Sacramento-San Joaquin Delta
Regional Ecosystem Restoration Implementation Plan

Ecosystem Conceptual Model

Tidal Marsh - Draft

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Status of Peer Review: Model has not yet completed the peer review process and final modifications may be required of the developers. Model may not be cited or circulated until that process is complete. It may be used in identifying and evaluating restoration actions with assistance from content experts. Model is appropriate for use by experienced evaluation team with input from content experts as necessary.

DO NOT CITE

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PREFACE

This Conceptual Model is part of a suite of conceptual models which collectively articulate the current scientific understanding of important aspects of the Sacramento-San Joaquin River Delta ecosystem. The conceptual models are designed to aid in the identification and evaluation of ecosystem restoration actions in the Delta. These models are designed to structure scientific information such that it can be used to inform sound public policy.

The Delta Conceptual Models include both ecosystem element models (including process, habitat, and stressor models); and species life history models. The models were prepared by teams of experts using common guidance documents developed to promote consistency in the format and terminology of the models http://www.delta.dfg.ca.gov/erpdeltaplan/science_process.asp .

The Delta Conceptual Models are qualitative models which describe current understanding of how the system works. They are designed and intended to be used by experts to identify and evaluate potential restoration actions. They are not quantitative, numeric computer models that can be "run" to determine the effects of actions. Rather they are designed to facilitate informed discussions regarding expected outcomes resulting from restoration actions and the scientific basis for those expectations. The structure of many of the Delta Conceptual Models can serve as the basis for future development of quantitative models.

Each of the Delta Conceptual Models has been, or is currently being subject to a rigorous scientific peer review process. The peer review status of each model is indicated on the title page of the model.

The Delta Conceptual models will be updated and refined over time as new information is developed, and/or as the models are used and the need for further refinements or clarifications are identified.

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OVERVIEW

Tidal marshes are a subset of estuarine wetlands defined by the presence of vegetation types uniquely adapted to sheltered intertidal zones of temperate and subtropical coastal plains (Chapman 1960, 1976, Mitsch & Gosselink 1993). They are found across a full range of salinity conditions from seawater on the immediate coast to freshwater tidal reaches of estuarine river systems. Marshes are transitional ecosystems that provide critical connections between adjacent subtidal and terrestrial ecosystems within the estuarine landscape (Levin *et al.* 2001). These "critical transition zones" often function as conduits for substantial fluxes of materials and energy (Ewel *et al.* 2001), and provide a variety of valuable ecosystems services related to the maintenance of biodiversity, fish and wildlife habitat, water quality, flood abatement and carbon sequestration (Costanza *et al.* 1997, Weslawski *et al.* 2004, Zedler & Kercher 2005). However, estuarine marshes and the biotic communities that depend on them are vulnerable to anthropogenic impacts (Holland *et al.* 2004, Snelgrove *et al.* 2004), and the functionality of these systems can be difficult to restore once severely impacted (Zedler & Kercher 2005).

The San Francisco Bay estuary is perhaps the most hydrologically-engineered estuarine wetland system in the United States, and an estimated 95% of the marsh area that existed there in 1850 has been altered or converted to other types of ecosytems (Josselyn 1983). The principal source of freshwater input to the estuary enters through the Sacramento-San Joaquin River Delta (Delta), which is the terminus of a watershed that drains about 40% of California's land area. Anthropogenic alterations of the estuary's hydrologic characteristics have profoundly affected the extent and functioning of the tidal wetlands, particularly in the brackish and tidal fresh portions of the upper estuary associated with the Delta. Although the conceptual model presented here is intended to capture the features and dynamics of tidal marshes in the Delta (e.g., Suisun Bay to the upriver extent of the tide), oligohaline and tidal freshwater marshes still remain poorly understood. Recent texts (e.g., Sharitz & Pennings 2006) still consider the review by Odum (1988) as the best treatment of these low salinity tidal ecosystems. Consequently, development of the current conceptual biological model often required us to judiciously borrow from the more extensive literature on temperate salt marshes in diverse regions.

This broad-view model explicitly acknowledges the importance of interactions among structural components of tidal marsh ecosystems and the hydrologic characteristics that are modulated by both extrinsic and intrinsic factors. The interaction of these factors control biological/ecological processes that support two of the more important ecosystem services of tidal marshes: essential habitat for biota and the net export of high-quality organic production. It also highlights the transitional position of tidal marshes between adjacent ecosystems, including terrestrial and aquatic interfaces that represent the dynamic and permeable boundaries of the tidal marsh; these interfaces may function as membranes through which the exchange of materials (organisms, surface/groundwater, etc.) and energy between upland and open water estuarine environments via the intervening marsh ecosystem may be modified or blocked, i.e., permeable to varying degrees (Kneib 1997, Levin *et al.* 2001).

We focus this conceptual model on the vegetated marsh proper (or marsh plain) that is depicted as the *Marsh Structure and Processes* box, explicitly recognizing variation in the types of emergent marsh vegetation (i.e., plant architecture) and associated sub-system contributions, as well as the *in situ* production of plants that leads to the support of a regionally characteristic animal biodiversity and food web. This box can be expanded to include more details of both physicochemical (e.g., sediment accretion, light attenuation) and ecological interactions (including trophic dynamics) that result in different marsh physical and biotic assemblage structures and/or enhance the production of specific plant or animal components. However, it is not the intention of the present broad-view model to provide that level of detail, although we have attempted to identify important feedback loops between biological and physical processes (e.g., plant growth and sedimentation) that affect intermediate outcomes and drivers (e.g., inundation regime affected by changes in elevation) of ecosystem functioning. Thus, the details of these physical, biological and ecological processes operating within the marsh are not included in this conceptual model, but can be added as a module if that level of understanding is required.

INTERFACES

The model highlights attributes of the fundamental structural and functional ecotones of tidal marshes that we describe as *Interfaces*. These represent a suite of physical boundary features of the system through which the effects of some drivers (e.g., water flow and associated material transport) on other components of the model can be modulated in ways that may be very specific to a situation, scale or location (Gosz 1991, Amoros *et al.* 1996).

Tidal marshes are transitional systems positioned between adjoining ecosystems with which they share usually permeable boundaries at said interfaces. One can envision a number of such interfaces at different spatial scales, including air-water, sediment-air, sediment-water, etc. In this conceptual model, we consider two broad categories of interfaces – terrestrial (or upland) and aquatic. These are structural elements in the terrestrial-marsh-aquatic landscape that largely affect the flow of water and anything transported in that medium across tidal marsh boundaries, but may also be associated with the movement of terrestrial organisms (e.g., pathways used by mammals to move between upland and intertidal ecosystems (Keusenkothen & Christian RR 2004, Talley et al 2006, and references therein) as well as aquatic organisms (e.g., rivulets and features of the tidal channel edges used by nekton to gain access to intertidal resources; Rozas *et al.* 1988, Williams & Desmond 2001). In some cases (e.g., marsh islands surrounded by water), there may be no terrestrial interface and so driver effects operating through the aquatic interface would dominate; for instance, many of the relict and restoring marshes in the Delta are islands, with hardened levee slopes constituting much of the interfaces with adjacent terrestrial or aquatic ecosystems (Mount & Twiss 2005, USFWS 2000).

Effects of drivers and the presence/amount of materials transported are modulated by the relative permeability of these interfaces (e.g., degree of shoreline armoring, such as levees or bulkheads, between the intertidal marsh and adjacent subtidal water bodies or the number and position of stormwater drainage channels at the upland interface) or the frequency and duration of exchange opportunities (i.e., water level flooding of tidal channels and the marsh plain). For example, although there is not always an easily demonstrable link between anthropogenic alterations in estuarine landscape structure and the abundance of certain estuarine fish populations (Healey 1994), the use of dikes to impound tidal wetlands interrupts hydrologic exchanges across the terrestrial and aquatic interfaces with adjacent ecosystems and has been associated with profound effects on vegetation, topography and the composition of animal assemblages (Daiber 1982). Even partial exchanges through breached dikes or water control structures (e.g., tide gates), while enabling tidal exchange between the marsh and adjacent aquatic system, modify other interface elements such as overbank exchanges along the exterior (non-tidal channel) edge (Pethick 2002). Therefore, the present conceptual model includes these interfaces as crucial filters (or modulators) on the driver effects connected with model outcomes. Although there are other interfaces of potential importance in this system (e.g., atmosphere/water, water/soil, atmosphere/soil), they are not explicitly presented in the model.

DRIVERS

There are six primary drivers (or ‘limiting factors’) considered in this model: (1) tides; (2) freshwater flows (i.e., base/modified riverine flows and surface- and ground-water drainage from uplands surrounding the Delta); (3) nutrients and pollutants; (4) incident light [or solar radiation]; (5) marsh plain elevation; and, (6) waves, as shown in Figure 1. All affect some aspect of ecosystem stability, productivity or consumer access to the marsh, and particularly intertidal (marsh plain) resources.

Hydrologic characteristics are the most fundamental driving forces in the development and functioning of wetlands (Mitsch & Gosselink 1993) and these are represented in the model by freshwater inputs, tidal flows, and wave energy. In addition to the seasonal precipitation that falls directly on the marsh, the principal freshwater inflows occur from local and regional watershed sources that enter the system at both the terrestrial (e.g., surface flow, groundwater, stormwater, agricultural run-off, etc.) and aquatic interfaces (tidal riverine flows). These flows are usually associated with seasonal and interannual variation in precipitation and snowmelt but also may be associated with management-related flow manipulations, all of which vary in predictability. Of particular importance from the standpoint of contributions of sediments, nutrients and some organisms and physical disturbance processes that influence marsh geomorphology are the occurrence and magnitude of flood events, especially when coincident with major tidal exchanges. As compared to the tidal riverine driver, the effects of freshwater flows on the structural characteristics and functionality of the terrestrial interface are understood to some degree and considered of moderate importance.

At the aquatic interface, there is an important and moderately understood link between tides and freshwater riverine flows that will modify water constituents, such as suspended sediments and salinity, and characteristics, such as temperature, depending on the mixture of freshwater and tidal volumes. Also, variation in freshwater discharges changes the volume of the marsh watershed above and beyond the influence of tidal exchange and so has a potentially important effect on the depth and duration of tidal inundation at any given elevation within the marsh system. The combined effects of the tidal and freshwater flows, along with wave energy, can have an important effect on the structure of the aquatic interface through erosion and sedimentation processes distributed along this interface; in some circumstances where the marsh interface is exposed to a navigational channel, vessel wakes can also affect sedimentation processes. Despite a predictable seasonal signal, the effect of freshwater flow on tidal volume is considered relatively unpredictable because of extreme inter-annual variation in freshwater availability and especially flooding events. Thus, the connection between freshwater flows and tides is shown as a dotted line (i.e., low predictability) but of high importance. The greater predictability of tidal pattern on factors such as the amount of extrinsic production imported to the tidal marsh system is reflected in the dashed line between tides and imported production. Although it may also seem reasonable to use a solid line at this link, the unpredictable influence of freshwater flows on the relationship should be accommodated. We have not shown the potential influence of water flow regulation on this process, which will likely increase the predictability, but decrease the variability, of the resulting flooding frequency and duration.

Water fluxes across the terrestrial and aquatic interfaces transport nutrients (N, P, etc.), sediments, and pollutants (e.g., chemical pesticides, mercury, etc.) that are then taken up (or captured, in the case of sediments) by marsh primary producers and consumer populations via bioaccumulation.

We have inserted a potentially important nexus (shown in the model as a red circle) at the aquatic interface that connects the structural features of the marsh edge with water characteristics that may modify the effects of tidal flows on the quantity or quality of production that is exported from the marsh system. Natural, vegetated edges have an inherent permeability that to some degree alters the flux of nutrients, sediments and other constituents across that interface, primarily by vegetation uptake of nutrients and other constituents, consumer consumption of food particles, cross-boundary movement of organisms, and increased sediment settling. Modified interfaces (e.g., dikes, dams, culverts) will limit permeability to the exchange of materials and organisms between the marsh and the distributary channels and open waters of the estuary (Sheaves *et al.* 2007). In such cases, the water characteristics on either side of the interface may be distinctly different. In contrast, a relatively permeable structure of natural, interconnected channels and rivulets at the aquatic interface will tend to reduce differences on each side of the interface and enhance exchange of materials and organisms.

Incident light from solar radiation has a crucial and well-understood effect on the growth of primary producers, although the effects of incident light on the activities and production of consumers is less well known. Consequently, the blue arrow from incident light to the structure and processes within the marsh system reflects a moderate understanding of the impact of incident light on the entire system (producers and consumers). In addition, different types of primary producer (e.g., emergent vascular plants, phytoplankton, benthic algae, submerged aquatic vegetation [SAV]) have different light requirements for optimal photosynthetic activity. A dotted blue arrow extending from the *Marsh Structure and Processes* box to incident light attempts to capture the shading effect (marsh architecture) of marsh plants (and perhaps animal populations) on the amount of incident light available for photosynthesis. For example, a dense canopy of tall emergent vegetation will reduce the light available for production of benthic algae on the surface of the marsh. In areas of high biomass, wrack, debris, dense populations of epiphytes, snails or other slow-moving or sessile animals covering the photosynthetic surfaces of vascular plants or SAV will likely reduce productivity. We have also taken into account the effect of water characteristics on incident light, reflecting the process of light attenuation by water turbidity (suspended sediments). If the water inflows or resuspension from the marsh is a source of suspended organic material, the turbid water can alter the photosynthetic activity of phytoplankton, macroalgae and SAV on the marsh plain or in adjacent creek channels.

Marsh elevation together with variation in tides determines the inundation regime experienced by specific locations in the tidal marsh, which in turn is associated with virtually every aspect of the structure and functioning of this system. The relationship between elevation and tidal inundation is crucially important, straightforward and well understood. We have synopsized these processes under the *Relative Surface Elevation Processes & Sediment Structure* portion, delineated by a light blue dashed circle, of the *Marsh Structure and Processes* box. Marsh surface elevation and surface sediment structure are the integrated, but spatially and temporally variable, outcome of these processes, influenced by the underlying geology of the substratum and varying with the balance between sea level rise, accretion or erosion of sediments and subsurface changes (root and rhizome production, decomposition) and subsidence that influences the surface elevation. Except for sea level rise, these processes often are influenced principally by the composition and productivity of the living components of the marsh system. Emergent vegetation slows the flow of water over the marsh plain and promotes the process of sedimentation of suspended organic and inorganic particles carried into the marsh (especially along aquatic interfaces) by either surface freshwater flows across the terrestrial interface or tidal flows across the aquatic interface. Organic matter resulting mostly from the *in situ* production of plant biomass accumulates in marsh sediments and contributes to this accretion. The structural support and growth of living roots and rhizomes of some robust vascular plant species also contribute to changing the elevation of the marsh substratum as well as other fine-scale structural features of the ecosystem, such as intertidal creek channels (Phillip & Field 2005, Teal & Weishar 2005) and aquatic features on the marsh plain (Hunter et al 2006). This varies seasonally as a function of variable below-ground vegetation growth and decomposition of organic matter. Consumption of these roots and rhizomes by terrestrial (e.g., birds and mammals) or aquatic (e.g., crabs) organisms, as well as diseases, drought or other factors that effect the robust growth of vascular marsh plants (e.g., brown marsh) can result in subsidence and reduction of marsh elevation. The relative interaction of processes that increase and decrease relative elevation of the marsh have been described in more detail in the Suisun Marsh Relative Surface Conceptual Model (SM RSE, Siegel unpubl.).

INTERMEDIATE OUTCOMES

The principal drivers act directly on a set of seven intermediate outcomes: (1) inundation regime; (2) a suite of water characteristics including but not limited to salinity, temperature, dissolved oxygen levels and turbidity; (3) emergent plant biodiversity and architecture; (4) *in situ* marsh production and biomass accumulation; (5) imported production; (6) aquatic animals; (7) terrestrial animals; and, (8) relative surface elevation. As described under Drivers, there are three additional intermediate outcomes that influence relative surface elevation: (9) accretion; (10) compaction and subsidence; (11) erosion and desiccation; and, (12) the subsurface component of *in situ* marsh production, biomass and decomposition. Many of these intermediate outcomes are inter-dependent and operate as drivers themselves through feedback loops. Thus, variation in intermediate outcomes is controlled both by interactions among multiple primary drivers and with each other to yield the final outcomes considered in this model.

Inundation regime (frequency, duration and depth) is driven largely by elevation, freshwater inflow and and tidal cycles; effects can be modulated through the complexity of the physical structure at the aquatic interface. Riverine flows also influences inundation regime by expanding or contracting the marsh tidal prism, and is influenced by tidal pumping of both surface waters and groundwater. The inundation regime is a key feature of all intertidal wetland systems (Mitsch & Gosselink 1993) from which many characteristics and dynamics of the biological communities derive (e.g., Rozas 1995, Kneib 1997).

Dissolved oxygen (DO) is a key requirement of all aerobic processes that occur in the flooded portions of the tidal marsh and is influenced by circulation patterns, diffusion with the atmosphere, generation by living plants (in light), and the respiration of living aquatic organisms (plants, animals and microbes). Behavior of mobile aquatic organisms (e.g., fishes) in response to DO levels can lead to short-term migrations into or out of marshes (diel light cycles) or seasonal use patterns (because DO levels are strongly affected by temperature) (Hackney *et al.* 1976). The influx of organisms to dendritic (blind-ended) marsh channels, pools, and sloughs can also affect water quality through the consumption of oxygen and release of nutrients in the case of aquatic animals, or the production of oxygen and uptake of nutrients in the case of phytoplankton. This accounts for the 2-way interaction between the water characteristics and imported production outcomes. The effect of water characteristics on the immigration and survival of mobile organisms in tidal marsh channels is considered very important, moderately understood, and relatively predictable. However, the effect of immigrating organisms on water characteristics is considered only moderately important and only moderately predictable because the relationship is likely very species-specific (e.g., rates of oxygen consumption and excretion rates of nitrogenous wastes vary considerably among species). Although

DO is also influenced to a lesser degree by salinity, that relationship was not considered to be sufficiently important in freshwater and oligohaline situations to merit specific treatment in this conceptual model.

The combined effects of water characteristics and imported production are expected to have strong effects at multiple levels within the *Marsh Structure and Processes* box in terms of recruitment of plant and animal propagules and the well-known effects of water quality (e.g., DO, temperature, salinity) on physiological processes that affect survival and production of biotic populations during periods of tidal inundation. Tidal water that inundates the marsh surface also functions much like the fluid in a heat exchange system, removing or contributing heat to the marsh depending on season or time of day; the effects of temperature on the physiology of most marsh plants and animals is generally well-known.

The presence of emergent plants defines tidal marsh ecosystems, and plant biodiversity is strongly affected by salinity because salt-induces stresses through osmotic effects, toxic effects, and interference with nutrient uptake (Batzer & Sharitz 2006). Consequently, tidal freshwater wetlands support much higher species richness than do saline marshes. Tidal inundation regime strongly influences horizontal zonation patterns in marsh plant communities (Batzer & Sharitz 2006). Together, salinity and tidal inundation gradients are the primary drivers of plant community composition and structure in most marshes, but shoot density and productivity are dependent on availability of nutrients.

In situ marsh production, biomass and decomposition is the largest ‘black box’ in the current model and includes all of the plant and animal production and respiration that occurs in the marsh. It requires a submodel to describe the complex production dynamics that drive system photosynthesis, respiration and the accumulation of living organic matter, and so must be considered separately at a finer scale despite the simplicity of our diagram. For purposes of the present model, this intermediate outcome serves as both a source (exports) and a sink (imports) for organisms and organic material in the estuarine landscape. The production of plant biomass is related to the composition of the plant assemblages, competitive interactions among the species for space and nutrients and herbivory effects. This can have strong feedback effects on production and standing stock biomass of living and dead plant tissues, consequently the boxes describing plant biomass and plant diversity/architecture are linked with a strong 2-way interaction. However, the effect of biomass production *per se* on the structure of the plant community is considered only moderately predictable because a variety of tidal marsh plant assemblages can be associated with either high or low annual production depending on edaphic and climatic conditions.

Terrestrial animals (mammals [including humans], reptiles, birds, insects, etc.) cross the terrestrial interface with the tidal marsh to use the resources (food, refuge, and habitat) available there. The type of resources that attract different species is wholly dependent on the structure and processes that occur within the marsh box, and so have low predictability in a general model. Also, the existing knowledge about the use of tidal marshes by terrestrial species is limited, and so while there are several examples of critical linkages between terrestrial organisms and marshes (e.g., see Carlton and Hodder 2003 and references therein) the importance of this habitat for survival and productivity of most terrestrial species is uncertain and needs additional study.

OUTCOMES

Sub-system contributions: *Habitat* is defined by the place where a particular species normally lives (Calow 1998) and so marshes tend to be defined in the context of the organisms that utilize unique emergent vegetation that grows under certain hydrologic regimes at the transition between terrestrial and aquatic ecosystems. However, many other species or certain life stages (often juveniles) are dependent upon - or at least use - portions of the tidal marsh for breeding, feeding or resting. Consequently, the rationale for this outcome is founded in the role of tidal marshes in providing a portion of either the required habitat or niche of many other terrestrial and aquatic species. For most species, the relative suitability of their habitat will be tied to the composition (and productivity) of the emergent plant assemblages and their structural attributes, particularly surface elevation. For example, birds and small mammals that use marshes as breeding areas would require a plant canopy of sufficient density to provide protection from predators, sufficient height to avoid submergence of nests and young by flood tides but sufficient adjacent foraging areas.

Animal biodiversity: The diversity of plant types along with embedded landscape elements (e.g., ponds and tidal channels) in freshwater tidal marshes provides complex structure that is believed to support a greater diversity of animals, especially birds and insects, than in saline marshes (Mitsch & Gosselink 1993). In general, marshes with greater plant biomass and adjacent beds of submerged vegetation (Rozas & Odum 1987, Strayer & Malcolm 2007) have the potential to support greater productivity at higher trophic levels, thus both plant community composition and productivity contribute to the community structure and production of animal assemblages. This outcome also supports cultural and sociological functions, such as enhancing recreational opportunities (e.g., bird-watching, fishing, etc.) as well as opportunities for research, education and cultural preservation.

Exported Production: Although considerable marsh production is processed and remains within tidal marshes, which thus act as traps and sinks for estuarine production, marsh production is also exported and considered to subsidize the broader estuarine ecosystem (Howe and Simenstad 2007). However, those materials that do leave the tidal marsh system tend to be of ‘high quality’ or special interest including living biomass such as fishes and migratory birds as well as both benthic (drift) and aerial (flying insects) invertebrates and zooplankton. The process may be either active (seasonal migrations) or passive in various degrees (e.g., trophic relays such as described by Kneib 2000 or simply the passive transport of small organisms by water flow). Other exported materials such as detritus and live plant material, contribute in some degree to the base of the bentho-pelagic, detritus-based food web in adjacent aquatic ecosystems. Benthic algae and phytoplankton may also be exported, but are likely imported as well, and the net direction of exchange is unclear. Also, the effects may be either beneficial or harmful. For example, in the presence of sufficient nutrients, toxic algal populations may incubate in stagnant ponded areas or poorly drained sloughs in tidal marshes and may be episodically released into the adjacent estuary by high tides or heavy rainfall (e.g., Lewitus *et al.* 2003). This is where the nexus (red circle in diagram) between structural elements of the aquatic interface and water characteristics, acting through tidal fluxes, can have an important but as yet poorly-understood (and so unpredictable) effect on the quality and quantity of production exported from the marsh.

ARROWS

(1) Estuarine ecosystems and associated biotic communities are profoundly influenced by freshwater inflow (e.g.,Meng *et al.* 1994, Kimmerer 2002a, Holland et al 2004, Kimmerer *et al.* 2005, Craft 2007). Direct sources of freshwater input to intertidal wetlands include surface and subsurface flows (e.g., stormwater runoff, groundwater, agricultural runoff, etc.) draining from adjacent uplands. These types of local - usually unidirectional - flows pass through the interface at the terrestrial boundary of the tidal marsh, altering hydrologic conditions and vegetation patterns, and transporting dissolved and suspended materials into the tidal wetland (for a general treatment of this topic see Amoros *et al.* 1996). Signals from these sources are detectable within the faunal components of tidal wetlands at the levels of individuals (e.g., chemical composition of tissues, Wigand *et al.* 2003) and communities (e.g., Holland *et al.* 2004). However, relatively little is known about how the porosity (e.g., interface perforated by drainage channels, rooted vegetation, soil particle composition, etc) and structural configuration (e.g., slope, soils and geology, presence/absence of armoring, etc.) of terrestrial-marsh interface influences the effects of upland freshwater inputs into tidal wetlands.

(2) Freshwater flows entering the subtidal estuary from its entire watershed (e.g., riverine flows) alter the volume of water in the estuary and modify the effects of tidal flows in the system. For example, the estuarine salinity gradient changes in response to riverine freshwater flows into the estuary (Jassby *et al.* 1995, Monsen *et al.* 2007). The volume of freshwater from this source could well determine the spatial extent of environmental conditions that favor development and persistence of oligohaline tidal marsh ecosystem in a region of the estuary. It could also determine the frequency and depth of tidal inundation (i.e., greater volume in the estuary means more intertidal unundation), as well as the suitability of a site for the support of native versus invasive species (e.g., Moyle *et al.* 2007). In the short term (e.g., during periods when water flows are controlled within an estuarine reach), the effects may be relatively predictable, but are much less predictable in the long term due to interannual variation in weather (e.g., precipitation events) and climate conditions (e.g., timing of snow-melt).

(3) The arrow intersecting the Aquatic Interface represents that portion of freshwater flows (Arrow 2) carried by tidal action across the aquatic interface at the lower

boundary of the tidal marsh where it borders the subtidal estuarine environment. It does not represent that portion of the water column that remains in channels and sloughs at high tide. Except in a turbulent mixing environment, the freshwater flows represented by Arrow 3 are expected to remain in the upper portion of the water column as the tide carries the water onto the marsh plain. Consequently, the volume of freshwater entering the estuarine system can in part determine the characteristics of water to which the flora and fauna of the marsh plain are exposed at high tide. The composition and structural configuration of the aquatic interface (slope, permeability due to presence or absence of networked channels, and/or the composition of the interface [e.g., rip-rap, earthen dikes, sand/mud] may modify some of the water characteristics as the tide filters through this edge environment (e.g., USFWS 2000).

(4) Materials dissolved and suspended in the water (Arrow 3), originating from a variety of sources in the estuarine watershed (e.g., Holland *et al.* 2004, Deegan *et al.* 2007, Smalling *et al.* 2007), passes through the filter of the Aquatic Interface and contribute to the pool of nutrients, pollutants and sediments entering the vegetated tidal marsh.

(5) Commensurate with the process described by Arrow 4, materials dissolved and suspended in the water originating from the adjacent terrestrial landscape (Arrow 1) pass through the filter of the Terrestrial Interface and contribute to the pool of nutrients and pollutants entering the vegetated tidal marsh.

(6) The influx of terrestrial animals (mammals, insects, spiders, reptiles, birds, etc) that cross the terrestrial interface (often via established pathways, runways, etc) to use the resources of the tidal marsh may have a variety of disturbance impacts on the system that are poorly understood, but are likely of relatively low importance in most circumstances. Tidal marshes are the principal habitat for relatively few terrestrial animals (e.g., rice rats, see Sharp 1967, Kruchek 2004), but terrestrial mammals and birds visit this habitat with sufficient frequency to have at least a local influence on the composition and quantity of vegegation and biota. Trampling by larger mammals (e.g., deer) can affect both above and below-ground production of marsh plant species, but such effects are generally isolated to discrete patches of habitat adjacent to uplands or isolated marsh hammocks (Keusenkothen & Christian 2004). Major seasonal disturbances of salt and brackish marsh vegetation (e.g., in the form of “eat-outs”) are known to occur as a result of feeding flocks of migratory birds such as the greater snow goose (Mitchell *et al.* 2006).

(7) The outflux of terrestrial animals returning to adjacent upland habitats through the terrestrial interface after using the resources of the tidal marsh is a sink of exported marsh-derived biomass and nutrients to adjacent systems. This is not a topic that is well-documented in the literature (Traut 2005). However, because the tidal marsh is a challenging environment for most terrestrial species, especially small mammals (Shure 1971, Martin *et al.* 1991), these exports are expected to be relatively minor and of marginal importance, except perhaps in the case of seasonal migratory populations of birds (see above).

(8) Some of the marsh production consumed by terrestrial animals will be deposited in adjacent upland ecosystems through the excretion of wastes and death of organisms, a portion of which likely contributes to the terrestrial nutrient and detritus pools. If not sequestered by the biological components of the terrestrial ecosystem, these nutrients and organic matter will be transported to the tidal marsh via freshwater flows (Arrow 14) across the terrestrial interface. This source of returning nutrients is not well researched, but is likely to be of low importance and predictability.

(9) Tidal action influences the characteristics and constituents of the water available to flood the surface of the tidal marsh by resuspending sediments and contributing to turbulence that mixes the water column in portions of the estuary. Tidal action interacts with freshwater flows to determine the location of important biological dynamic nodes within the system, such as the estuarine turbidity maximum (ETM); in the San Francisco Bay/Sacramento-San Joaquin Estuary, the location of a 2‰ isohaline at the bottom of the water column (determined in part by tidal action has been associated with the ETM and several important measures of biological activity (Jassby *et al.* 1995).

(10) Tidal cycles, in concert with freshwater flows (Arrow 2) directly determine the inundation regime (frequency, duration and depth of flooding) experienced by intertidal ecosystems (including tidal marshes). The tide is the principal physical driver that interacts with topography (i.e., elevation) to determine the inundation regime (e.g., spring tides flood the marsh surface longer and deeper than neap tides) experienced by the tidal marsh and all of its biotic components. Such hydrologic relationships are well-understood, crucially important, and are among the most predictable dynamic components of the estuarine system that defines a tidal wetland (Reed 1993).

(11) (**a**) Tides also provide an important driver for the movements of nekton from the open estuary, channels and sloughs into their habitats within or adjacent to tidal marshes. The relationship is neither simple nor clearly understood, particularly for oligohaline and freshwater tidal marshes. Based on the current scientific literature and our research observations, we have depicted nekton movement as being mediated through an important nexus involving species- and size-specific behavioral responses of nekton (because nekton, by definition, are capable of self-directed movements against currents) to the structural configuration of the aquatic interface (Williams & Zedler 1999, Desmond *et al.* 2000) and the characteristics of water quality surrounding the tidal marsh habitat.

Estuarine nekton enter intertidal marsh environments in predictable species- and size-specfic patterns on rising tides (e.g., Kneib & Wagner 1994, Bretsch & Allen 2006), with the timing (stage of tide and duration of stay) likely related to relative levels of risk aversion to tidal stranding (Kneib 1995), physiological responses to water quality (Kirby-Smith *et al.* 2003), especially dissolved oxygen levels (Bell & Eggleston 2005, Tyler & Targett 2007), and/or perceived or actual risk of predation.

(**b**) Nekton follow the receding tides out of marshes in similar species- and size-specific patterns of progression into permanent subtidal waters or intertidal refugia (see Kneib 1997).

These bi-directional tidal migrations also affect water characteristics in and around the marsh because large numbers of nekton consume oxygen, excrete measurable levels of nutrients (Haertel-Borer *et al.* 2004), and their feeding activities may contribute to sediment resuspension (Smith & Merriner 1985, Palmer 1988). The complexity of the interactions involving nekton activity, structural configuration of the aquatic interface and water quality characterisitics are of potentially great importance to the functioning of tidal marsh systems, but are neither well-understood nor predictable in the Bay/Delta system.

(12) Contributions of nekton activity to available nutrient, pollutant and sediment pools available for transport into the tidal marsh (as mentioned for arrow #11b, above) are only moderately understood and only as predictable as the presence/abundance of nekton populations at a particular site.

(13) The effects of nekton on *Marsh Structure and Processes* are very species-specific and so inputs should be entered through individual species models. For example, (as described for arrow #11a, above) some species (mostly marsh residents) enter the intertidal marsh as soon as the tide allows, while others (e.g., seasonal migrants, such as juvenile salmon, or occasional visitors) enter late in the flooding tide and leave early on the ebb, often as a consequence of differential tolerances to the risk of stranding.

(14) Much of the nutrients and pollutants carried in the waters that enter the marsh across both the Terrestrial and Aquatic interfaces are assimilated and accumulate in marsh plant and animal tissues. This is a well-established, predictable and important consequence of water flows into tidal marshes (e.g., Wigand *et al.*, 2003, Holland *et al.* 2004, Craft 2007, Deegan *et al.* 2007, Smalling *et al.* 2007). However, some nutrients such as ammonia and nitrate can also enter the marsh predominantly by bulk precipitation (Jordan *et al.* 1983). In addition, unvegetated mudflats (not included in *Marsh Structure and Processes*), that are relatively rare in mature marsh ecosystems but quite common in restoring wetlands in the Delta, may be much larger sinks for nutrients than the vegetation marsh (*ibid*). Nutrients and pollutants are also exported from the marsh, both in terms of the residual not assimilated/accumulated in the marsh and also that generated by the marsh. The net flux of nutrients can vary, depending on the tidal regime, composition of marsh flora and fauna, and freshwater contributions, but tidal emergent marshes have been found to be net annual exporters of nitrogen species (Valiela *et al.* 1978) but have been found to be nitrate + nitrite sinks in other situations (Spurrier, JD & Kjerfve 1988). Thus, the predictability of the overall effect of nutrient flux is low due to the variability in both the nutrient inputs and the structure of the marsh vegetation and substrate.

(15) In addition to providing the principal mechanism for the flux of nekton populations into and out of tidal marsh habitats, the interaction of tides and freshwater flows in the estuary also provide a mechanism by which planktonic

organisms and early life stages (eggs/larvae, plant propagules, etc) of larger aquatic and marine organisms enter the marsh system as other imported production. The relative contributions of freshwater inputs from different portions of the watershed determine the pool of potential external production available for importation to the tidal marsh proper with each tide (e.g., allochthonous organic material such as detritus of marine or terrestrial origin).

(16) Water flows (primarily tides, but also storm runoff across the marsh plain) interacting with the structural characteristics of the aquatic interface can affect the timing and amount of marsh production that is exported. While both channelized and sheet flow can export production, especially on spring tides, modified marshes have more restricted Aquatic Interfaces that are much more restrictive except during extreme events. For example, strong spring tides that occur with high seasonal riverine flows may overtop a dike, weir, or other barrier at the boundary of the tidal marsh and open estuary, thus allowing the escape of a pulse of materials (detritus), nekton or aquatic insects that might otherwise remain confined to the boundary of the tidal marsh. The interaction of tidal activity with the composition and configuration of the aquatic interface (e.g., unaltered channel edge versus a diked or otherwise altered edge) represents a potentially important, but poorly understood nexus that has a strong effect on the ability of aquatic animals to gain access to tidal marsh plain.

(17) The water quality conditions experienced by organisms that passively enter the system with inflows of tidal or other directional aquatic flows will determine, in part, whether or not they survive, grow, or reproduce in the marsh system. Individual species responses and physiological tolerances to interactions between variations in tidal flooding and salinity are likely to determine the species composition, productivity and sustainability of oligohaline tidal marsh systems (Spalding & Hester 2007). Water quality conditions in the shallow channels and sloughs associated with the tidal marsh can be quite different from those in the open estuary. The predictability and understanding of the effects of water quality characteristics on external production that is ultimately imported to tidal marshes of the Bay/Delta, is relatively low.

(18) Except perhaps for the colonization of plants that define the marsh ecosystem, and the introduction of exotic species that can profoundly alter the structure and function of the marshes, the importance of other imported production to marshes of the Bay/Delta is not known.

(19) (**a**) Flux of solar energy is critically important to marsh primary production and influences the activities of marsh animals as well. The relative contributions of benthic algae and vascular plants to marsh primary production and the relative importance of different pathways (e.g., herbivory versus detritivory) to marsh secondary production (e.g., Kneib 2003, Janousek *et al.* 2007) make the availability of light a complicated issue in this system. For example, some species of benthic algae, and much of the microbial assemblage, have higher rates of productivity under conditions of diffuse insolation than in direct sunlight, as when the soil is shaded by emergent vascular plants. The productivity of different species of vascular plants in tidal wetlands also varies due to different

optimal light (and temperature) levels. The structure and species composition of mostly plants, but also some of the larger slow moving animals of the tidal marsh (e.g., snails, clumps of bivalves), may affect the amount of incident solar radiation that impacts sediment and leaf surfaces, which affects the productivity of a portion of the primary producers. The effect of shading may reduce productivity of some species (e.g., mostly emergent vascular plant species), but may enhance the productivity of other more shade tolerant species (e.g., benthic diatoms), and so the effect on overall productivity is not very predictable.

(**b**) The structure of the marsh community, especially plant species composition and growth forms, as well as the presence of abundant epiphytes or slow-moving/sessile mollusks can reduce the amount of incident insolation received by other flora and fauna in the tidal marsh system. The importance and predictability of this feedback is likely minor in most tidal marsh systems, but may have a limited effect on biodiversity and total primary and secondary production from the ecosystem.

(20) Wave energy and heavy rainfall have erosive effects not only on the aquatic interface of established marshes, but may also impair the establishment and growth of young tidal marsh plants with undeveloped root systems even at considerable distances from the marsh edge (Mwamba & Torres 2002).

.(21) Erosion and dessication can reduce marsh production and biomass along the edges of the tidal marsh, and prevents the recruitment of plant seedlings the growth of which would tend to stabilize banks and channel edges. Removal of plant biomass by erosion may also have a positive effect by maintaining hydrologic flows through channels which otherwise might be blocked by plant growth (e.g., *Phragmites* example from NJ or something from CA if appropriate)

(22) Erosion has a negative, but generally unpredictable effect on net accretion. The uncertainty is associated with the less than predictable frequency and intensity of erosive forces (e.g., wind and rainfall).

(23) Development and sustainability of tidal marshes depends on the accumulation of sufficient sediment to maintain an appropriate level of elevation relative to tidal inundation (i.e., keeping up with relative sea level rise; Patrick & DeLaune 1990; Warren and Niering 1993). Once an emergent marsh is established this can occur through the passive accumulation of suspended sediments during tidal flooding (arrow #14) and the reduction of currents flowing across the vegetated marsh plain and subsequent settling of suspended sediments and other material, the active capture of deposition of sediments by filter-feeding organisms (e.g., bivalves) or the accumulation of organic matter from plant production. Thus, marsh production, biomass accumulation and decomposition processes contribute to both the source of accreting organic matter and enhancement of settling; a source of sediments (terrestrial or aquatic) is all that is necessary.

The accumulation of organic matter from above- and below-ground plant production and subsequent rates of decomposition is an important source of material in established marshes. Rates of decomposition, especially in below-ground production, differ substantially along a salinity gradient. Below-ground decomposition rates are substantially slower in tidal freshwater marshes (Craft 2007), and consequently this is often the dominant mechanism of accretion in those marshes. Decomposition rates are greater at higher salinities and there is a shift toward the importance of trapping suspended sediments (via both passive—reductionreduction of current flows—and active—filter-feeding organisms—mechanisms) as the principal means of accretion in salt marshes. This also explains why freshwater tidal marsh plains tend to be relatively flat while tidal salt marshes often exhibit distinct elevation gradients and include features such as natural levees along tidal creek channels (Odum 1988).

(24) Sediments that accrete on marsh plains tend to compact over time, with the degree of compaction related to sediment composition (Patrick & DeLaune 1990). Sediments with high organic content, such as occur in tidal freshwater marshes tend to exhibit greater compaction over time due to microbial decomposition and the capacity for fine-grain sediments (e.g., silts and clays) to become more compact (Mount & Twiss 2005). Existing marshes deprived of an external source of sediments by artificial dikes and levee systems (Mount & Twiss 2005), or by deep dredging of adjacent tidal channels, often subside considerably as a result of compaction and the disruption of the delicate balance between sediment accretion, compaction and erosion that determines relative elevation over time.

(25) (**a**) Sediment accretion has an unpredictable, but potentially important effect on marsh animal species composition and production that is not well understood. This is particularly true for predicting the potential success of invasive species. For example, the deposition of large amounts of fine sediments could ihibit recruitment or smother settled larvae or interfere with the ability of small filter-feeders to maintain themselves in the marsh system.

(**b**) There are potential positive effects of filter-feeding organisms, in particular, on accretion rates (e.g., deposition of pseudofeces and binding of sediments) that contribute to the building and maintenance of the marsh plain, by sequestering and consolidating settled materials in pseudofeces or covered by extracellular material. In contrast, burrowing activities of other species, such as crabs (Rudnick *et al.* 2005) can quickly counter the effects of accretion and cause erosion and slumping of tidal marsh creek banks..

(26) Compaction of sediments provides some resistance to erosion, but is likely of minor importance compared to other factors. Erodability of the marsh substratum is determined more by sediment composition (sediments with high organic content tend to erode more easily), the robustness of rooted vegetation, and the strength of the erosive forces from stormwater inputs across the terrestrial interface, sediment resuspension by rain (Torres *et al.* 2004) or animal activities (e.g., crab burrows, Rudnick *et al.* 2005), wind-driven waves or tidal flows (Wood & Widdows 2002). Sediments of freshwater marshes tend to be more easily eroded than those of saline marshes because there is generally a lower root biomass (i.e., bulk density) (Odum 1988, Craft 2007) and finer particle size (i.e., lower sand content) in freshwater marsh substrata.

(27) (**a**) Comparable to accretion processes, compaction of sediments and subsidence may also influence the biodiversity and production of certain smaller animal species in the marsh system by interfering with their ability to burrow into the marsh sediments or altering the flooding regime, changing the suite of competitors and predators or altering food delivery.

(**b**) However, as with accretion (arrows #25a&b), burrowing and feeding activities of certain faunal groups may have either a positive or negative effect on compaction. Thus, these effects, though of potential moderate importance to the structure and functioning of the marsh system, are not predictable without knowledge of the existing assemblages.

(28) (**a**) Marsh plant production and the translocation of below-ground biomass can have a strong effect on emergent plant diversity and architecture (e.g., density of above ground shoots and plant height often correspond to the amount of production and biomass stored below-ground).

(**b**) There is a reciprocal effect of plant diversity on production and biomass through positive interactions (Bertness & Shumway 1993) among species and growth forms that alter microclimate and edaphic factors.

(29) The amount of plant production available directly influences the potential to support the production of motile secondary consumer populations (e.g., Kneib 2003). There are a number of mechanisms, most notably through the local provision of organic matter for detritivores.

(30) A direct positive relationship between plant diversity or complexity of plant architecture is related to the provision of more niche space and diversity among the animal components of the marsh.

(31) The composition of marsh flora and fauna, their productivity, and metabolic activity (e.g., respiration) all influence the characteristics of tidal water that periodically floods and drains the marsh. For example, water that is distributed over the marsh surface on neap tides will be shallower than on higher amplitude spring tides and so will warm more rapidly during the day and cool more rapidly at night. This in turn would have an effect on dissolved oxygen concentrations and perhaps salinity in cases where evaporation is an issue (e.g., shallow marsh pools).

(32) One of the more important products of the various abiotic and biotic processes included in *Marsh Structure and Processes* (arrows #20-#30) is the dynamic maintenance of the marsh elevation. The elevation will vary on a seasonal basis, commensurate with variability in suspended sediment inputs to the marsh, marsh plant productivity, climate events, etc.

(33) Elevation has an important, well-understood and very predictable effect on the inundation regime of tidal marshes. The relationship between elevation and the frequency and duration of tidal inundation is the basis for our understanding of many zonation patterns in tidal marshes (Daiber 1982).

(34) *In situ* marsh production of plants and animals together with all of the biotic and abiotic processes that structure the ecological interactions within this environment

(including the amount of marsh production that is used in place or sequestered) determine the potential amount of production that is available for export as either living, mobile organisms, as well as passively transported production in the form of plankton or detrital production. This arrow represents the export of all marsh production other than that exiting the system through mobile populations of larger nektonic species, which are described by Arrow #16. The aquatic interface is not considered important in the export of organic matter of marsh origin in Arrow #34 because the material moves passively with water flows exiting the tidal marsh to the open estuary.

(35) Mercury is a pollutant of special interest in the Bay/Delta, and here the output from the DRERIP mercury model is linked to the pollutant pool of the present model.

ADDITIONAL SUB-MODELS AND ELEMENTS THAT COULD BE INCORPORATED IN FUTURE ITERATIONS

- ***Tropho-dynamic model*** of ecological interactions linking primary production to the food web structure and production flows into, through, and out of the tidal marsh system.

- ***Landscape-level models*** that address the effects of variation in structural features of the tidal marsh environment (e.g., tidal channel complexity, channel width, channel length, edge:area ratios, etc.) on the population or production dynamics of specific plants and animals

- ***Additional modular docking links*** to integrate other component models with the general tidal marsh model. These links would identify the most effective points within the tidal marsh model structure to input the outcomes from other DRERIP models.

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Figure 1. DRERIP Tidal Marsh Biological Model – Broad View