



A Landscape-level Model for Ecosystem Restoration in the San Francisco Estuary and its Watershed

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ABSTRACT

The CALFED Bay-Delta Program is an ambitious effort to restore ecosystems and improve reliability of ecosystem services in California's Central Valley. Key issues for CALFED and its Ecosystem Restoration Program (ERP) include (1) meeting societal demand for multiple, potentially conflicting ecosystem services; (2) the tradeoff among more or less environmentally intrusive approaches to solving problems; (3) whether restoration should focus at the ecosystem level or on individual species; (4) the appropriate response to uncertainty; and (5) the tension between action and investigation. A long-term, landscape-scale perspective is essential for framing the scientific questions underlying these broad issues. We introduce a landscape-scale conceptual model that illustrates linkages, including material flows and animal migration, among the major ecosystem components being described in detail in a series of review papers. This model shows how linkages between ecosystem com-

ponents result in remote consequences of locally applied restoration actions. The network of linkages is made more complicated by human interventions, which add components not previously a part of the landscape (e.g., salmonid hatcheries) and alter or even reverse causal relations. A landscape perspective also helps identify conceptual gaps in CALFED's restoration strategy, such as climate change and human population growth, which should be explicitly considered in forecasts of the long-term prospects for restoration. A landscape perspective is no panacea; in particular, the effects of restoration at this scale will be difficult to detect. Nevertheless, we advocate integrating investigations of processes at nested, smaller scales as an approach for evaluating effects of individual restoration actions and of the entire program. We believe CALFED and other large restoration programs will be most successful if they are able to integrate both societal expectations and scientific study at the landscape level.

KEYWORDS

model, landscape ecology, restoration, spatial scale, temporal scale

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INTRODUCTION

Meeting disparate human demands for reliable supplies of water is an increasing challenge in many regions of the world (Postel et al. 1996; Vörösmarty et al. 2000). The task is particularly daunting in the watershed of the San Francisco Estuary, which encompasses about 40% of the area of California. This extensive watershed, home to nearly 15 million people, encompasses virtually all of the state's Central Valley, the Sacramento and San Joaquin rivers, and their tributaries. The state's citizens support the protection of ecological functions and viable populations of native species within this region, but they also require continued delivery of ecosystem services (Costanza et al. 1997), particularly delivery of fresh water. Management and restoration activities in the watershed of the San Francisco Estuary have attempted, with limited success, to reconcile incompatible societal goals (Van Eeten and Roe 2002).

The landscape of central California has been dramatically altered since the arrival of European settlers. The estuary has become highly urbanized, with attendant problems of diminishing water quality, hardening of shorelines, and impacts from dredging (Nichols et al. 1986). The agricultural land uses that dominate the watershed demand ample fresh water and protection from flood damage, while at the same time releasing large quantities of pesticides and herbicides (Kuivila and Foe 1995). Ecological linkages and processes in both the estuary and the watershed have been heavily modified by anthropogenic alteration of physicochemical processes, as well as the introduction of numerous non-native species of plants and animals (Cohen and Carlton 1998; Moyle 2002). Many native species have been reduced in abundance or driven to extinction, and at present 36 species of plants and 31 species of animals in the Central Valley are protected under federal and state endangered species laws (CALFED 1999).

Conflicting societal goals in the Central Valley are particularly evident in the allocation of water.

Precipitation in central California has a pronounced seasonal pattern, with a long summer dry season, and a north-to-south gradient of increasing aridity. California's native animals and plants respond to these gradients through spatial variation in occurrence and

life-history adaptations to seasonal variation in precipitation (Bailey 1998; Moyle 2002). In contrast, the human response to temporal and spatial variation in precipitation has taken the form of engineering to accommodate a pattern of demand concentrated in the summer and toward the south; complex water storage and delivery systems export a substantial fraction of the available water out of the Sacramento and San Joaquin watersheds. These changes have irreversibly altered the landscape of central California and created conflicts between direct human uses of water and the needs of fish and wildlife.

The CALFED Bay-Delta Program was initiated in 1995 in an attempt to resolve these conflicts (Van Eeten and Roe 2002; Jacobs et al. 2003). The geographic focus of CALFED is centered on the Sacramento-San Joaquin Delta, but also includes the rest of the San Francisco Estuary and the entire Sacramento-San Joaquin watershed below the major dams (Figure 1). This endeavor, now managed by the California Bay-Delta Authority (CBDA, <http://calwater.ca.gov/>), includes programs to restore ecosystems, ensure a reliable water supply, improve water quality, improve stability of levees protecting urban and agricultural land, and minimize conflicts between water supply and protection of native fishes (Table 1). Each of these programs has a large spatial extent and a decades-long temporal scope. Each program is a substantial undertaking on its own; the idea that all programs can proceed and succeed simultaneously is ambitious, if not unrealistic.

In this paper we focus principally on the CALFED Ecosystem Restoration Program (ERP), emphasizing large-scale, long-term restoration actions and other activities in the watershed. The goals of the ERP (Table 2) are directed toward ecosystem improvement, using a broad definition of "restoration" that represents a trend away from species-specific management toward broader and more comprehensive approaches that recognize key ecosystem processes (CALFED 2000). However, ERP goals imply a level of ecological understanding that may not yet exist. Gaps in scientific knowledge of the ecology of the San Francisco Estuary and the Central Valley lead to considerable uncertainty regarding the most effective strategies and management actions to achieve ecological goals and to support desired land and water uses. Furthermore, attempts to apply ecosys-

tem-level remedies can conflict with the state and federal legislation that enforces protection of individual endangered species.

Pressure from various stakeholders has forced the ERP to proceed before clearly defining specific objectives, or developing explicit models that link restoration actions

to those objectives. For example, initial expenditures toward ecosystem restoration began in 1995, yet the ERP strategic plan, including goals and general objectives, was not published until 2000 (CALFED 2000). The goals and objectives are only now being unambiguously linked to suites of actions and performance measures.

Thus, the need remains for a clear articulation of how the ecosystem is likely to respond to various restorative measures and other human activities and how those responses relate to restoration goals. Herein, we introduce a landscape-scale conceptual model as a framework for this articulation.

Early in its development, the ERP attempted to codify the state of knowledge supporting restoration in the San Francisco Estuary and Central Valley by commissioning a series of review papers (or “white papers”) on key topics (Table 3). Several of these papers have been completed and several are nearing completion. Detailed information is or soon will be available on several key species of fishes (Sacramento splittail *Pogonichthys macrolepidotus*, Moyle et al. 2004; delta smelt *Hypomesus transpacificus*, Bennett submitted; and Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*), Williams and Yoshiyama in prep.). Additional information is available on subtidal (Kimmerer 2004) and marsh (Brown 2003a; Orr et al. 2003) habitats in the San Francisco Estuary (including the Delta) and regional effects of global climate change are being examined (Dettinger et al. in prep). However, the status of commissioned papers on the remaining topics is uncertain. Thus, the ERP lacks cogent descriptions of many



Figure 1. Map of California showing the Central Valley and its watershed along with the San Francisco Estuary. The Sacramento-San Joaquin Delta, keystone to water management in this system, occupies a central place in restoration efforts as well.

Table 1. Overview of CALFED programs, projected costs of Stage 1 implementation, goals, main ecosystem amenities addressed, and required intervention into ecosystem operation. [Source of information in columns 1-3: CALFED Bay-Delta Program, 2000. California's water future: a framework for action.]

<i>Program</i>	<i>Stage 1 Cost (\$M)</i>	<i>Goal</i>	<i>Amenities Addressed</i>	<i>Intervention</i>
Water use efficiency (includes storage, conveyance, and transfers)	\$2956	Accelerate adoption of cost-effective behaviors that conserve/recycle water	Irrigation Drinking water Hydropower Recreation At-risk biota Edible biota	Ambiguous
Water supply reliability	\$2361	Improve reliability of water supply, despite unpredictable availability and competing demands; capture peak flows	Irrigation Drinking water Hydropower Recreation At-risk biota Edible biota	More
Ecosystem restoration	\$1340	Restore species and ecosystem structure/function; improve habitat; enhance/mimic natural processes	At-risk biota Edible biota Recreation	Less
Water quality	\$955	Provide good quality drinking water, despite some natural constituents (e.g., salt, organic C)	Drinking water	More
Levees	\$444	Protect land uses depending on intact levee system	Productive soils Freshwater biota	More
Watersheds	\$300	Promote locally led actions that contribute to goals of other programs	None specifically	Ambiguous
Science	\$300	Develop scientific knowledge needed to implement, monitor, and evaluate programs; communicate knowledge to managers and public	None specifically	Ambiguous

of the important physical and biotic elements of riverine ecosystems, and the influences of toxic materials and water diversions. Furthermore, it is difficult to identify gaps among these topics at the ecosystem scale. Nevertheless, the topics of these papers make logical building blocks for examining the Central Valley in the context of landscape restoration.

Integration of topic areas at the landscape scale is necessary because the ERP is geographically broad and must be considered in the context of other CALFED programs, as well as other human activities and ecological processes in the watershed. The purpose of this paper is to examine linkages among major ecosystem components that may be important from a restoration perspective. The linkages presented reflect our interpretations of the scientific literature on the watershed of the San

Francisco Estuary and our personal experience. We provide a general conceptual model of CALFED's ecological landscape, then discuss the consequences of this model for landscape-level restoration, including key ecosystem responses and implications for restoration efforts.

KEY ISSUES FOR ECOSYSTEM RESTORATION

Several key issues must be considered in designing ecosystem restoration efforts. Each of these issues has implications at the scale of individual projects or individual ecosystems, but each also influences restoration success at the landscape scale.

A first issue is the fundamental conflict within CALFED: meeting societal demand for multiple ecosystem services. This conflict is most closely focused on

Table 2. Strategic goals (CALFED 2000b) and their main associated ecosystem amenities for CALFED's Ecosystem Restoration Program. Expected conflicts between goals are also shown.

<i>Strategic Goal</i>	<i>Target Amenities</i>	<i>Conflicting Goals</i>
1 Recover at-risk native species	At-risk biota	3
2 Rehabilitate natural processes to enhance natural biotic communities	At-risk biota Edible biota	3
3 Maintain harvestable populations of selected biota (including some nonnative species)	Edible biota Recreation	1,2,5
4 Restore habitat types for ecological and public values	Recreation Aesthetic appeal	
5 Prevent and reduce impacts of nonnative species	At-risk biota Aesthetic appeal	3
6 Reduce water and sediment toxicity	At-risk biota Edible biota Drinking water	

the historical and ongoing ecological impacts of a highly engineered water supply system. The system of reservoirs, canals, river channels, and diversions is operated to provide water at selected places and times, with results that often deviate markedly from the natural flow regime. Although much of the present conflict stems from reduction in river flow and use of natural channels for moving water, particularly in the Delta, additional conflict arose throughout the Central Valley when construction of major dams blocked access by anadromous fishes to their high-elevation spawning sites.

The importance and intensity of current conflicts over ecosystem services can be inferred from an overview of CALFED programs and goals. The projected cost of each program during Stage 1 implementation is a crude measure of importance (Table 1). Most (61%) of CALFED's resources are devoted to enhancing the availability of water for human uses. Although some of these "beneficial uses" of water include maintenance of valued biota (e.g., in wildlife refuges), the vast majority is used directly by humans, especially for irrigation and drinking. Ecosystem restoration, which gets 15% of CALFED expenditures, is the only CALFED program that primarily strives to enhance biota. Overall, agricultural production (via irrigation water and levee protection) and drinking water are the ecosystem services receiving the greatest CALFED investments.

Escalating societal demands on a limited supply of water will certainly lead to conflicts among stakeholders for access to water and its associated services. Although the details of such conflicts are not predictable, the management approaches being implemented to enhance the main ecosystem services of concern suggest that profound conflicts between meeting the goals of ecosystem restoration and the goals of other CALFED programs are imminent. In particular, the programs striving primarily to enhance delivery of irrigation and drinking water and to protect current land uses in floodplains and the estuary (via levee protection) will require even more human intervention in an already highly engineered ecosystem (Table 1). For example, water storage capacity in the Sacramento and San Joaquin basins is already 80% and 135% (respectively) of mean annual runoff (CALFED 2000). Additional engineering to enhance delivery of irrigation and drinking water is likely to undermine efforts to restore ecosystem structure and function, if that is to be accomplished with minimal intervention. The Environmental Water Account (Kimmerer 2002b) attempts to resolve conflicts between endangered species protection and water deliveries, but its ancillary ecosystem-level benefits are unknown.

Other areas of conflict arise even under the rubric of ecosystem restoration. The range of ecosystem services targeted by the ERP is narrower than that for all

CALFED programs (Table 2). The value to society of some of these services may be difficult to quantify. For example, the extent to which the delivery of recreation and aesthetic appeal is enhanced by a particular management action is difficult to assess, because different people may view the same action as either improving or degrading these services. On their surface, actions to meet ERP goals do not seem to interfere with the delivery of each other's services. A main exception stems from the fact that some of the harvestable populations to be maintained by the ERP are nonnative (e.g., striped bass, American shad, largemouth bass) and likely have substantial impacts on native species that are largely unmeasured but may be substantial (Lindley and Mohr 2003). Maintaining nonnative populations at levels high enough to provide substantial harvest will compromise CALFED's ability to achieve other ERP goals. Similarly, measures to protect certain kinds of "wildlife-friendly" agriculture from conversion to urban or other land uses serve to support ecosystem services compatible with cultivation of crops, but preclude provision of other ecosystem services such as habitat for endangered species.

A second issue is the tradeoff between highly technological approaches to solving problems and less ecologically intrusive approaches. Examples include the use of salmon hatcheries as mitigation for dams versus restoration of salmon habitat; the widespread use of agricultural biocides versus biological or other pest control methods; and the construction of levees to reduce local flooding impacts, as opposed to expansion of floodplains. In each case, the alternative approaches imply costs to different sectors of society, further complicating the selection of an approach.

A third issue is whether restoration or environmental protection should be focused at the ecosystem level or at the level of individual species. The ERP has explicitly stated a preference for ecosystem-level protection, chiefly through restoring physical habitat. That focus does not preclude actions to conserve a single target species, such as restoration of riverine habitat for spawning by salmon, as long as such restoration improves overall ecosystem conditions. This approach contrasts starkly with the prevailing implementation of endangered species legislation, which focuses not only on individual species, but on individual organisms.

A fourth issue is how to manage in the face of ongoing uncertainty. The ERP proclaims adaptive management as its mode of dealing with uncertainty. Traditional approaches to management and restoration determine a course of action through the use of "best available science," a regulatory term of ambiguous meaning (Bisbal 2002). An alternative approach specifically designed to address uncertainty is adaptive management (Holling 1978; Walters 1986; Walters and Holling 1990). In contrast to "learning by doing," adaptive management explicitly lays out causal links and potential outcomes before action is taken; establishes programs of research, monitoring, and evaluation to assess progress toward goals; provides a formal feedback loop for improving both ecological understanding and future management; and, where possible, treats management actions as explicit experiments. In its early stages, adaptive management is also valuable for clarifying the current state of ecological understanding and how such understanding may help to establish priorities for restoration; however, adaptive management is difficult to apply in practice, especially over large geographic areas, and has been criticized as unworkable (Van Eeten and Roe 2002). Although adaptive management has been applied at local scales (e.g., Montagna et al. 2002), it may be intractable at landscape-level scales because of the difficulty in measuring outcomes and attributing them reliably to specific causes.

A fifth issue is the tension between the need for rigorously selected, cost-effective restorative measures, and the need, both political and practical, to meet targeted goals relatively quickly. When CALFED was initiated the pressure to show positive ecological results was overwhelming, with the result that numerous restoration and other projects were launched with little formal planning, no explicit conceptual models, and no provision for assessment or learning. One danger is that the appearance of accomplishing things (e.g., spending money, moving earth, stocking fish) can be uncritically construed as actual improvement in ecosystem performance. To this day there has been no landscape-scale summary of real change in ecosystem performance in the CALFED action area; hence, although these problems are being addressed, we currently cannot state definitively what progress has been made toward meeting ERP goals.

THE ROLE OF CONCEPTUAL MODELS IN RESTORATION

The principal scientific problem facing management or restoration at any scale is uncertainty, which manifests in a variety of distinct forms. First, a lack of relevant data results in ignorance about ecological processes, leaving planners and stakeholders without a scientific basis for choosing restoration actions.

Second, alternative but reasonable interpretations of data may suggest different actions or even preclude many actions. Third, alternative theories about ecosystem function, each more or less consistent with the available data, may suggest very different management or restoration strategies. In the latter cases, the uncertainty lies in not knowing which interpretation or strategy is most concordant with ecological reality. Finally, because the outcome of any restorative action is probabilistic and contingent on other conditions that may not be controllable, the likelihood of success of even "correct" actions is uncertain.

In all of these cases, clarity about the nature and consequences of the uncertainty can support more effective decisions about restoration, and may suggest a path toward resolution of alternative perceptions through targeted research or pilot studies. This clarity can be achieved through the development of explicit conceptual models about important processes involved in restoration. Conceptual models are a key element of adaptive management because they facilitate clear description and open discussion of alternative outcomes (Walters 1986; CALFED 2000). A conceptual model is an explicit description of an object or phenomenon. For our purposes, a conceptual model describes current knowledge about how some aspect of the ecosystem works, how it is affected by environmental conditions and human activities, and how it is likely to respond to management interventions.

Although they often incorporate flow diagrams, conceptual models can take any form that conveys effectively the knowledge of interest.

For large, complex ecosystems, such as the San Francisco Estuary and its watershed, conceptual models are useful for describing phenomena at a range of spatiotemporal scales, as well as linkages between scales. Healey et al. (in prep.) present several conceptual mod-

els of this system, ranging from a grand overview of interactions among socioeconomic, environmental, and biological factors, to a focused depiction of how restoration in the gravel reaches of a salmon stream might work. Each model illustrates key ecological processes and management issues particular to its respective spatiotemporal scale. All are germane to the ERP goals.

An emphasis on applying conceptual models to describe ERP projects has resulted in some confusion within the CALFED community. Much of the difficulty in developing conceptual models arises from the idiosyncratic nature of concepts themselves; conceptual models of the same topic developed by two people may look very different. One of the greatest challenges in developing conceptual models is to identify common and alternative beliefs among participants. Conceptual models have been used (1) as heuristic tools, (2) to explain how proposed restoration actions are expected to work, (3) to highlight differences in understanding and expectations of the ecosystem, and (4) as a basis for predicting outcomes of restoration actions (Walters 1986; CALFED 2000).

An example illustrates the importance of explicit conceptual models. In its early days ERP emphasized the restoration of "shallow-water habitat" to support greater abundance of fish species of concern. The implicit underlying conceptual model assumed that these species were habitat-limited and would increase in abundance if additional habitat were created (CALFED 1997). The assumption that marshes were essential nursery habitats for juvenile stages of open-water fishes was mainly inferred from other geographic areas (e.g., Kneib 1997). In the San Francisco Estuary, some open-water species make considerable use of marshes and marsh channels (Meng et al. 1994); however, recent research suggests that species of greatest conservation concern may not use shallow subtidal habitat (Brown 2003b). The threatened delta smelt, for example, is predominantly an open-water species (Moyle et al. 1992; Moyle 2002; Bennett submitted), and Sacramento splittail and juvenile salmon may survive or grow better on floodplains than in subtidal habitat (Sommer et al. 1997, 2001; Moyle et al. 2004). The fundamental assumption that restoring shallow-water habitat would lead to an increase in the abundance of fishes of concern, therefore, was not supported by data specific to this system. Had the initial conceptual model been more explicit, the lack of site-specific sup-

port for a fundamental assumption would have been exposed, and the need for research and planning alternatives would have been apparent earlier.

A MODEL OF LINKAGES IN THE LANDSCAPE

Our conceptual model of the entire landscape of the San Francisco Estuary and its watershed below major dams illustrates linkages among ecosystem components (Figure 2). The components are connected geographically, from upland terrestrial habitats through the riparian zones to the rivers, and then to the estuary, including both open waters and tidal marshes. Three principal stressors overlaid on these geographic components are contaminants, which may influence any portion of the landscape, diversion pumping at the major export facilities in the south Delta, and climate change.

The species of fish treated individually in review papers have been singled out because of their conservation status and the belief that they are strongly influenced by management activities in the Delta. Other species of fish and all terrestrial species are not treated individually but are subsumed under the ecosystem components, although ecosystem-level restoration is assumed to benefit them.

Linkages between pairs of ecosystem components fall into six classes (Table 3). Linkages between organisms and their habitats are explicit only for the three taxa treated in review papers. An additional element in Table 3 illustrates explicit linkages between human activities and all other ecosystem components.

Most of the linkages between ecosystem components are physical flows of materials, particularly water. Although the dynamics of these flows and their dependence on external forcing may be complex in reality and at a fine resolution (e.g., sediment flux from the Sacramento River to the estuary, Wright and Schoellhamer 2004), they are conceptually straightforward. Water, which entrains nutrients, organic matter, sediments, and other substances, generally flows from terrestrial through riparian to river habitats and then downstream to the estuary, although floods can reverse that direction by depositing river-borne material on land. Flows from the rivers to the estuary are unidirectional, whereas tidal flows between the estuarine channels and tidal marshes,

and between the estuary and ocean, are bi-directional.

Considerably more complex, but still conceptually tractable, are biotic transports of material through

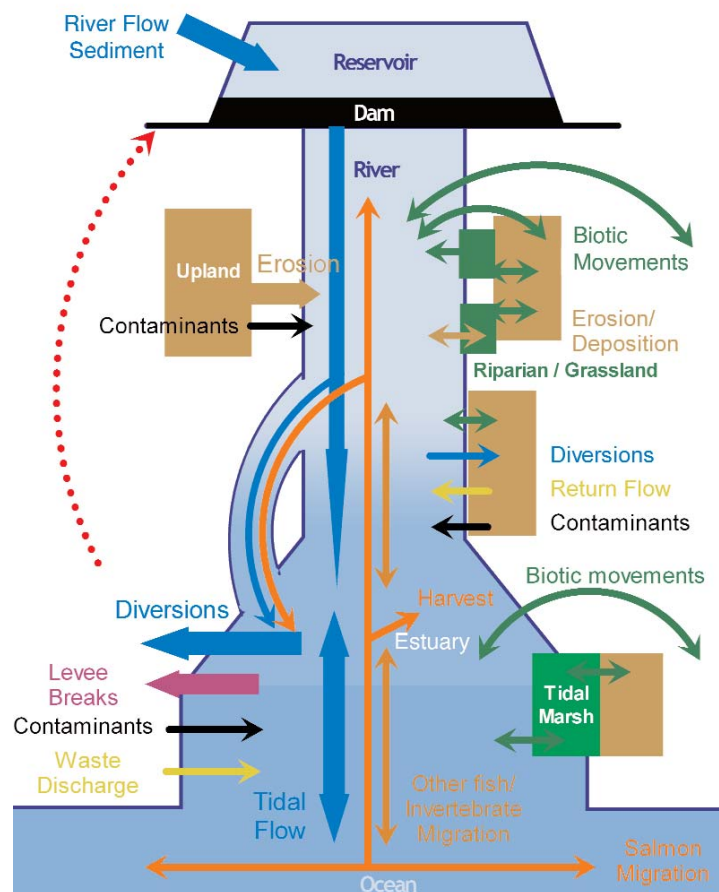


Figure 2. Schematic diagram of the Central Valley landscape, showing spatial relationships among elements, including those discussed explicitly in review papers. The Sacramento-San Joaquin Delta, the landward portion of the San Francisco Estuary and focus of water supply issues and restoration efforts, is shown as a triangular region. Areas of physical habitat (brown and green) illustrate the grading from terrestrial, through riparian and marsh habitat, to open-water habitats of rivers and the estuary. Climate change influences all elements of the system, including timing and possibly quantity of freshwater flow. Important stressors include contaminants and waste discharge, which are concentrated in various parts of the system, and diversions, which occur throughout the freshwater portions of the system, but are of greatest concern in the southern Sacramento-San Joaquin Delta. Salmonids range from the upper reaches of rivers to the Pacific Ocean; other anadromous species may have a smaller range but still link freshwater and brackish to saline habitats; and even resident fish species may undergo significant migrations.

migration and feeding. The most dramatic example of these fluxes is the spawning migration of adult salmon, which migrate and usually die far up the river systems, contributing their biomass and marine-derived nutrients to the stream ecosystems. The importance of these nutrients, high in Alaskan streams (Kline et al. 1990), is unknown for Central Valley streams. Similarly, migratory waterfowl that feed with-

in the estuary or Central Valley may transfer substantial biomass within or beyond the region (Lovvorn and Baldwin 1996).

Other migrations at the landscape scale, although generally of shorter distance, include anadromy by striped bass (*Morone saxatilis*), American shad (*Alosa sapidissima*), Pacific lamprey (*Lampetra tridentata*), river lam-

Table 3. Potential or known linkages between landscape components. Numbers indicate the nature of each linkage, according to the key. The linkages are read from left to right; for example, the river influences the estuary through movement of materials driven by river flow, as well as by the migration of organisms (e.g., downstream migration of juvenile anadromous fish) and to some extent the movement of organic matter through predation, e.g., when striped bass or other anadromous fish feed in the rivers and then migrate to the estuary. The influence of the estuary on the river occurs mainly through movement of organisms, since water does not flow uphill. Global human influences on climate are neglected here.

Information or material flow to:

Flow from:	Terrestrial	Riparian	River	Estuary	Marsh	Contaminants	Diversions	Salmon	Splittail	Smelt	Climate Change	Humans
Terrestrial	-	1										6
Riparian	1	-	1									6
River			-	1,2		1	1	3	3			1,6
Estuary			2	-	1,2	1	1	3	3	3		6
Marsh				1,2	-			3	3			6
Contaminants	4	4	4	4	4	-		4	4	4		4
Diversions				5		1	-	5	5	5		6
Salmon	2	2	2	2	2			-				6
Splittail		2	2	2	2				-			6
Smelt				2	2					-		6
Climate Change	1, 3	1, 3	1, 3	1, 3	1, 3	1, 3	1, 3	1, 3	1, 3	1, 3	-	6
Humans	1,5,6	1,5,6	1,5,6	1,5,6	1,5,6	1,6	1,6	5,6	5,6	5		-

Key to numbers in table:

- 1** Movement of materials through flow (water, nutrients, organic matter) or debris fall
- 2** Movement of organisms (life-cycle or short-term migration, predation, carcasses)
- 3** Provision of physical habitat including food supply and temperature
- 4** Toxic effects
- 5** Removal of organisms
- 6** Ecosystem services to humans (water, food, recreation, aesthetics); restoration

prey (*L. ayresi*), Sacramento splittail (*Pogonichthys macrolepidotus*), and several other species (Moyle 2002). A potentially important flux occurs through the catadromous migration of non-native mitten crabs, *Eriocheir sinensis* (Veldhuizen 2000). At a smaller scale, feeding links organisms in different habitats. Examples include birds that prey on fish in marshes, rivers, or open waters; salmon that prey on terrestrial insects; and estuarine or riverine fish that prey on invertebrates on floodplains or marshes at high water stages.

Toxins, changes in freshwater flow, and water diversions have direct and indirect effects on biological components. Linkages with human activities include harvest, restoration, and discharges of wastes into water and air, all of which contribute to material flows. The ecological landscape affects humans primarily by providing ecosystem services, but rivers also affect humans through floods.

A few examples illustrate the utility of considering ecological linkages explicitly in designing restoration projects. Unidirectional flows of materials and bidirectional movement of organisms link the rivers with the estuary. By all measures of quantity or effect, flow of materials is by far the most important. The estuary is heavily influenced by freshwater flows (Jassby et al. 1995; Kimmerer 2002a, 2002b), as well as by loading of nutrients (Hager and Schemel 1992), organic matter (Jassby et al. 1993), sediments (Schemel et al. 1996), planktonic organisms (Jassby et al. 2002), and contaminants (Kuivila and Foe 1995). Thus, the physical, chemical, and biological conditions in the estuary are heavily dependent on those in the river, whereas the reverse is not true. Diadromous migrations, arguably the only significant natural mechanisms by which the estuary influences the rivers, appear to have a relatively minor influence except in certain locations and seasons, and then only in terms of biology and perhaps nutrient chemistry.

By contrast, some other linkages important for restoration are tight and bidirectional. For example, tidal flows, migrations of organisms, and predatory interactions closely link tidal marshes with open water (Dame et al. 1986; Kneib 1997). Thus, dredging in channels and rising sea level may increase erosion of marshes and reduce the success of marsh restoration, while

marsh reconstruction and expansion may alter the sediment regime, therefore affecting water clarity in channels (Orr et al. 2003). Marshes also provide habitat for species that otherwise use open water (Kneib 1997). An increase in habitat complexity through restoration of brackish marshes could provide habitat for species of concern, whereas restoration of freshwater wetlands is equally likely to provide habitat for introduced waterweed (*Egeria densa*), which harbors mostly introduced fishes, including predators such as black basses (*Micropterus* spp., Brown 2003b).

Linkages between ecosystem restoration and human land and water use involve the most significant conflicts in the CALFED arena (Table 3). Human intervention can cause linkages to reverse direction, as when river flow increases through deliberate releases from reservoirs to meet demand for water exports in the Delta (Figure 2). In addition, an inherent conflict exists between restoration and destruction of physical habitat. This is most obvious in the gravel-bedded streams where gravel restoration and enhancement proceed side-by-side with the gravel mining that is at least partially responsible for the need for restoration. Longer-term conflicts exist between urbanization of agricultural land and either preservation of agriculture, in part to support wildlife, or reclamation to aquatic habitat. Conflicts also exist between creating impoundments for human water supply and allowing salmon access to high-elevation spawning grounds. Explicit conceptual models can help clarify the sources, alternative solutions, and likely consequences associated with such conflicts.

Among the conflicts between the goals of the ERP and those of other CALFED programs, the sharpest relate to alternative uses of freshwater, especially water supply for humans versus use of water for ecosystem protection and restoration. Another significant conflict has arisen because plans to increase shallow habitat to produce more organic carbon (ERP), and to store water in the Delta (an element in the water supply reliability program), were incompatible with actions to contain methylation of mercury (elements in the water quality program). A landscape-level model portraying key linkages among major ecosystem components provides a useful framework for organizing knowledge relevant to CALFED-wide conflicts.

DETAILED MODELS WITH SMALLER SCOPE

A tractable model of the entire Central Valley landscape is necessarily too coarse to allow an outline of the many interactions among ecosystem components that could influence the outcome of restoration actions. Here we limit ourselves to describing the major interactions among rivers, salmonids, and contaminants in an effort to illustrate how a conceptual model of modest scope and intermediate detail might be used to understand complex ecosystems and inform managers about restoration options. The basis for this discussion includes our beliefs that describing reference conditions can help identify ecosystem linkages that currently are degraded, and that repairing degraded linkages is crucial to achieving restoration goals.

Identifying specific objectives for ecosystem restoration implies knowledge of a desired condition or trajectory for the restored system. An understanding of historical conditions is useful in identifying a desired condition, but rarely leads directly to objectives for restoration, since in most cases a return to a pre-development state is precluded by current infrastructure, presence of non-native species, extinctions, or other irreversible alterations. In addition, knowledge about historical conditions usually must be inferred, which introduces at least some uncertainties. Nevertheless, contrasting a conceptual model of historical ecosystem dynamics with models of current ecological dynamics can reveal effective opportunities for management intervention.

Pre-industrialized conditions provide a reasonable reference for informing restoration of rivers and salmonids (Figure 3). River conditions before 1850, including sediment transport processes, water flow, and habitat configurations, were largely inferred on the basis of physiography and climate rather than from direct historical measurements. Physiography, including geology, topography, and other land-form elements, controlled the shape of river channels, size and composition of sediments, and water chemistry. Climate, especial-

ly precipitation and temperature, regulated the amount and timing of water that flowed down river channels, which in turn influenced rates of sediment transport, channel stability and morphology, and the spatial distribution of sediments. Interactions among channel morphology, sediment composition, freshwater flow, and water temperature controlled the availability of habitat for salmon. The distribution and abundance of salmon were presumably determined largely by variation in habitat availability, as evidenced by the precipitous decline in salmon runs after access to habitat was cut off by dams (Yoshiyama 1999). Variable oceanic conditions can affect survival of salmon to adulthood and presumably caused variability in run size of salmon populations (Francis and Hare 1994).

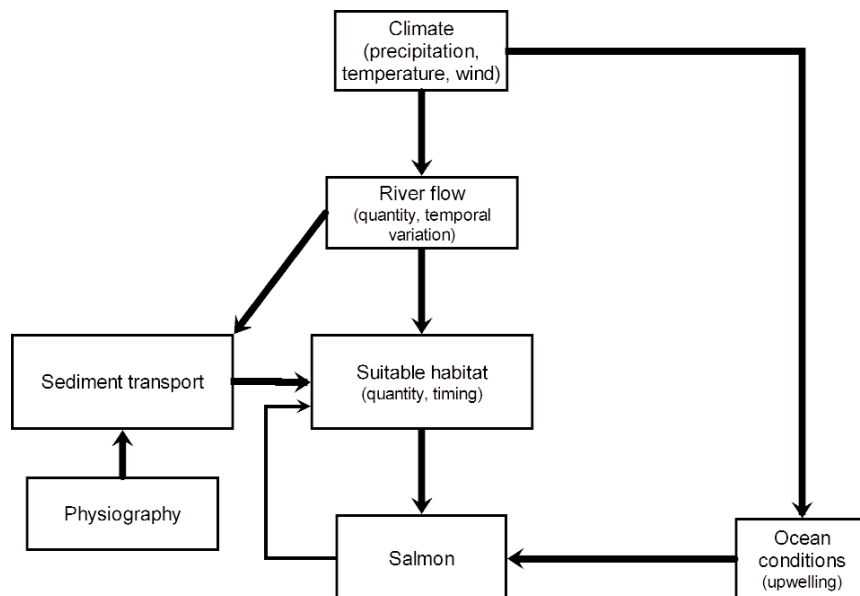


Figure 3. Simple diagram representing drivers of salmon production in the Central Valley prior to European industrialization. Arrow thickness is increases with scale and intensity of effects. Production was largely controlled by regional climate and physiography, which regulated the amount and availability of suitable habitat. Habitat suitability is defined by a suite of environmental parameters that enable salmon to complete their life cycle. Generally, more habitat or better timing of resource availability produces more salmon. The feedback loop from salmon to habitat represents construction of redds by adult salmon, which cleans the gravel and may enhance its suitability for future spawners. Delivery of marine nutrients to streams via salmon carcasses, an important feedback loop in salmon streams in Alaska and Canada, has unknown importance in Central Valley streams. The role of oceanic conditions in salmon production is also unknown, but is presumed to be important in this model. Note that contaminants and exotics played no role in salmon production.

Salmon abundance remained high despite substantial human harvest (Yoshiyama 1999).

Today, the factors that controlled historical river dynamics during the pre-industrial era are overwhelmed by human land and resource uses (Figure 4). Dams deny salmon access to historical spawning areas. Although winter river flows still respond strongly to climate, during most of the year flow is controlled by dams and diversions. Furthermore, climate is being affected by anthropogenic emissions of greenhouse gases. The linkage between global and regional climate change is poorly understood, but involves at least temperature increases and shifts to earlier seasonal peaks in freshwater runoff (Dettinger and Cayan 1995) to the likely detriment of some salmon races. Physiography still influences sediment composition, but the distribu-

tion and transport of sediment have been disrupted by dams and land use. Water chemistry, which historically would have influenced only the homing patterns of salmon, now involves toxic contaminants that may impair local habitat quality (Saiki et al. 1995). The composition, distribution, and abundance of contaminants are controlled by a complex array of sources, pathways, and linkages (Hinton 1998). The availability of suitable habitat remains crucial to salmon dynamics, but habitat quality and quantity are now largely functions of anthropogenic actions rather than natural factors. Furthermore, harvest and introduced non-native predators directly reduce salmon abundance, and harvest can also change maturity schedules and timing of salmon runs (Hankin et al. 1993). Counteracting harvest and predation is the influence of hatcheries, which in at least some streams enhance salmon abundance and

support an ocean fishery. This influence is not benign; it may reduce abundance of wild stocks through competition for food or space, or through increased fishing effort (Lichatowich 1999). Introduction of hatchery Chinook salmon could also adversely affect genetic integrity of wild salmon (Hedrick et al. 2000).

Although the current, highly modified ecosystem is better suited than the pre-industrial ecosystem for reliably providing quantities of water to humans, it is less well suited for supporting naturally spawning populations of salmon. The river ecosystem has been converted from one in which availability of salmon habitat fluctuated widely through time and space, to one in which habitat availability is consistently low and localized, and hatchery production is consistently high.

Comparison of the historical and current models highlights opportunities for restoration in which human controls on key ecological processes (e.g., flooding) can be relaxed, or where certain anthropogenic factors (e.g., contaminants, harvest) can be altered. Each proposed restoration action requires one or more conceptual models to provide insight into the potential mechanism for restoration,

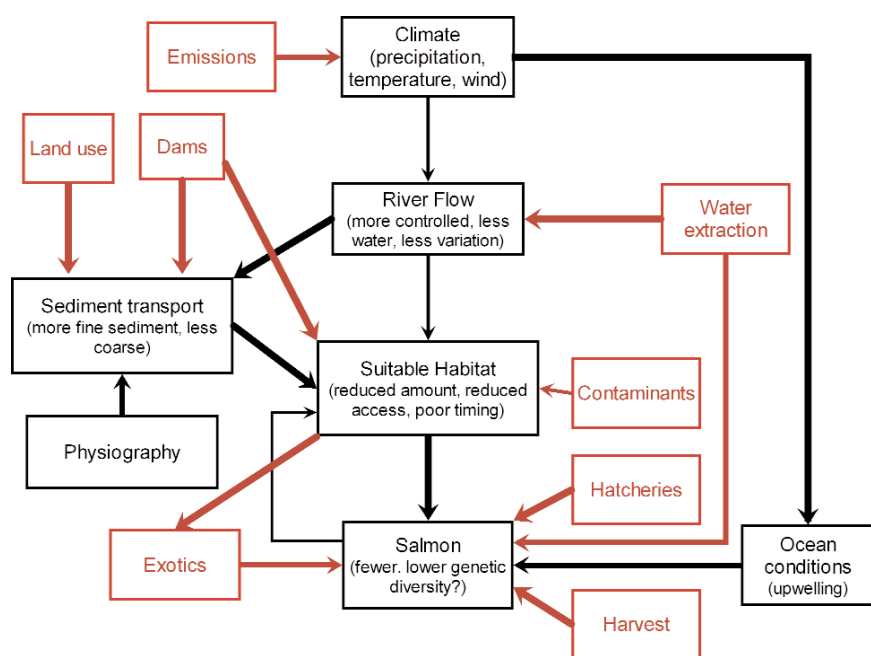


Figure 4. Simple diagram representing modern drivers of salmon production in the industrialized Central Valley. Arrow thickness increases with effect size. Natural factors (climate and physiography) still play roles, but are dwarfed by anthropogenic factors (shown in red). Much historical salmon habitat has been cut off permanently by dams, making dams a greater constraint on habitat availability and suitability than river flows. Sediment transport, river flow, and habitat suitability are greatly influenced by human alterations of the ecosystem. In addition, evolutionarily novel drivers, such as contaminants, exotic predators, entrainment, and hatcheries affect salmon in diverse ways. Overall, the factors limiting salmon production are more numerous, the pathways more complex, and conditions less suitable than during pre-industrial times.

as well as the possibilities for interference with or by other system elements or actions. In addition, explicit models at the landscape scale should be developed to place the restoration action in a broader context and allow comparison of it with other actions.

EFFECTS OF INTERACTIONS AT THE LANDSCAPE SCALE ON RESTORATION

CALFED intends to restore ecosystems and improve ecosystem services at the landscape scale. Ideally, restoration and other activities should be prioritized through consideration of large-scale ecological linkages and their attendant services. If these linkages are not recognized, tradeoffs in resource allocation among ecosystem elements tend to be decided on the basis of short-term economics.

Landscape linkages do exist, and they may magnify or interfere with restoration efforts, as examples demonstrate. Biological linkages, such as migrations of organisms, are analogous to movements of materials, but perhaps more importantly they represent how ecological processes in one geographic area can be influenced by agents in others. For several prominent species in the San Francisco Estuary ecosystem, the distribution of different life stages across the landscape, including the coastal ocean, precludes successful restoration when each landscape element is considered in isolation. The apparent need for a system-wide view generally has not resulted in extensive efforts to model or understand the landscape.

Principal exceptions include papers on splittail (Moyle et al. 2004) and salmonids (Williams and Yoshiyama in prep.), both of which include the entire life cycle of the species.

Contaminants are sufficiently pervasive throughout the system to have potential effects on all biota. There have been several demonstrations of effects of contaminants on bioassay organisms (Kuivila and Foe 1995), individual fish collected from the field (Bennett et al. 1995), and localized benthic fauna (Hornberger et al. 2000). A bioassay for the pesticide diazinon in the Sacramento and San Joaquin watersheds showed that risks to fishes were low, but at least some invertebrates were vulnerable to ambient concentrations (Giddings et al. 2000). However, no study has shown that population size of

any aquatic species has been affected by contaminants. The difficulty of demonstrating population-level effects of contaminants all but guarantees Type II errors, that is, failing to detect effects that are important. In addition, contaminants may interact quite subtly with other processes, leading to erroneous conclusions about relationships between stressors and biota. Contaminants may also cross boundaries between landscape components (e.g., transport of sediment-bound contaminants from rivers to the estuary, Bergamaschi et al. 2001). Thus cross-boundary effects must be kept in the forefront of discussions of restoration and habitat protection at the landscape scale.

Because diversions of water can remove fishes and other organisms from rivers and the estuary, they can serve as an effective example of a linkages between landscape elements. Diversions have received more management and public attention than any other individual stressor in the Central Valley (e.g., Stevens et al. 1985; Brown et al. 1996), and substantial funding has been directed to redressing management challenges associated with diversions (e.g., Environmental Water Account). Nevertheless, there has been little rigorous examination of the effects of diversions at the population level for any species. Even the large diversions of the Central Valley Project and State Water Project in the southern Sacramento-San Joaquin Delta have only recently been examined with any degree of statistical rigor. Results published to date do not suggest a substantial effect on migrating salmonids (Newman and Rice 2002), and the early assertion that export pumps were the sole cause of the decline in striped bass was not confirmed by detailed analysis (Kimmerer et al. 2000, 2001). We believe that a more comprehensive view of the life cycles of these species – a landscape view – would reveal at least the potential for other factors to be more important in population dynamics. Nonetheless, individual delta smelt remain within the upper estuary and appear to be vulnerable to export entrainment, although export effects on the smelt population remain unclear (Bennett in review). Although it would be unwise to dismiss diversions as a significant stressor, their role in driving declines of desirable species may have been inflated in the past.

Direct interactions between humans and other ele-

ments of the landscape are arguably the most important and complex linkages to be addressed by conceptual models in emerging review papers. These interactions take two general forms: exploitation of ecosystem services, including harvest, and the alteration of morphology, flow patterns, and other attributes of the physical system. These alterations include restoration and management activities. To our knowledge, no one has yet undertaken a comprehensive analysis of the various CALFED programs and how they might interact or interfere with each other. In this case, a landscape model such as ours is too skeletal to inform specific management decisions; but it does have heuristic value in pointing out important gaps in knowledge.

External forcings with known or expected trends that may influence the long-term trajectory of restoration efforts include global and regional climate change, interruption of sediment supplies in rivers and the estuary, human population growth, and various socioeconomic trends. Only climate change is addressed explicitly in a review paper. Regional climate change is likely to produce warmer winters, increasing the proportion of precipitation falling as rain, and earlier snowmelt, leading to an earlier peak in annual runoff (Roos 1989; Dettinger and Cayan 1995; Dettinger et al. in prep.). Because dam operators must meet objectives for flood control as well as water supply, these shifts will result in lower storage levels in spring or higher flood risk. Lower storage and growing demand will exacerbate the effects of decreasing snowpack and early runoff. These changes will almost certainly lead to conflict over the need for additional storage, the reliability of water supply to farms and cities, the degree of acceptable risk from flooding, and the availability of water for ecosystem maintenance.

Global models of climate change are providing increasingly reliable forecasts (IPCC 2001). Barring unforeseen socioeconomic development or catastrophe, consequences can be forecasted with reasonable confidence. Given the severity of these consequences, development of restoration alternatives in the face of climate change seems ripe for long-term analysis, gaming, and modeling. Such analyses may be beyond the scope of ERP review papers, but could be adopted as interagency efforts, perhaps led by CALFED.

Other consequences of long-term environmental and demographic trends can be predicted, many operating at scales larger than the individual landscape elements in Figure 2. These predictions suggest that ERP's current emphasis on relatively small-scale projects with local impacts well might be misplaced, and that analyses are needed of the landscape-scale, long-term consequences of multiple simultaneous trends.

TOWARD A LANDSCAPE VIEW

We believe that a long-term, landscape perspective is necessary to address some of problems discussed in the previous sections. This perspective is an essential basis for a restoration science, although many more impediments must be overcome in actually achieving restoration at the landscape scale in a democratic society. A few examples illustrate the value of a landscape perspective in providing the necessary understanding, but also hint at the difficulties. In the Pacific Northwest, study and management of salmon stocks has long occurred at the landscape scale in response to recognition that these stocks move between upper rivers and the ocean, yet restoration success has remained elusive (Williams et al. 1999). The principal environmental challenge facing the restoration efforts in Chesapeake Bay is nutrient loading in tributary watersheds; recognition of this problem has led to research and management that address both watersheds and the bay itself, although source reduction has proved difficult (D'Elia et al. 2003). Realization that management of freshwater in central Florida affects not only the Everglades but also Florida Bay has led to landscape-scale assessment and management efforts, the results of which have been mixed (McIvor et al. 1994; Redfield 2000). Although none of these efforts has been entirely successful in achieving restoration goals, there is now general acknowledgement that a landscape perspective is an essential element of solutions to large-scale problems. This perspective has not yet fully permeated thinking at CALFED.

A landscape perspective cutting across programs is specifically suitable for addressing the five key issues discussed above. Recognition of large-scale linkages can lead to consideration of new approaches to restoration or other CALFED program goals and actions, different than those arrived at from smaller-

scale perspectives. For example, flooding has historically been managed by construction of stronger, more extensive levees. An alternative approach, using floodplains to absorb the destructive energy of floods, also facilitates growth of flood-tolerant vegetation and provides habitats for salmon and other aquatic fauna. Similarly, integration of hatchery operations and ocean harvest management with restoration would enhance the probability of restoration success and provide program flexibility, while supporting moderate harvest rates.

Although a landscape perspective is invaluable, there are three reasons that it may be difficult to maintain. First, environmental scientists are generally inclined (and funded) to work on problems at tractable scales with limited scopes. For example, salmon can be affected by a broad array of factors, such as the geomorphic and hydrologic conditions that shape riparian forests, and the climatic influences that effect survival in the open ocean. That is a broad scope of endeavor for one scientist or even a small team of scientists. Second, agency jurisdictions typically focus on selected regions (e.g., the Delta) or topics (e.g., storage and transfer of water). This is true even for CALFED: although all of the major resource agencies are CALFED members, CALFED itself has no authority over such aspects of management as hatchery operations, harvest, land use, or permitting. Third, and perhaps most important, understanding and solving environmental problems is difficult enough at a local scale, but the same problems magnify tremendously at the landscape scale because of an increased number of factors that need to be considered and increased uncertainty of causal relations.

An additional challenge underlies large-scale adaptive management. Although the effects of single restoration actions at a local scale may be detected by a suitable combination of replication in time and space, there is no opportunity for rigorous replication at the broader system scale. Response variables must be aggregated across the landscape, and responses may be so confounded by natural and anthropogenic factors that signals arising from restoration may be obscured. For that reason large-scale adaptive management generally is not compatible with the principles of experimental design, even with the application

of usually suitable Bayesian approaches. Careful selection of models (Walters 1997) and innovative approaches to statistical inference (Holling and Allen 2002) may overcome this limitation, but there are few examples of successful models at the landscape level that incorporate smaller-scale processes explicitly (but see DeAngelis et al. 1998 for one example).

The solution to this dilemma is to integrate a landscape perspective with careful investigations of underlying ecosystem processes at nested smaller scales (Williams 1999), using suitable models to apply inferences drawn from results of smaller-scale investigations (Walters 1997). This stretches our paradigm well beyond a simple view of the landscape as an integrated suite of systems. It requires a clear consensus view of how outcomes at the landscape scale rest on cumulative processes at the smaller scales, together with a commitment to investigate processes at the smaller scales as part of larger-scale restoration.

CONCLUSIONS

The review papers commissioned by the CALFED Ecosystem Restoration Program and Science Program are intended to make alternative conceptual models and their assumptions clear and explicit, and present information that supports or refutes each model. Nevertheless, relying exclusively on individual models for information about how to conduct restoration would be a mistake in light of the landscape-level interactions discussed above. Moreover, policy and economic considerations may have at least as much weight as scientific considerations in deciding which actions to implement.

The current focus on relatively small-scale restoration projects fails to address the larger-scale issues that may be pivotal to program success. The system-scale conceptual model presented here illustrates the ways in which linkages and a large-scale view should be considered in restoration. These linkages include the influences of remote actions, such as the effect of ocean harvest on Chinok salmon escapement, and the interactions of hatchery operations in one watershed with protection of natural production in other watersheds. Influences from outside of the modeled system could alter trajectories on the CALFED landscape to

an extent even greater than restoration efforts or other actions within the landscape. These influences include climate change, ocean conditions, and various human activities, including responses to climate change and human population growth. Consequences of population growth and economic growth are important missing elements in the analysis of the CALFED landscape.

We suggest that these external factors should be integrated with the large-scale linkages discussed here in an effort to put CALFED, and in particular the ERP, in a broader context. This would not only assist future evaluation, but would also allow the focus of the ERP to shift, if necessary, toward actions that incorporate the broader-scale ideas that are needed to realize program goals.

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