Sacramento-San Joaquin Delta
Regional Ecosystem Restoration Implementation Plan

Ecosystem Element Conceptual Model

Tidal Marsh

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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 emergent 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 (Simenstad *et al.* 2000; 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 functions, goods and services related to the maintenance of biodiversity, fish and wildlife habitat, water quality, flood abatement and carbon sequestration (Rabenhorst 1995, 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 both direct and indirect 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 and Sacramento-San Joaquin River Delta 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 land uses (Josselyn 1983). The principal source of freshwater input to the estuary enters through the Sacramento and San Joaquin rivers; their inland delta (the Delta) 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 in Figure 1 is intended to capture the features and dynamics of tidal marshes in the Delta (e.g., Suisun Bay to the upriver extent of the tides in the Delta), oligohaline and tidal freshwater marshes generally 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.

Although one of our principal objectives in developing this model involves identifying the dominant processes and interactions that characterize restoring marshes at various stages of development, the model is intended to characterize the dynamics of "equilibrium" marshes at their mature state of geomorphic and ecological functioning (Pestrong 1972, Reed 2002, Williams *et al.* 2002). Our rationale is that restoring marshes are considerably variable and that trying to capture intermediate stages of development (e.g., positions along a development "trajectory"; Simenstad & Thom 1996 [however, see Zedler & Callaway 1999]) would introduce too much variability for a single model, and because the ultimate objective of restoration is the self-sustaining, equilibrium condition. However, we have sought were appropriate to describe important processes that influence restoration trajectories and affect the ecosystem functions, goods and services that marshes provide in various landscape settings that are found in the Sacramento-San Joaquin Delta.

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 (e.g., Zeff 1999, Kirwan & Murray 2007). The interaction of these factors control biological/ecological processes that support two of the more important ecosystem services of tidal marshes: provision of essential habitats for biota (e.g., Visintainer *et al.* 2006) and the net export of high-quality organic production (e.g., Kneib 2004). 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 (Lawrence *et al.* 2004, Kneib 1997, Levin *et al.* 2001).

A variety of distinct landscape elements such as channels, sloughs, ponds and pannes are common features that are embedded in intertidal marsh mosaics and are prominent in many of the interactions across the marsh interfaces. These elements contribute spatial heterogeneity, and may serve important functions as sources/sinks in metapopulation dynamics involving marshes (e.g., Dean *et al.* 2005), conduits for the transport or retention of water and waterborne materials (e.g., sediments, nutrients, pollutants), as well as corridors for the active movement of animals through the ecosystem (e.g., Rozas *et al.* 1988). While implicitly acknowledging the importance of these landscape features in connecting marshes with adjacent ecosystems, we focus the present version of 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 BETWEEN TIDAL MARSHES AND ADJACENT UPLAND AND AQUATIC ENVIRONMENTS

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, Lawrence *et al.* 2004).

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 tidal 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) and are functionally different from a widely connected tidal marsh-aquatic interface. 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 OF EQUILIBRIUM MARSH FUNCTIONS

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) sediments, nutrients, and pollutants; (4) incident insolation [light or solar radiation]; (5) marsh plain elevation; and, (6) waves. 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. The occurrence and magnitude of flood events, especially when coincident with major tidal exchanges, are of particular importance from the standpoint of contributions of sediments, nutrients and some organisms, and physical disturbance processes that influence marsh geomorphology. 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 throughout the marsh but particularly 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 influence of tidal pattern on factors such as the amount of extrinsic production imported to the tidal marsh system is considered only moderately predictable due to the variable influence of freshwater flows on the relationship. 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. The more heterogeneous or complex these interfaces, the higher the potential capacity for these geochemical and sedimentation processes.

We have inserted a "nexus" (shown in the model as a red circle) which represents the lateral (not the vertical, sediment-water column) aquatic interface that is a particularly important feature of intertidal marshes—the marsh-channel margin and tidal channel (drainage) outlets—that are considered important ecotones through which the flux of materials, organisms and energy is modulated (e.g., Whigham et al. 2008). The structural, geochemical and other characteristics of the marsh edge control the effects of tidal flows on the quantity or quality of production that is imported into and exported from the marsh system. Natural vegetated edges punctuated by tidal drainage channels and sloughs of various sizes have an inherent permeability related to both the composition and effective length of the marsh-aquatic interface (Zeff 1999). The irregularity of such natural marsh edges increases 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. The shallow littoral edges of marsh systems often are associated with high standing stocks of fishes (e.g., Allen 1982, Moyle *et al.* 1986, Nobriga *et al.* 2005). These same areas sometimes develop beds of submerged (SAV) and floating (FAV) aquatic vegetation that essentially extend the structurally complex vegetated intertidal zone into the subtidal zone of protected sloughs and channels. This provides additional permanent habitat – or important low-tide staging habitat – for aquatic organisms associated with marshes (Allen 1982, Castellanos & Rozas 2001) albeit including non-indigenous species that may be considered deleterious to endemic communities (e.g., see Brown 2003, Nobriga & Feyrer 2007 for different patterns in extensively modified wetland edges with abundant SAV).

Constrained interfaces (e.g., dikes, dams, culverts) that shorten the length of the marsh-aquatic edge will limit permeability to the exchange of materials and mobile 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 sloughs, channels and rivulets at the aquatic interface will tend to reduce differences on each side of the interface by enhancing the 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 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. The arrow extending from the *Marsh Structure and Processes* box to incident light attempts to capture the lack of understanding and the low predictability of 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, and are influenced by the underlying mineralogical characteristics of the substratum. Surface elevation varies with the balance between sea level rise, accretion or erosion of sediments and subsurface changes (root and rhizome production, decomposition) that may result in either augmentation or subsidence of the substratum. 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 contribution varies seasonally as a function of variable belowground 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 affect 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 eight 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) nekton; (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 tidal cycles; effects can be modulated through the complexity of the physical structure at the aquatic interface and geomorphology of the marsh plain. Riverine flow 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 duality 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. This is represented in the model as interacting through the nexus. However, the effect of immigrating organisms on water characteristics, also interacting through the nexus, 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 (see Temperature conceptual model); 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 salinity strongly affects plant biodiversity and productivity because salt induces stresses through osmotic effects, toxic effects, and interference with nutrient uptake to which plants exhibit distinctly different responses due to species-specific physiological adaptations (Batzer & Sharitz 2006). Consequently, tidal freshwater wetlands support much higher species richness but lower vascular plant production than do saline marshes. Tidal inundation regime strongly influences 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 also are dependent on availability of nutrients which arises in part from substrate grain size and geochemical characteristics.

In situ marsh production, biomass and decomposition represent 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. These factors 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 freshwater and oligohaline 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

In this section, we focus on the ecological functions, goods and services of tidal marshes, and focus on how physical processes drive the biology and ecological interactions that in turn produce outcomes that are largely physical in character.

Habitats for many species: *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. Marshes are defined by the presence of specific types of intertidal vegetation, so the very existence of marsh (natural, restored or created) represents the outcome of habitat provision for a certain suite of species. This outcome is represented in the model as a yellow border surrounding the *Marsh Structure and Processes* box, which combines the structural provision of habitat (a model outcome) and important ecological processes within the marsh that contribute to other intermediate and ultimate outcomes of interest.

Many aquatic and terrestrial species, or certain life stages (often juveniles), are dependent upon - or at least use - portions of the tidal marsh for breeding, feeding or resting. For most species, the relative suitability of their habitat will be tied to the composition (and productivity) of the emergent plant assemblages and its 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 also may require access to adjacent estuarine or terrestrial foraging areas. Some aquatic Species-of-Special-Concern in California, such as Sacramento splittail (*Pogonichthys macrolepidotus*), require the type of brackish water nursery habitat associated with the shallow sloughs and channels of tidal marshes in the Delta (e.g., Moyle *et al.* 2004). However, these same habitats may also be susceptible to invasion by exotic submerged aquatic macrophytes such as *Egeria densa*, which appears to provide habitat that is more favorable to non-native fishes, and particularly piscivorous fishes (Simenstad *et al.* 1999, Brown & May 2006, Brown & Michniuk 2007, Toft *et al.* 2007).

Based on the information from the BREACH I (Simenstad *et al.* 1999) reference sites in relict natural marshes, the freshwater tidal marshes of the Delta were historically more complex than we document today, perhaps because of the channel levee development and underlying disturbance regimes of the un-regulated hydrology that by flooding and wood recruitment promoted more topographic complexity through overbank flooding.

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: A considerable amount of annual marsh production is sequestered or processed and enters tidal marsh food webs, but much is also exported and considered to subsidize the broader estuarine ecosystem (Howe and Simenstad 2007). Those materials that do leave the tidal marsh system tend to be of 'high quality' or special interest, and include 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 involving nekton populations such as described by Kneib 2000, or simply the passive transport of small benthic and planktonic organisms by water flow). Other exported materials such as detritus and live plant production, 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.

LINKAGES

The following numbered discussions correspond to individually numbers arrows in the Broad View Conceptual Model shown in Figure 1 that link drivers and outcomes.

(1) **Freshwater flows at the terrestrial interface.** Estuarine ecosystems and associated biotic communities are profoundly influenced by freshwater inflow (e.g., Meng *et al.* 1994, Kimmerer 2002a & 2002b, Holland *et al.* 2004, Kimmerer *et al.* 2005, Buzzelli *et al.* 2007, 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) **Riverine freshwater inflows and the tides.** 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 inundation), 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). Refer to the Transport conceptual model for more discussion on this relationship.

(3) **Freshwater flows at the aquatic interface.** The arrow intersecting the aquatic interface represents that portion of freshwater flows (Linkage #2) carried by tidal action across the aquatic interface at the lower boundary of the tidal marsh where it borders the subtidal estuarine environment. During large river discharge conditions, tidal exchange is moderated and river flows become the dominant influence on water characteristics—salinity, temperature, DO and turbidity—through (freshwater) tidal exchange and flooding. It does not represent that portion of the water column that remains in channels and sloughs at high tide. Where salinity intrudes into the proximity of marshes (at the downestuary margin of the Delta), freshwater flows represented by Linkage #3—being less dense than saline waters—may remain in the upper portion of the water column as the tide carries the water onto the marsh plain, depending on the extent of vertical mixing in the water column. 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 (such as rip-rap, earthen dikes, sand/mud) may modify some of the water characteristics as the tide filters across this interface through the nexus (e.g., USFWS 2000).

(4) **(a) Aquatic interface and nutrients, pollutants, and sediments.** Materials dissolved and suspended in the water (Linkage #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), and pass through the filter of the aquatic interface and contribute to the pool of nutrients, pollutants and sediments entering the vegetated tidal marsh. As above, the mass flux of

these constituents depends on the filtering effect of the aquatic interface and thus its specific characteristics.

(b) Nutrients, pollutants, and sediments and aquatic interface. Although the flux can be less because marshes are often considered to be net sinks or balanced, rather than major sources, of sediments, some nutrients, and pollutants (e.g., Anderson *et al.* 1997), some of these materials are passed back through the aquatic interface, often in transformed form (e.g., different nutrient species, microbially-enhanced sediment particles). However, under some circumstances, marshes have been documented to provide a significant net export nitrate and ammonium (Childers & Day 1990, Page *et al.* 1995) as well as mercury (see Linkage #35 and DRERIP mercury model). The extent of nutrient retention in the marsh and the resulting export across the aquatic interface is also highly dependent on nutrient loading (e.g., landscape setting) and the stage of wetland development, wherein phosphorus is driven by geochemical processes that diminish with age of a restoring wetland but nitrogen is driven by biological processes generally increases over time (Craft 1996).

(5) **Terrestrial interface and nutrients, pollutants, and sediments.** Commensurate with the process described by Linkage #4, materials dissolved and suspended in the water originating from the adjacent terrestrial landscape (Linkage #1) pass through the filter of the terrestrial interface and contribute to the pool of nutrients and pollutants entering the vegetated tidal marsh. The magnitude of this linkage depends on the degree and nature of the terrestrial connectivity.

(6) **Terrestrial animals and marsh structure and processes.** The influx of terrestrial animals (mammals, insects, spiders, reptiles, birds, etc.) that cross the terrestrial interface (often *via* established pathways, runways, etc.) to use and contribute to the resources of the tidal marsh may have a variety of contributions (e.g., prey, nutrients) and effects (e.g., predation) on the system that are somewhat documented in cases such as bird use but otherwise poorly understood. We consider them to be of relatively low importance in most circumstances. Except for the salt marsh harvest mouse (*Reithrodontomys raviventris*) in marshes that are not extensively impacted by encroaching urban development (Shellhammer 2005), relatively few terrestrial animals utilize tidal marshes for their primary habitat for (e.g., rice rats, see Sharp 1967, Kruchek 2004), but terrestrial and semi-terrestrial mammals, birds, reptiles and amphibians visit this habitat with sufficient frequency (Greenberg & Maldonado 2006) to suggest at least a local influence on the composition and quantity of vegetation and biota. Trampling by larger mammals (e.g., deer) can affect both above and belowground 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) **Terrestrial animals and the terrestrial interface.** 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 ecosystems. 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 probably relatively minor and of reduced importance where that interface is constrained by urban and other development. However, marsh residents such as the salt marsh harvest mouse require sufficient refuge within this interface to allow them to escape higher tides and flooding events. Where it occurs, the extent and importance of this outflux is also likely proportional to the degree of connectivity and species-specific permeability of the terrestrial interface. Bird populations (see 6, above) may also routinely cross this interface especially when they are seasonally migratory, or in areas where—as a consequence of residential development along the terrestrial interface—mammalian predators such as house cats are abundant and forage on bird populations nesting in tidal marshes (Takekawa *et al.* 2006). Given the degree of knowledge about salt marsh harvest mice and birds in the Bay/Delta, we consider these interactions at or across the terrestrial interface to be of medium importance, understanding and predictability,

(8) **Terrestrial animals and nutrients, pollutants, and sediments.** In addition to organic matter and nutrients deposited as excretion or other processes (e.g., molting, predation by marsh residents) directly within the marsh (see Linkage #6, above), 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 (Linkage #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) **Tides and Water Characteristics.** Tidal action influences the characteristics and constituents of the water available to flood the surface of the tidal marsh by controlling the distribution of salinity along the riverine-tidal gradient and vertical salinity concentration that could contribute to water characteristics entering the marsh. Tides also contribute 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); at the western margin of the Sacramento-San Joaquin Delta, the location of a 2 psu isohaline (termed *X2*) 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). It is relatively unknown whether or how concentrations of sediments, organic detritus and organisms uniquely associated with features like ETM enter tidal marshes in mainstem or peripheral islands, but it is likely a rare event and occurs along the western margin of the Delta (e.g., Suisun Marsh) when freshwater flows from the Sacramento and San Joaquin are seasonally low or water management results in extensive diversions of Delta water out of the system. It has been recently argued that greater variability in salinity regime in the Delta would improve conditions for natural ecosystems and native aquatic species at risk, and be more deleterious to non-native species (Lund et al. 2007, Norbriga 2007).

(10) **Tides and Inundation Regime.** Tidal cycles, in concert with freshwater flows (Linkage #2) directly determine the inundation regime (frequency, duration and depth of flooding)

experienced by intertidal ecosystems such as 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). During winter outflow events, the tidal inundation regime can be significantly modulated by river flows (Linkage #2), especially in the tidal freshwater domains, with relatively little modification by tides.

(11) (**a**) **Aquatic interface and nekton.** Tides also provide an important driver for the movements of nekton (fish and other organisms that can propel themselves against currents) 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 fish movement as being mediated through the marsh edge 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-specific 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 and the aquatic interface.** Nekton follow 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 characteristics 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) **Nekton and nutrients, pollutants, and sediments.** Contributions of nekton activity to available nutrient, pollutant and sediment pools available for transport into the tidal marsh (as mentioned for Linkage #11b, above) are only moderately understood and only as predictable as the presence/abundance of nekton populations at a particular site.

(13) **Nekton and marsh structure and processes.** 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 Linkage #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 (e.g. Kneib 1995, 2003). The amount of foraging time available for nekton, coupled with species-specific tolerances to stranding risk, will determine the potential for nekton populations to affect intertidal prey assemblages, deposit nutrients and other associated ecological interactions within the marsh proper.

(14) **(a) Nutrients, pollutants, sediments and marsh structure and process.** 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 assimilation 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 vegetated marsh (*ibid*). Freshwater and tidal flows transport sediments required for tidal marshes to capture and maintain elevation relative to sea level. Thus, most sediment becomes entrained in the marsh, athough episodic storm events may also lead to the erosion of sediments depending on the structural geomorphic and vegetative characteristics of a particular site (Gabet 1998, Callaway 2001).

(b) Marsh structure and process and nutrients, pollutants, sediments. 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. Tidal emergent marshes tend to be net annual exporters of nitrogen species (Valiela *et al.* 1978) but have been found to be nitrate + nitrite sinks in some 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) **Tides and freshwater flow and imported production.** 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 (see hydro model) 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); see Organic Carbon and Aquatic Food Web models.

(16) **Tides and freshwater flow and exported production.** Water flows (primarily tides, but also storm runoff across the marsh plain) interacting at the nexus with the structural and biological (e.g., consumers of detritus) characteristics of the aquatic interface can affect

the timing and amount of marsh production that is exported. The relative contributions of tidal and riverine energy and the presence of engineered features that affect flow patterns (e.g., diversions and pumps) can exert a very strong influence on the distance to which exported production can be transported and thus support aquatic organisms external to the marsh. While both channelized and sheet flow can export production, especially on spring tides, restored marshes most often have more relatively small aquatic interfaces (e.g., breaches through large levees left otherwise intact) that are much more restrictive except during extreme events when flow overtops the remnant levees. 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) **(a) Water characteristics and imported production.** The water quality conditions experienced by planktonic 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.

(b) Water Characterization and Incident Insolation. Water characteristics can also alter the incident insolation driver of photosynthetic production within the *Marsh Structure and Processes* box through light absorption by suspended particles (i.e., turbidity). We distinguish this process from the flux of nutrients, pollutants and pollutants and sediments into and out of the marsh system (Linkages #14a and #14b, above) although it is certainly influenced by the contributions of the marsh to external turbidity (through Linkage #14b to #4b) and interacting with the nexus of the aquatic interface.

(18) **Imported production and marsh structure and process.** In addition to the flux of pelagic phytoplankton and zooplankton, imported production-driven dispersal is the primary colonization mechanism for establishment of emergent marsh vegetation and benthic invertebrates (endemic and exotic species). Given that most species have seasonal reproductive and growth patterns, the timing of imported production arrival, combined with extant environmental conditions, may very well determine the pattern of plant recruitment and assemblages of organisms at restoring marsh sites where the reintroduction of tidal inundation occurs at different seasons. Except perhaps for the colonization of plants that define the marsh ecosystem, and the introduction of exotic species that can potentially alter the structure and function of the marshes, the importance

of other imported production to marshes of the Bay/Delta is not known. In particular, there is little information on the net flux of phytoplankton and zooplankton in mature marshes. Stable isotope food web studies indicate that northern San Francisco Bay marshes, including relatively young restoring marshes, are supported primarily by autochthonous macrophytic production rather than pelagic production from the Bay (Howe & Simenstad (2007). There is also relatively little information on the use of tidal freshwater/oligohaline habitats as spawning or nursery areas for some species of special interest in the Delta. For example, the principal spawning habitat for the threatened delta smelt (*Hypomesus transpacificus*) is unknown (Bennett 2005), but species such as topsmelt (*Atherinops affinis*) and Atlantic silversides (*Menidia menidia*), which have similar early life histories (i.e. demersal eggs, pelagic larvae, lunar/semi-lunar spawning cycles), are known to use vegetation along the marsh edge as spawning substratum (Allen 1982, Middaugh 1981).

(19) (**a**) **Incident insolation and marsh structure and processes.** Flux of solar energy is critically important to marsh primary production and influences the activities of marsh animals as well. While the effect of solar radiation on primary production could be considered a universal feature of the environment, the net productivity of various primary producers can vary by the plants' positions in the marsh landscape. For instance, 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 emergent marshes. 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 - mostly of plants - but also of some larger, slow-moving tidal marsh animals (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) **Waves and rainfall effects on erosion.** 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). The effects of waves are likely very scale dependent, at the landscape setting scale in terms of overall wind stress and at finer scales within the marsh, e.g., along channels vs. the

interior of the marsh (Davidson-Arnott *et al.* 2003). Wave resuspension of sediments has been a noticeably limiting process at marsh restoration sites in some settings of San Francisco Bay (Williams & Orr 2002) but may be less of a factor in the confined distributary channels of the Delta unless restoring sites involve extensive wind fetch across large expanses of open water when flooded.

(21) **Erosion and desiccation effects on production, biomass, and decomposition.** Erosion and desiccation can reduce marsh production and biomass along the edges of the tidal marsh and prevent the recruitment of plant seedlings, the growth of which would tend to stabilize banks and channel edges. Although the role of natural disturbance in promoting production, biomass and decomposition is poorly understood in the presently hydrologically-controlled system, evidence from the BREACH I studies in the Delta (Simenstad *et al.* 1999) suggest that historically surface elevation processes and sediment structure may have historically created more heterogeneous marsh mosaics that contribute to greater vegetation biodiversity and complexity. Whether these processes still persist sufficiently to allow accretion and erosion, and perhaps large wood recruitment, that creates topographically complex marsh surfaces (and particularly along natural levees) over long term (e.g., Hood 2007), has not been assessed.

The erosion processes that produce tidal channel networks also influence vegetation production processes and (through Linkage #28b) plant biodiversity and architecture. Because composition of vegetation assemblages varies with distance from tidal channel bank and channel size (Culberson 2001, Sanderson *et al.* 2000, 2001) the patterns of distribution over the marsh plain and their contribution to aboveground and belowground production (Linkages #28a & b), and the processes that control relative surface elevation processes and sediment structure (Linkages #22, # 23, #24 and #26), are organized around the patterns and controls on tidal channel structure.

Removal of plant biomass by erosion may also have a positive effect by maintaining hydrologic flows through channels which otherwise might be blocked by (often non-indigenous) plant growth (e.g., Weinstein & Balletto 1999; Toft *et al.* 2007).

(22) **Erosion effects on accretion.** 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). , However, restoring wetland settings with patchy marsh or low plant density, and long fetch across adjacent, unvegetated reaches may experience considerably higher surface sediment erosion (Williams & Orr 2002).

(23) **Production, biomass and decomposition effects on accretion.** Development and sustainability of tidal marshes depends on the net accumulation of sediment and belowground organic matter sufficient 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 (Linkage #14a) as a consequence of 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. Given that the availability of sediments in the Delta is low relative to other regions of the estuary, accumulation of organic matter is expected to be more important than mineral sedimentation as a mechanism of sediment accretion in Delta marshes (Culberson 2001, Reed 2002, Culberson *et al.* 2004).

The accumulation of organic matter from above- and belowground plant production and subsequent rates of decomposition are an important source of material in established (both natural and restored) marshes, particularly in regions of the Delta that have lower suspended sediment concentrations than other regions of the Bay-Delta (e.g., North/San Pablo bays). Rates of decomposition, especially in belowground production, differ substantially along a salinity gradient. Belowground decomposition rates are slower in tidal freshwater marshes (Craft 2007), and consequently this is often the dominant mechanism of accretion in those marshes. Thus, trapping suspended sediments (*via* both passive—reduction of current flows—and active—filter-feeding organisms—mechanisms) is a 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) **Accretion effects on compaction and subsidence.** 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). Marshes deprived of an external source of sediments by artificial dikes and levee systems, by deep dredging of adjacent tidal channels, or by regional reductions in sediment supply, 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 (Mount & Twiss 2005). Under these conditions, the role of plant-derived organic matter accumulation (Linkage #23) becomes even more important.

(25) (**a**) **Accretion effects on animal biodiversity and productivity.** Sediment accretion has an unpredictable, but potentially important effect on marsh animal species composition and production that is not well understood. The possible importance of this linkage is emphasized given that: (a) the Delta is relatively sediment poor; (b) the important role of accretion from *in situ* sources of organic production in the maintenance of relative surface elevation; (c) the importance of relative surface elevation to the inundation regime; and, (d) the importance of inundation regime in determining marsh biocomplexity and productivity. This relationship is of particular importance for predicting the potential success of invasive species. For example, the deposition of large amounts of fine sediments might inhibit recruitment or smother settled larvae or interfere with the ability of small filter-feeders to persist in the marsh system. Conversely, the lack of accretion could result in the persistence of compacted, consolidated sediments that restrict plant and animal recruitment and persistence.

(**b**) **Animal biodiversity and productivity effects on accretion.** 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 benthic organisms such as crabs (Rudnick *et al.* 2005, Gutiérrez *et al.* 2006) can both dramatically increase accretion (and burial of organic matter) and cause erosion (as well as slumping of tidal marsh creek banks). While the effect of animal biodiversity and production on accretion could be locally important, it is likely to be as patchy as the dispersion patterns of the animal assemblages, and of less overall importance across a broader landscape scale.

(26) **Compaction and subsidence effects on erosion and desiccation.** 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 aquatic and terrestrial interfaces (Gabet 1998, Callaway 2001), sediment resuspension by rain (Torres *et al.* 2004) or animal activities (e.g., crab burrows, Rudnick *et al.* 2005), and wind-driven waves or tidal flows (Wood & Widdows 2002). Sediments in freshwater marshes tend to be more easily eroded than those of saline marshes in part because there is generally a lower root biomass (Odum 1988, Craft 2007) and finer particle size (e.g., lower sand content) in freshwater marsh substrata. Erosion and compaction also lower relative surface elevations and, in areas without extensive vegetative cover, will reduce desiccation opportunity by increasing the amount of time inundated.

(27) **(a) Compaction and subsidence effects on animal biodiversity and productivity.** 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, either by directly inhibiting colonization or by modifying the marsh plain elevation and changing the suitability for organisms adapted to specific tidal inundation frequency and duration regimes. This might occur by interfering with their ability to burrow into the marsh sediments or by altering the flooding regime experienced by organisms, as well as by altering temporal or spatial patterns of food delivery, or changing the suite of competitors and predators within the animal assemblages. However, examples of this interaction are rare.

(**b**) **Animal biodiversity and productivity effects on compaction and subsidence.** As with accretion (Linkages #25a & #25b), burrowing and feeding activities of diverse faunal groups may have either a positive or negative effect, and complex interaction effects, on compaction both directly through their activity (e.g., burrowing, feeding) and indirectly through reduction in macro- and microalgae that modify sediment characteristics such as its cohesiveness (Boyer and Fong 2005). The relative significance of these (Linkages #27a & #27b) faunal responses to or effects on compaction, although likely of potential moderate importance to the structure and functioning of the marsh system, are neither well known nor predictable without knowledge of the various fauna involved.

(28) (**a**) **Production, biomass and decomposition effects on emergent plant biodiversity and architecture.** Marsh plant production and the translocation of belowground biomass can have a strong effect on emergent plant diversity and architecture (e.g., density of aboveground shoots and plant height often correspond to the amount of production and biomass stored below ground). This effect may be particularly evident in the biological processes driving the prominent patterns of vegetation zonation found in the Bay/Delta marshes (Culberson 2001). Because marsh production is an important contributor to the maintenance of marsh plain elevations away from the elevated zones adjacent to tidal channels (where sediment accretion is more prominent), the processes that regulate that production and its variability (e.g., salinity) also affect the species and diversity of plants in representative (elevation) zones.

(**b**) **Emergent plant biodiversity and architecture effects on production, biomass and decomposition.** 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. This can particularly influence the occurrence of small, understory plants, and particularly benthic microalgae, where architecture of dominant species forms an overstory that extensively shades the benthos and underlying plants.

Plant zonation, especially as structured around tidal channel networks (see Linkage #21), can also influence where plant recruitment and subsequent production development, especially in the presence of disturbance or in the case of restoring tidal marshes. Rand (2000) noted that seed distributions along a New England salt marsh gradient strongly paralleled adult plant abundance patterns, suggesting that seed dispersal was particularly localized, with limited movement out of parental environments. In contrast post-dispersal factors responsible for determining species distribution patterns were determined by intolerance to abiotic conditions in the lower marsh zones and to competitive suppression by dominant plants in higher marsh elevations. Whether these pre- and post-dispersal transitions and elevation differences affect marsh vegetation assemblage structure and production in Bay/Delta marshes has not been extensively evaluated.

(29) **Production, biomass and decomposition effects on animal biodiversity and productivity.** 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) **Emergent plant biodiversity and architecture effects on animal biodiversity and productivity.** High biodiversity in aquatic ecosystems is considered to be a desirable attribute to promote stability and resistance to invasive species and disturbance effects (Lawton 1997, Levin et al. 2001). A direct positive relationship between plant diversity or complexity of plant architecture on animal biodiversity and productivity is related to the provision of more niche space and diversity among the animal components of the marsh. Although we are applying this most directly to the effect of emergent marsh plant architecture on animal biodiversity and productivity, it is also applicable to submerged aquatic vegetation at the aquatic interface of tidal channel: marsh margins, where Toft (2000), Toft *et al.* (2007) and Simenstad *et al.* (2007) describe extensive associations of

epibenthic invertebrates associated with water hyacinth (*Eichhornia creassipes*) and other submerged aquatic vegetation (SAV; e.g., pennywort, *Hydrocotyke umbellate*) root structure, some of them unique to the SAV. The fact that the non-indigenous hyacinth supported non-indigenous amphipods (*Crangonyx floridanus*) and isopods (*Caecidotea racovitzai* and *Asellus hilgendorfii*) that were not prevalent in fish diets, contrasting strongly with the indigenous amphipod *Hyalella azteca* associated with pennywort and was heavily preyed upon by fish, suggests that plant architecture can play a significant role in structuring animal diversity and productivity.

(31) **(a) Marsh structure and processes effects on water characteristics.** 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 thermal exchange process can directly affect water temperatures in adjacent tidal sloughs (Enright and Burau, pers. comm.) and would have an effect on dissolved oxygen concentrations and perhaps salinity in cases where evaporation is an issue (e.g., shallow marsh pools).

(b) Water characteristics on marsh structure and processes. Salinity and temperature are the primary characteristics of water directly influencing the biotic structure of marshes, by influencing the physiological tolerances of the plant and animal assemblages that can colonize and persist in the marsh. But, dissolved oxygen and turbidity can also influence marsh biota under extremely low or high concentrations, respectively. Indirect effects, such as through sediment accretion related to suspended concentrations of mineral and detritus particles (i.e., turbidity) are manifested through the aquatic interface and associated processes (e.g., Linkages #4a through #14a and *Relative Surface Elevation Processes & Sediment Structure*).

(32) **Marsh structure and processes effects on elevation.** One of the more important products of the various abiotic and biotic processes included in *Marsh Structure and Processes* (Linkages #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. This pathway is part of a critical feedback loop between internal marsh processes and inundation regime (Linkages #13, #32 & #33).

(33) **Elevation effects on inundation regime.** 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). This pathway is part of a critical feedback loop between internal marsh processes and inundation regime (Linkages #13, #32 & #33).

(34) **Marsh structure and processes effects on exported production.** *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 Linkage #16. Although the aquatic interface is likely the primary interface of transfer of exported production from the vegetation marsh, the net export of organic matter across that interface (Linkage #34) may be comparatively insignificant (e.g., compared to production within tidal channels and open water) because under normal tidal flows emergent vegetation functions as a filter such that the marsh plain tends to be a sink for passively-transported particles. Any unfiltered materials that reach the aquatic interface would likely follow the water flows exiting the tidal marsh to the open estuary. High freshwater flows, however, may scour the marsh of organic matter and the filtering of the aquatic interface may be much less a factor.

(35) **Mercury effects on nutrients, pollutants, and sediments.** 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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