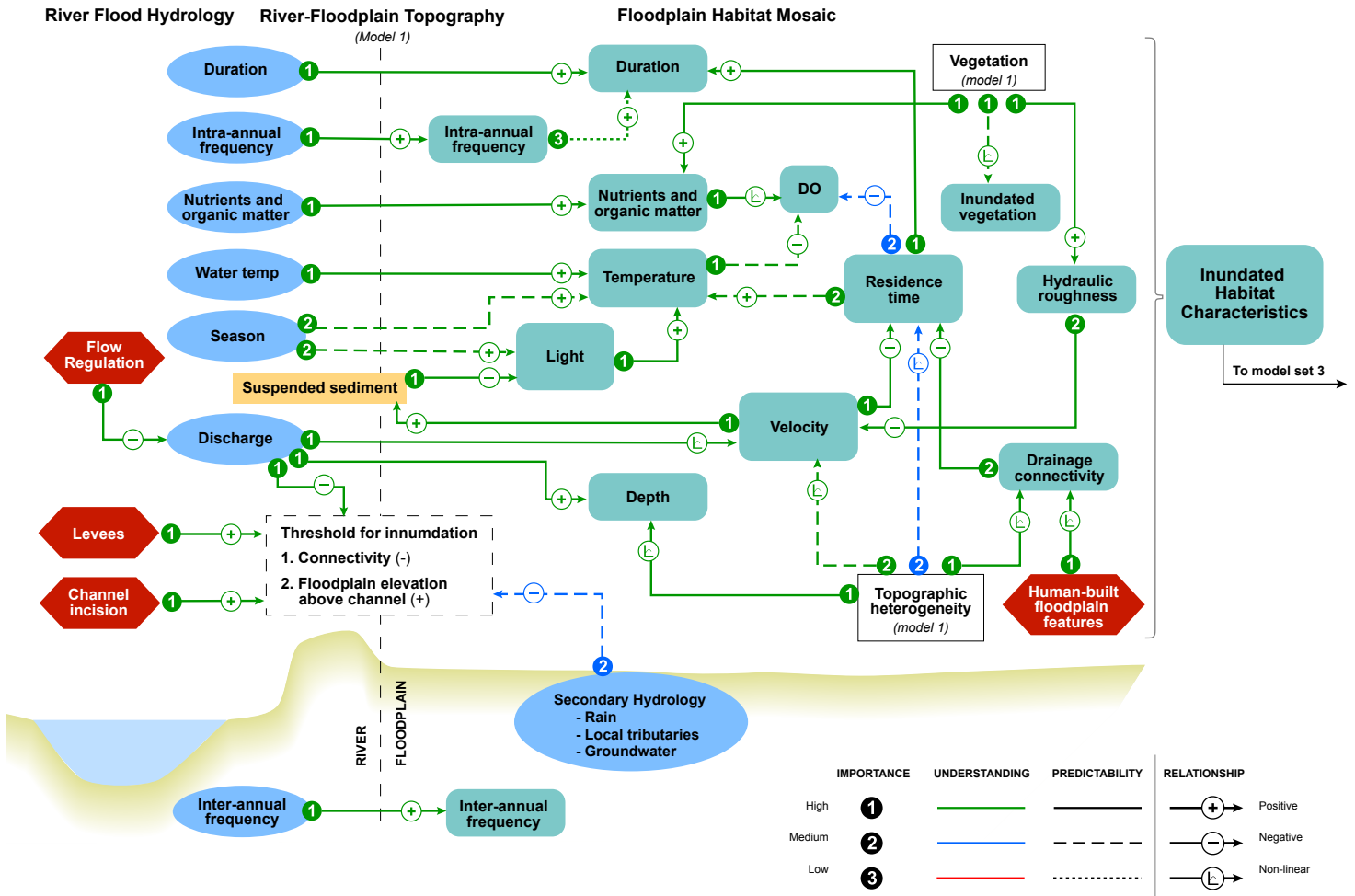
Figure 6 Model 2 ("inundating the template") depicting the processes that result in floodplain inundation and generate a set of inundated habitat characteristics. A cartoon diagram of a river and floodpain, containing four primary elements: (1) river flood hydrology with hydrological characteristics derived from flow data (e.g., discharge and duration) as well as water quality characteristics (e.g., water temperature); (2) To the right of the river is a levee with a dashed line extending vertically from the levee crown, representing river-floodplain topography—the topographic relationship between the river channel and floodplain, including the relative elevation of the channel and floodplain surfaces, and features that connect the river and floodplain such as levee breaches, sloughs, and side channels. The dashed vertical line, along with the box "threshold for inundation," graphically illustrates that the riverine flood hydrology characteristics do not begin to influence habitat characteristics on the floodplain until the flows exceed this threshold (the exception is rising river stage, through groundwater connectivity, can influence characteristics of the water quality and quantity within floodplain wetlands prior to the connection of surface waters). In this model, modifying factors, denoted by red polygons, act to increase the threshold for inundation; (3) If the threshold is exceeded, then river water enters and inundates the floodplain and interacts with the habitat mosaic created in Model 1. (4) The interaction of riverine flood hydrology with floodplain habitat mosaic results in a variety of inundated habitat characteristics, which are the primary inputs to Model 3.

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floodplain that are important to the species or processes described in Model 3 (Figure 6).

Model Scale, Objectives, Structure, and Outcomes

Model 2 illustrates processes and conditions that: (1) result in inundation of a given floodplain; and (2) influence habitat characteristics on the floodplain during the period of inundation. In this model, the physical template is relatively static, unlike Model 1 which emphasizes the dynamic processes that, over time, create, alter, and maintain the physical habitat template. Model 2 can be used to evaluate strategies to alter inundation patterns (e.g., frequency, duration, season of inundation) and to influence habitat conditions within the inundated floodplain (Table 2).

While Model 1 depicts processes and patterns that can vary across the spatial scale of the model (e.g., the diverse elements of the shifting mosaic), Model 2 is more appropriate for a relatively discrete patch of floodplain that is undergoing an inundation event. Even relatively small floodplain sites can have considerable spatial and temporal heterogeneity during an inundation event (Ahearn and others 2006). For Models 2 and 3, this heterogeneity is discussed in the narrative but is not specifically illustrated in the conceptual models.

The outcomes of this model are a variety of inundated habitat characteristics that are the primary inputs to Model 3. These characteristics directly affect biota and processes during the inundation period, and influence the production of desired outputs such as juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and phytoplankton.

Model Summary
Inundation and Connectivity

The **inundation threshold** is the river stage at which connectivity begins between river surface water and the floodplain. A primary control on this threshold is the **floodplain elevation** above the river channel; the greater the elevation, the greater the inundation threshold (i.e., a higher discharge and stage is required to exceed the threshold). **Channel incision**

increases the elevation difference and thus increases the inundation threshold. **Connectivity** also affects flooding dynamics by decreasing the inundation threshold. **Levees**, both natural and human-made, generally have higher elevations than the adjacent floodplain, which increases the stage required for river water to overtop the levee and then inundate the floodplain. In this model, connectivity refers to low points or breaches in a flanking levee that provide preferential flowpaths and allow waters to inundate the floodplain at a lower stage than would be required to overtop the levee. For natural levees, sloughs and crevasses can provide this connectivity, while with man-made levees, connectivity can be provided by accidental or intentional breaches, or with weirs. In the model, intact constructed levees are shown as a modifying factor that decreases connectivity and increases the threshold for inundation.

Secondary hydrology includes sources other than river flow. These include direct precipitation that contributes to elevated water tables and surface water on the floodplain, groundwater inflows, and tributaries that dissect the floodplain. These other sources can initiate floodplain inundation and also mix with surface water from the main river. In some systems, secondary hydrology can cause significant floodplain inundation without inundation from the primary river. Additionally, secondary hydrology can contribute to variability in the water quality of the floodplain, for example by contributing nutrients (Schemel and others 2004). In this model, secondary hydrology is shown to reduce the threshold for inundation; secondary hydrology doesn't directly affect the connectivity or relative elevation of the river and floodplain, but it can begin the process of inundation and so is shown to reduce the threshold.

To increase the **frequency**, **depth**, or **duration** of inundation, management actions can address the inundation threshold. Possible actions include flow releases (e.g., increasing **discharge**) and increasing connectivity by breaching or removing natural or flood-control levees (Opperman and others 2010). The relative elevation difference between floodplain and river channel can also be reduced. Floodplain surfaces can be graded to a lower elevation. A specific example of this is the grading of a swale that extends from

a river channel up into a floodplain (Williams and others 2009). The addition of roughness to a channel can also increase the stage for a given discharge and thereby reduce the elevation difference between river and floodplain. Large wood or other features can add such roughness and, at one time, large wood strongly influenced the stage at which floodplain inundation occurred. Large-scale land lowering is also possible but generally carries high costs compared to these other strategies to reduce elevation differences. Replicating the inundation dynamics that secondary hydrology sources provide, management actions can direct water from other sources (e.g, pumped groundwater or through irrigation canals) on to the floodplain to create inundation (e.g., as occurs on the Yolo Widlife area).

Inundated Habitat Characteristics

Once the threshold for inundation is exceeded and river water enters the floodplain the **floodplain habitat** mosaic becomes inundated. Model 2 focuses on how river flows and secondary hydrology interact with the habitat mosaic to create specific **inundated habitat characteristics**. These characteristics structure the biotic and abiotic environment for several important "outputs" that depend on inundated habitat, such as Sacramento splittail (*Pogonichthys macrolepidotus*), juvenile Chinook salmon, and the production of phytoplankton (Model 3). The habitat mosaic is an important driver of these characteristics as are **river hydrology** and processes that occur within the water column. **Topographic heterogeneity** and the composition of **vegetation** that is inundated can influence the production of these important outputs.

To illustrate the model, I'll describe two interrelated inundated habitat characteristics—**hydrological residence time** and **duration**—that are particularly important for several of the management outputs (Model 3). Below I review how hydrological factors, the habitat mosaic and other inundated habitat characteristics influence residence time and duration, as well as how residence time and duration, in turn, influence other inundated habitat characteristics.

Hydrological residence time is the length of time that a given unit of water remains in a given place and thus reflects the exchange rate of water at that place. Residence time can be calculated in many ways. One simple method is dividing the volume of the area of interest (e.g,. floodplain site) by the flow rate. Residence time is inversely related to water **velocity**. Residence time differs from duration in that **duration** refers more simply to the amount of time that a given area is inundated; an area can have longduration inundation by water with either very long residence time (e.g., a pond) or very short residence time (e.g, a river). The **hydraulic roughness** of the habitat mosaic's vegetation affects residence time by influencing water velocity; the mosaic's topographic heterogeneity influences velocity and **drainage connectivity**, which affect the exchange rate of water and rate of floodplain draining—longer draining time leads to longer residence time.

The duration of floodplain inundation is largely a function of the duration of river inputs and, after inputs cease, by the factors that control residence time. The duration of river flows above the inundation threshold determines how much water is being contributed to a floodplain, and for how long, while residence time influences how long that water remains after inputs cease. Duration increases with the **intra-annual frequency** of floods, depending on the interval between floods. Re-flooding a patch before it has drained extends the inundation duration and generates greater variability in inundation depth.

The duration of floodplain inundation has an important influence on the ability of native fish to spawn and rear (Models 3B and 3C). Residence time is a major influence on food web productivity (Model 3A), largely through its influence on or association with a number of other inundated habitat characteristics. For example, residence time is correlated positively with **temperature**. A volume of water with high residence time on a floodplain can absorb more solar input than a volume with low residence time. Because low-velocity water has less energy to transport sediment, residence time (inversely related to velocity) correlates with decreasing turbidity and greater **light** penetration as **suspended sediment** settles out of the water column. High residence time water on the floodplain is often associated with low

velocity, warmer and clearer water—all factors associated with food-web productivity.

Management options for influencing residence time include manipulating vegetation and topography to alter hydraulic roughness and drainage connectivity. For example, portions of the Yolo Bypass are graded, maintained with low hydraulic roughness, and otherwise managed for rapid drainage, decreasing the residence time of those areas. The residence time of floodplain sites separated by internal levees can be controlled by the number, size and location of breaches connecting those sites. Managed flooding, by manipulating river flows and/or the threshold for inundation (e.g, through weirs), can also influence residence time. Because residence time increases during the draining phase (e.g. after river inputs cease), for a given total volume of flood water, several pulses separated by intervals of time can increase the amount of time that a floodplain experiences high-residence-time draining, compared to a single larger or longer pulse (Ahearn and others 2006).

Management options to affect duration, beyond those for residence time, are primarily achieved through flow manipulations (river and secondary hydrology) or inundation threshold. For example, for a given flood event, reducing the inundation threshold by notching a weir would allow river flows to enter the floodplain for a longer period of time, thereby increasing duration.

MODEL 3: MANAGEMENT OUTPUTS FROM INUNDATED FLOODPLAINS

Model 3 illustrates how the inundated habitat characteristics, developed in Model 2, interact with a few other key elements to influence the production of biota of direct interest to Delta restoration planners, including algae, zooplankton, splittail, and juvenile Chinook salmon.

Model Scale, Objectives, Structure, and Outcomes

Model 3 comprises an overall framework (Figure 7) with three sub-models for aquatic food webs, splittail, and juvenile Chinook salmon. For the fish, the sub-models focus on the floodplain-specific portions of species' life histories. Species such as splittail and Chinook salmon are influenced by many factors external to the floodplain model that are not captured or described here. Broader perspective on salmon life history can be found in the DRERIP species model and in Williams' (2009) paper; Moyle and others (2004) extensively review of splittail life history.

The spatial and temporal scales for Model 3 are similar to Model 2: a discrete floodplain that undergoes inundation during a single flood event or flood season. The primary inputs to Model 3 are the inundated habitat characteristics created in Model 2 and the outputs are those of direct management interest, such as splittail or algal carbon.

Model 3A: Food Web

Inundated floodplains produce phytoplankton and other algae (Ahearn and others 2006), sources of biologically available carbon that are particularly important to downstream food-limited ecosystems such as the Sacramento–San Joaquin Delta (Sobczak and others 2002). Phytoplankton and attached algae (periphyton; Figure 8) are likely the primary sources of carbon that drive floodplain food webs (Sobczak and others 2002; Ahearn and others 2006), so this model (Figure 9) focuses on those algae rather than on macrophytes or the detrital loop that involves terrestrially derived organic matter. The flow of energy from algae to zooplankton and other invertebrates influences floodplain resources for native fish. The primary outputs of this model are phytoplankton (biologically available carbon for downstream export), zooplankton, and other invertebrates that provide primary inputs to subsequent models (3B and 3C).

Algae (Phytoplankton and Periphyton)

This narrative focuses more on the production of phytoplankton than periphyton because periphyton have received comparatively little study in floodplains and its relative importance is not certain (Ahearn and others 2006). The most important variables that influence algal growth are the limiting factors of temperature, light, and nutrients, along with
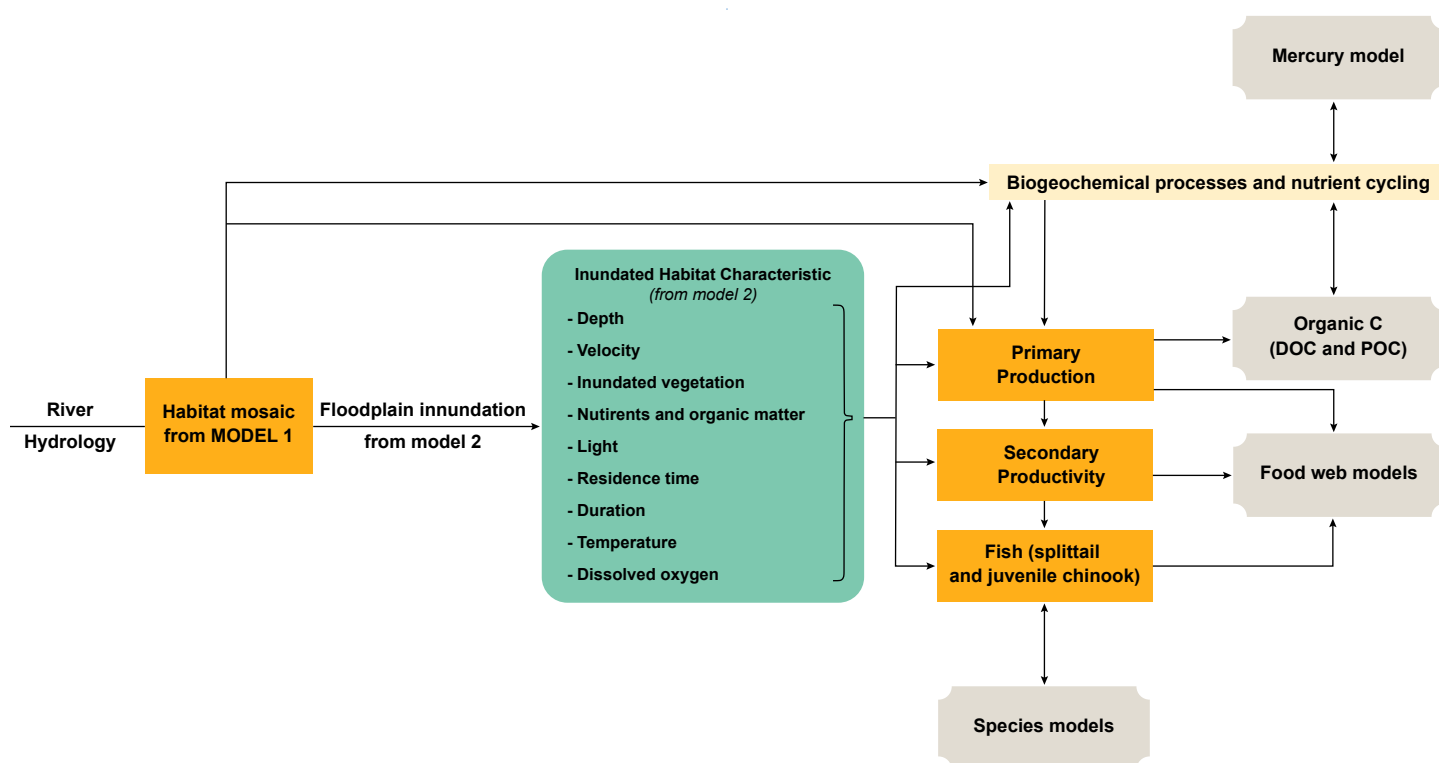
Figure 7 The generalized structure of the sub-models within Model 3 ("management outputs from inundated floodplains"). From the left, a habitat mosaic (output of Model 1) is inundated by water from the river and secondary hydrology sources (Model 2 threshold for inundation) to produce inundated habitat characteristics (central green box; Model 2). These characteristics are the primary environmental variables influencing the floodplain biota of management interest during the period of inundation. To the right of the inundated habitat characteristics box is a simplified food web. The main components of this food web include the primary outputs that managers seek from inundated floodplains. These models can interact with species models (splittail and Chinook salmon) and models for organic carbon and mercury.

Figure 8 Primary productivity in the Cosumnes River floodplain. Long duration, high residence time flooding promotes the growth of phytoplankton and periphyton, seen here as clumps of algae attached to wetland plants. (Photo by Jeff Opperman).

residence time and grazing pressure by zooplankton and macroinvertebrates.

Algal growth is positively correlated with **light** and **temperature** (Cushing and Allan 2001). Flooding in the spring, with more sunlight and warmer temperatures, leads to greater productivity of phytoplankton than winter flooding. Sheibley and others (2006) found that nitrate removal from the water column on the Cosumnes floodplain increased with increasing water temperature, which was attributed to increased uptake activity by phytoplankton. However, increasing water temperature can cause shifts in species composition and warmer temperatures favor cyanobacteria that can produce nuisance or harmful blooms (Jassby and others 2003).
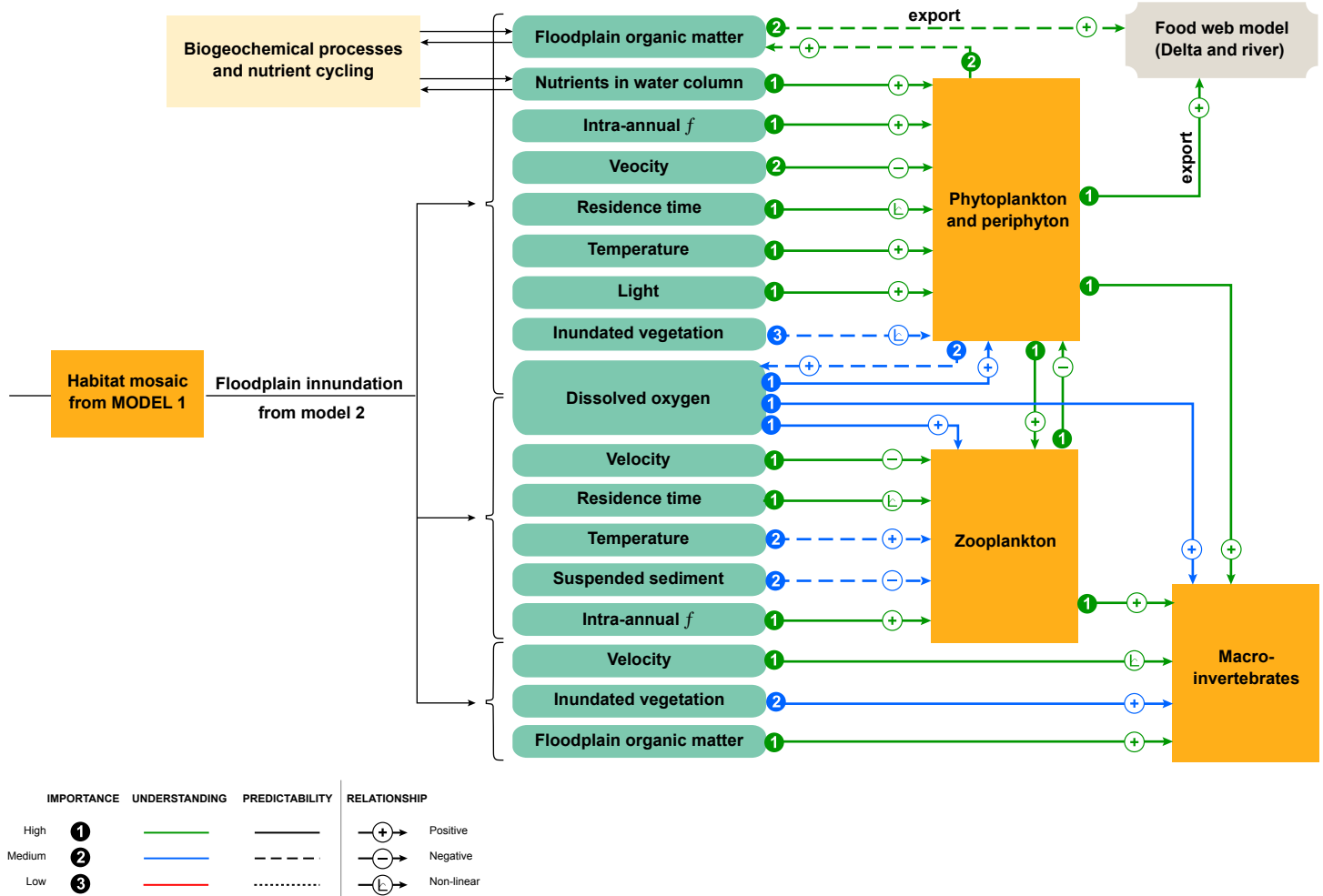
15

Figure 9 Model 3A: a floodplain food web. Management outputs include algae (phytoplankton and periphyton), zooplankton, and invertebrates

Algal growth depends on the uptake of **nutrients** from the water column. These nutrients can be supplied in dissolved form through river inflow or from the processing of organic matter through **biogeochemical pathways**. On the Cosumnes River Ahearn and others (2006) reported that phytoplankton were initially nitrogen-limited; later in the season, the proportion of nitrogen-fixing phytoplankton increased, and the system shifted to being phosphorous-limited (Grosholz and Gallo 2006). Phytoplankton blooms can deplete the water of nutrients leading to declines in productivity. Subsequent inundation (Ahearn and others 2006), mineralization of organic matter, or inflows of nutrients from other sources, e.g. other tributaries

(Schemel and others 2004) can replenish nutrients in the water column and continue to maintain phytoplankton growth.

Phytoplankton productivity is initially positively correlated with **residence time** (Schemel and others 2004; Sommer and others 2004; Ahearn and others 2006); phytoplankton concentrations are low during inundation events when residence time is low, because of both dilution and displacement. High-**velocity** flows can flush phytoplankton from the floodplain and transport them downstream (Cushing and Allan 2001); if residence time is shorter than phytoplankton growth rate, biomass will not accumulate (Schemel and others 2004). Long residence time

can result in a depletion of nutrients and reduced productivity, which is why this is shown as a non-linear relationship. Further, during long residence-time inundation, zooplankton can graze phytoplankton and reduce standing biomass; both grazing pressure and nutrient depletion (and specifically nitrogen limitation) can result in a shift in the phytoplankton community toward nitrogen-fixing phytoplankton that are resistant to grazing (Grosholz and Gallo 2006).

Phytoplankton concentrations tend to be greatest during the draining period of an inundation event, because of increasing residence time (Schemel and others 2004; Ahearn and others 2006). Researchers have recommended that total phytoplankton production from a given floodplain could be maximized by increasing the intra-annual frequency of floods to increase the total proportion of time in draining-phase conditions. Ahearn and others (2006) reported that phytoplankton productivity peaked 2 to 5 days after disconnection with the river (and cessation of river inflow).

Zooplankton and Macroinvertabrates

Zooplankton in Central Valley floodplains include *Daphnia*, and *Cladocerans* and rotifers. The most important variables that influence zooplankton production are hydraulic residence time and the availability of food resources (e.g., phytoplankton and periphyton). Zooplankton can consume both algal and detrital carbon. Laboratory trials with *Cladocerans* suggested that zooplankton may be food limited if phytoplankton concentrations drop below a level that correspond to 10 µg L^{-1} Chl *a*, (Muller–Solger and others 2002). Detrital organic matter appears to be a less important food resource and even where detrital carbon dominates the carbon budget, phytoplankton availability most strongly controls zooplankton growth (Muller–Solger and others 2002; Sobczak and others 2002). Phytoplankton productivity is greatest during the draining stage, and on the Cosumnes floodplain Chl *a* was measured at 19 and 18 µg L^{-1} during two draining periods in 2005, approximately four times the level found in the river (Ahearn and others 2006). In the Yolo Bypass, phy-

toplankton density can be high enough to produce a Chl *a* concentration of up to 23 µg L^{-1} (Schemel and others 2004), which indicates that floodplains during the draining stage can produce concentrations of phytoplankton that provide adequate food resources for zooplankton growth.

Zooplankton density initially increases with residence time, because of low velocities and reduced transport rates, and to increases in the availability of algae. With further increases in residence time, zooplankton reach a peak density and then begin to decline (Baranyi and others 2002). Grosholz and Gallo (2006) found that zooplankton densities peaked about 2 to 3 weeks after disconnection between river and floodplain (draining phase), and therefore recommended several pulses during the year, separated by 2 to 3 weeks, to maximize production of the zooplankton eaten by juvenile fish. The decline in zooplankton with increasing residence time is caused by a reduction of the food base and predation by fish. Despite warmer water and higher productivity, the Yolo Bypass didn't support significantly higher densities of zooplankton than did the adjacent Sacramento River; even though residence time in the bypass was significantly longer than in the river, the residence time was still probably insufficiently long for zooplankton to develop and reproduce completely (Sommer and others 2004).

Drift macroinvertebrates, including chironomids and terrestrial invertebrates, were the primary food resource for juvenile Chinook in the Yolo Bypass (Sommer and others 2001) and, were positively correlated with flow (discharge and flow velocity). In the Yolo Bypass, these organisms attain high densities soon after inundation, providing a food source to fish that is available before food web productivity that depends on long residence times can develop (Sommer and others 2004). Thus, higher-velocity water at a floodplain site may increase the amount of drift and terrestrial invertebrates that are transported to a site. However, high velocity water can also displace inverterbrates from the site downstream (Cushing and Allan 2001) so, within this conceptual model, the relationship between velocity and inverterbrates is shown to be nonlinear.

Macroinvertebrates feed on a broad range of food resources, and thus macroinvertebrate productivity will generally increase with the increasing availability of food resources.

Macroinvertebrates are often associated with floating and emergent plants, and vegetative structure correlates with higher densities of macroinvertebrates (Welcomme 1979).

Model 3B: Sacramento Splittail

Sacramento splittail may be one of the few native California fish that can be considered an obligate floodplain spawner, with population dynamics closely associated with annual patterns of flow and floodplain inundation (Moyle and others 2004). For example, the strength of splittail year class (age-0 abundance) correlates highly to the **duration** of Yolo Bypass inundation (Sommer and others 1997). Below, I review the most important variables that influence splittail spawning and rearing on floodplains (Figure 10).

Adult splittail move into inundated areas in late February or early March and spawning occurs in March and April; however, spawning can occur later in April and into May as well. The spawning time range is perhaps as broad as late February to early July, but later than May is "highly unusual" (Moyle and others 2004). Recent research from the Yolo Bypass suggests that spawning is most likely to occur near the vernal equinox (late March) (Feyrer and others 2006b). Splittail young-of-the-year (YOY) have been observed leaving floodplain habitats in May (Moyle and others 2004). These various observations suggest that floodplain inundation from March through May is conducive to successful splittail spawning.

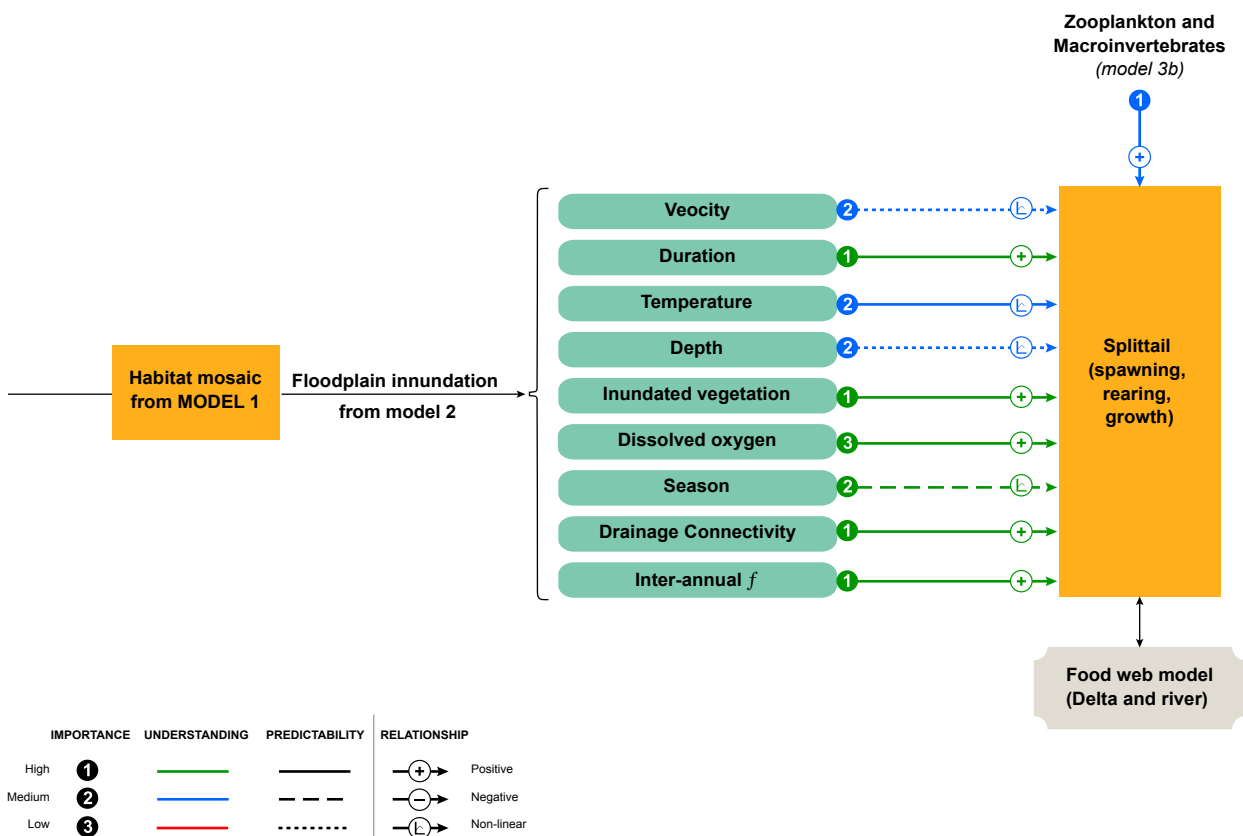Long-duration floodplain inundation is necessary for successful spawning, incubation and initial rearing

Figure 10   Model 3B: factors that influence splittail spawning and rearing on inundated floodplains

of larval splittail. Splittail eggs require 3 to 5 days to hatch and larval and juvenile splittail will remain on the floodplain while conditions are appropriate (Moyle and others 2004). Emigration from the floodplain appeared to be related to fish size as most YOY leaving the Yolo Bypass were between 30 to 40 mm in length. This size range suggests that a duration sufficient for fish to reach this size will be optimal (Feyer and others 2006b). Longer duration flooding that allows adults time to feed on earthworms on floodplains before they spawn may also improve spawning success. The energy gained by adults feeding on worms may improve their condition and egg production (Moyle and others 2004). Thus the optimal duration will allow for adults to enter floodplains, feed, and spawn; for eggs to incubate and hatch; and then provide sufficient duration for the YOY to reach 30 to 40 mm in length. The strongest year classes of splittail occur in years with prolonged inundation of floodplains (e.g, Yolo Bypass, Cosumnes) during March and April (Moyle and others 2004).

Splittail eggs are adhesive and adhere to **vegetation** for incubation (Moyle and others 2004). On the Cosumnes River floodplain, spawning was observed in open areas <1.5 m deep with "dense growths of annual terrestrial plants; dead cocklebur plants may be especially favored because they provide shelter from predators and high flows and are a source of invertebrate prey" (Moyle and others 2004, citing Crain and others 2004). In the Sutter Bypass, spawning sites were characterized by both annual and perennial vegetation (Moyle and others 2004, citing R. Baxter, unpublished data). Larval fish may also prefer to rear within inundated terrestrial vegetation (Moyle and others 2004).

For successful floodplain rearing, YOY splittail must be able to emigrate from the floodplain. Certain floodplain features can serve as barriers or stranding areas for juvenile fish; in particular, human-built features such as gravel pits, canals, and berms can prevent emigration back to the river (Sommer and others 2005). Splittail populations can be maintained without annual occurrence of the appropriate spawning conditions on floodplains, both because occasional strong year classes can maintain populations and because there is some spawning even in very dry

years (e.g., along channel margins) (Moyle and others 2004). However, splittail populations will generally increase with increasing **frequency** of appropriate spawning and rearing conditions on floodplains.

Model 3C: Juvenile Chinook Salmon

Juvenile Chinook salmon have been documented to use floodplain habitats in California (Whitener and Kennedy 1999; Sommer and others 2001). Fall-run Chinook have been observed rearing in the Yolo and Sutter bypasses and spring-run Chinook may also use these habitats (Sommer and others 2005; Feyer and others 2006a). Juveniles from the Cosumnes River's small fall run have been documented utilizing the Cosumnes floodplain (Swenson and others 2003). Within various floodplain habitats, researchers have reported that juvenile salmon had faster growth rates than salmon rearing in adjacent river-channel habitat (Figure 11; Sommer and others 2001; Limm and Marchetti 2009; Jeffres and others 2008). Below

Figure 11 Juvenile Chinook salmon have faster growth rates on floodplains than within main-channel rivers. Fish on the left were reared within enclosures in the Cosumnes River channel while those on the right were reared on the Cosumnes River floodplain. Source: Jeffres and others (2008). Photo by Jeff Opperman.
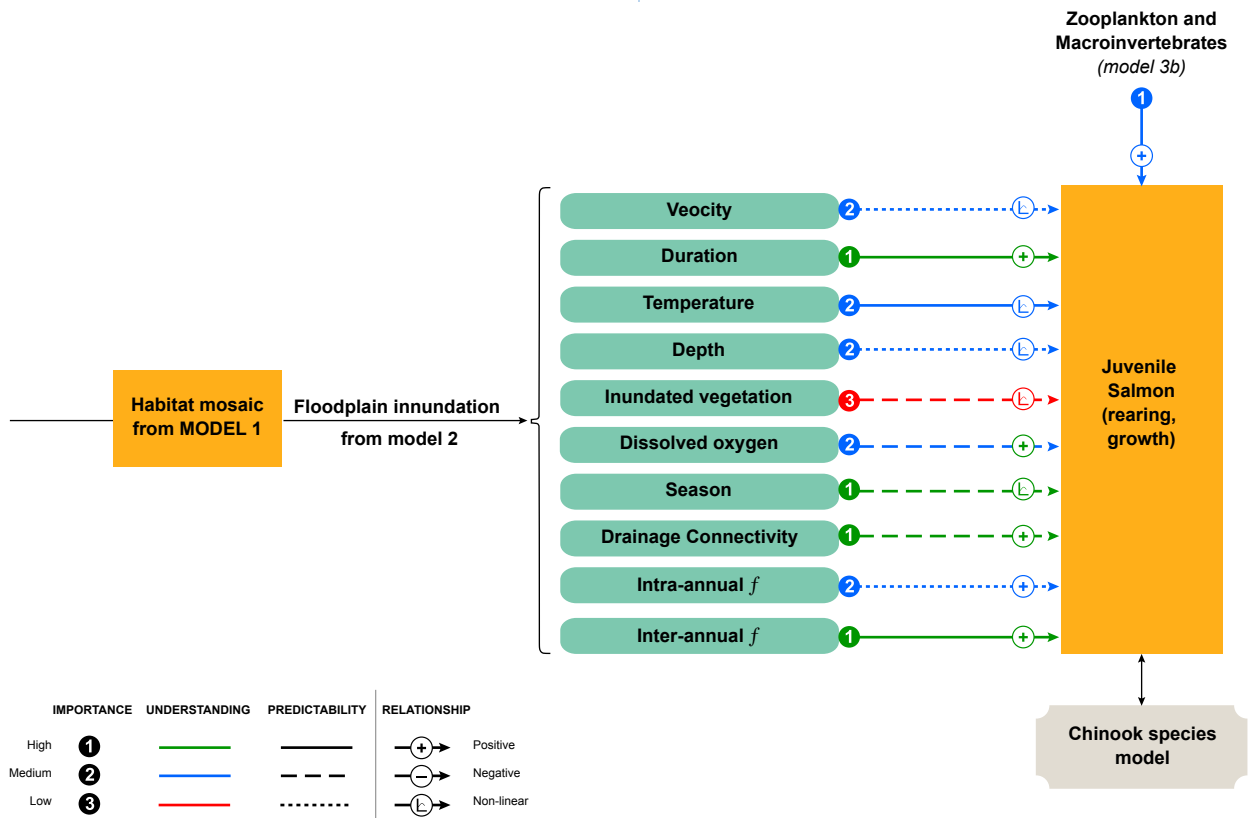
Figure 12 Model 3C: factors that influence juvenile Chinook rearing on inundated floodplains

I review the primary variables that influence salmon rearing on floodplains (Model 3c; Figure 12).

The higher growth rates of juvenile Chinook on Central Valley floodplains, relative to river habitats, has largely been attributed to the greater availability of prey within floodplain habitats (Sommer and others 2001; Jeffres and others 2008). For example, prey items can be 1 to 2 orders of magnitude greater in floodplains than in adjacent rivers: Dipterans in the Yolo Bypass (Sommer and others (2001) and zooplankton biomass in the Cosumnes floodplain (Grosholz and Gallo 2006).

Juvenile salmon have been reported to use a wide range of habitats on the Yolo Bypass, ranging from rice stubble to bare ground (Ted Sommer, California Department of Water Resources pers. comm., 2004) It is not well established what **vegetation** types are preferable for juvenile Chinook on floodplain. The most important characteristic of vegetation is likely to be its effect on prey availability, and secondarily as cover. In river channels, juvenile Chinook prefer relatively shallow habitats (15 to 60 cm) (Bjorn and Reiser 1991), although **depth** may not be particularly important for Chinook use of floodplains because Ahearn and others (2006) found that, during various portions of the flood-draining cycle, both deep and shallow portions of the floodplain were highly productive. Juvenile salmon are generally considered to prefer low-**velocity** habitats (Bjorn and Reiser 1991) but the velocity preferences of salmon on floodplains has not been well studied. Presumably, however, salmon use floodplains in large part because of the availability of low-velocity, shallow habitat.

Salmon have specific and well-studied **temperature** tolerances. However, tolerable or optimal temperatures are influenced by food availability (Myrick and Cech 2004). Optimal temperatures for growth of Chinook juveniles are considered to be 13 to 18 °C (Moyle 2002). Floodplains often have warmer water

temperature than do rivers, and these temperatures near the upper end of the optimal range may benefit rearing salmonids. For example, the Yolo Bypass was up to 5 °C warmer than the river (Sommer and others 2001) and off-channel habitats along the upper Sacramento River were 2 to 4 °C warmer than the river (Limm and Marchetti 2009). Thus within the range of temperatures generally observed within rivers and floodplains during the common period of inundation (winter to early spring), salmon growth can be considered to increase with temperature. Sommer and others (2001) note that the increased prey availability in the Yolo Bypass likely offset any increased metabolic requirements from the warmer floodplain water (relative to the Sacramento River). It is possible that floodplains could experience very high temperatures during spring flooding that could be detrimental to salmon. However, juvenile Chinook within enclosures on the Cosumnes River floodplain continued to grow rapidly even as daily afternoon temperatures reached levels considered lethal to salmon (25 °C) (Jeffres and others 2008). This observation suggests that the salmon were able to tolerate these temperatures because of the high density of prey (Myrick and Cech 2004).

Salmon require well-oxygenated water. Floodplain conditions can produce low levels of **dissolved oxygen** (e.g., long residence time and decaying vegetation) that are lethal to juvenile Chinook. For example, a patch of low dissolved oxygen (DO) water on the Cosumnes floodplain (3 mg O^2 L^{-1}) was quickly lethal to juvenile salmon within an enclosure (Jeffres and others 2008). However, it is not known how common such conditions are and salmon would likely avoid low DO patches of water. Further, as described for temperature, the availability of food influences tolerances to DO. Therefore, even though the relationship between DO and salmon has been well studied, there are several unknowns for transferring information about this relationship to floodplain environments. In general, however, it can be assumed that higher DO is better for salmon on floodplains.

The migration of juvenile salmon coincides with peak flows and so also coincides with access to floodplains. However, the specific timing of emigration varies from run to run, from river to river, and from year to year. Most fall-run fish emigrate between December and March (Williams 2006). Non-native fish begin to access the floodplain later in the spring (Crain and others 2004). Flooding in the winter and early spring will therefore tend to benefit native over non-native fish species. Floodplain benefits for juvenile Chinook should increase with increasing **duration** of flooding (thus this is a linear positive relationship). However, even relatively short periods of access may provide benefits because fish reared in enclosures on floodplain habitats showed rapid growth in a 2-week interval on the Cosumnes River floodplain (Jeffres and others 2008). For successful floodplain rearing, juvenile salmon must be able to emigrate from the floodplain. Emigration may be triggered by rising water temperatures or other cues and multiple flood pulses may facilitate emigration from the floodplain. Floodplains have not appeared to be population "sinks," and preliminary evidence suggests that salmon reared in the Yolo Bypass have long-term survival rates that are similar to or higher than salmon reared in the river (Sommer and others 2005). However, certain features can serve as barriers or stranding areas for juvenile fish; in particular, human-built features such as gravel pits, canals, and berms can prevent emigration to the river.

SYNTHESIS

These conceptual models can help identify the key processes and potential management options that can be used to influence the production of various floodplains outputs. For example, to understand the key processes and management options for juvenile Chinook salmon, one can work backward through the models, beginning with Model 3C (Figure 12). This model indicates that the most important factors for salmon are food resources (zooplankton and macroinvertebrates), and inundated habitat characteristics that are physical (drainage connectivity) and hydrological (flood duration, season, and inter-annual frequency).

Model 2 (Figure 6) examines inundated habitat characteristics, and indicates that the hydrological characteristics identified above depend on the corresponding characteristics of river flows (e.g., season of river flood to season of inundation) along with resi-

dence time influencing duration of inundation. More important, the river hydrological characteristics cannot become inundated habitat characteristics unless the inundation threshold is exceeded. All of these various factors can potentially be influenced by management options. For example, the inundation threshold can be manipulated by physical interventions such as levee setbacks or breaches, and discharge can be influenced by reservoir operations. Reservoir operations (e.g., managed flood releases) can also influence the hydrological factors of duration, season, and inter-annual frequency. Drainage connectivity can be managed through removal of potential barriers for salmonid emigration from the floodplain site (e.g., berms or pits).

Model 3A (Figure 9) examines food resource factors, and indicates that zooplankton and macroinvertebrates are influenced most strongly by a range of inundated habitat characteristics—including residence time, velocity, and intra-annual frequency—and the availability of their own food resources: algae (phytoplankton and periphyton) for zooplankton, and algae and zooplankton for macroinvertebrates. In turn, algae are influenced by light and temperature (both of which are strongly influenced by flooding season; Model 2), and residence time.

Management options for influencing the factors that control the availability of salmon food resources include reservoir operations that influence flooding season (to influence the light and temperature that promote algal productivity) and the intra-annual frequency. Grosholz and Gallo (2006) recommended that multiple flood pulses, spaced 2 to 3 weeks apart, would maximize zooplankton productivity because multiple pulses will have multiple draining phases. Hydrological residence time is generally longest during draining phases (Ahearn and others 2006), which leads to high algal productivity, followed by high zooplankton concentrations and then population crashes. Thus increasing the intra-annual frequency results in multiple pulses that "re-set" the floodplain food web. For a given volume of water, multiple smaller pulses, rather than one large pulse, could increase the total number of days in the high-residence-time draining phase, thus increasing produc-

tivity at multiple levels of the floodplain food web: algae, zooplankton, and Chinook salmon.

The complexity of processes and interactions described in the models can be summarized with a few overarching concepts. Ecologically functional floodplains—that is, those that can sustainably produce a full range of management outputs—require hydrological connectivity with their adjacent rivers across a wide range of flow levels. Connectivity is clearly essential for the exchange of organisms and organic matter between river and floodplain. Disconnected floodplains (e.g., those on the "dry side" of levees) or rarely connected floodplains (e.g., those on relict floodplain surfaces inundated very infrequently) can still support riparian forests but, absent the geomorphic processes mediated by hydrological connectivity, most riparian species will cease recruitment, and the forest structure and composition will shift toward more upland characteristics (Ward and others 2002).

In addition to connectivity, a diverse range of flow levels and events are necessary to maintain functional floodplains and their associated outputs. Infrequent, high-magnitude flood events create and maintain the habitat mosaic, including topographic features, such as side channels and oxbow lakes, and vegetative community diversity is maintained by the processes of erosion and deposition. Long duration, spring floods are essential for food-web productivity and the spawning and rearing of native fish.

From a management perspective, flow variability and connectivity are necessary, but not sufficient to maintain production of desired floodplain outputs; functional floodplains must exist at sufficient geographic scales for these processes to operate and for outputs to be measurable and meaningful (Opperman and others 2010). The conceptual models presented here focused on a generalized floodplain "site" and do not specifically address scale or spatial context.

Spatial scale is important for two reasons. First, many of the processes that maintain the habitat mosaic, such as meander migration and channel avulsion, can only occur on sites that are sufficiently large enough for these processes to occur. Second, the benefits provided by the floodplain habitat mosa-

ic (e.g., habitat for riparian songbirds) are generally proportional to the size of the floodplain site.

Similarly, the production of management outputs from floodplain inundation are also roughly proportional to the spatial extent of a floodplain site or aggregation of sites. For example, due to its small size (approximately 100 ha) the Cosumnes River floodplain undoubtedly provides a much smaller contribution to splittail spawning than does the Yolo Bypass (24,000 ha). Given its scale, the inundation of the bypass may have population-level effects on splittail, because year–class strength is correlated with the duration of inundation of the bypass (Sommer and others 1997).

As described in the conceptual models, numerous options exist for managers to increase the connectivity and flow variability of floodplain sites, including levee setbacks and breaches, weirs and other control structures, and managed releases from reservoirs. A fundamental management challenge is accomplishing these actions at the spatial scales necessary to contribute to the recovery of Delta floodplain species and communities. While restoration program funding can contribute to important increases in the extent of functional floodplain, other strategies may be required (Opperman and others 2009). Opperman and others (2009, 2010) describe several approaches for expanding the area of hydrologically connected floodplain including promoting agriculture that is compatible with periodic inundation, developing markets for the ecosystem services that floodplains provide, and linking floodplain restoration with flood-damage reduction projects. California—with its flood season discontinuous with the agricultural growing season, its strong need for floodplain ecosystem services such as groundwater recharge, and its unacceptably high flood risk for Delta and Central Valley urban areas—is well-positioned to explore how these various mechanisms can promote floodplain land use that is economically and environmentally sustainable, and contributes to the recovery of the Delta ecosystem.

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