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Author

Kimmerer, Wim

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WIM KIMMERER
ROMBERG TIBURON CENTER
SAN FRANCISCO STATE UNIVERSITY

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ROMBERG TIBURON CENTER
SAN FRANCISCO STATE UNIVERSITY

DEDICATION

I dedicate this work to the memory of Don Kelley.

KEYWORDS

Ocean, hydrology, geochemistry, tidal processes, physical forcing, fisheries, water management, water diversions, conceptual model, San Francisco Estuary, California

ABSTRACT

This paper reviews the current state of knowledge of the open waters of the San Francisco Estuary. This estuary is well known for the extent to which it has been altered through loss of wetlands, changes in hydrography, and the introduction of chemical and biological contaminants. It is also one of the most-studied estuaries in the world, with much of the recent research effort aimed at supporting restoration efforts. In this review I emphasize the conceptual foundations for our current understanding of estuarine dynamics, particularly those aspects relevant to restoration. Several themes run throughout this paper. First is the critical role physical dynamics play in setting the stage for chemical and biological responses. Physical forcing by the tides and by variation in freshwater input combine to control the movement of the salinity field, and to establish stratification, mixing, and dilution patterns throughout the estuary. Many aspects of estuarine dynamics respond to inter-annual variation in freshwater flow; in particular, abundance of several estuarine-dependent species of fish and shrimp varies positively with flow, although the mechanisms behind these relationships are largely unknown. The second theme is the importance of time scales in determining the degree of interaction between dynamic processes. Physical effects tend to dominate when they operate at shorter time scales than biological processes; when the two time scales are similar, important interactions can arise between physical and biological variability. These interactions can be seen, for example, in the response of phytoplankton blooms, with characteristic time scales of days, to stratification events occurring during neap tides. The third theme is the key role of introduced species in all estuarine habitats; particularly noteworthy are introduced waterweeds and fishes in the tidal freshwater reaches of the estuary, and introduced clams there and in brackish water. The final theme is the rather heterogeneous set of results from monitoring and research in the estuary. For example, some topics have been subjects of intense activity both in research and monitoring (e.g., physical dynamics of the upper estuary, phytoplankton blooms), while others have received little attention (e.g., microzooplankton). In addition, both research and monitoring have emphasized some regions of the estuary (e.g., the Sacramento-San Joaquin Delta) over others (e.g., San Pablo Bay). In addition, ecological modeling and synthesis has emphasized lower trophic levels over higher. Opportunities for restoration in the open waters of the estuary are somewhat limited by the lack of scientific basis for restoration, and the difficulty in detecting ecosystem responses in the context of high natural variability.

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SUMMARY

Estuarine ecosystems are extraordinarily complex, with interactions that can be observed only indirectly, and often with great difficulty. The San Francisco Estuary is one of the most-studied estuaries in the world, but it reveals its secrets slowly. Yet, we have learned a great deal about this ecosystem. In particular, recent years have seen revisions and refinements to several key conceptual models about the estuarine ecosystem. These revisions have come about through two key elements of the regional scientific enterprise: an institutional commitment to long-term monitoring; and an active, vibrant community of scientists pursuing their research interests, with substantial funding for research relevant to management of the estuary and its watershed.

This paper describes my view of the current state of knowledge of the open waters of the San Francisco Estuary, which includes waters from the mouth at the Golden Gate to the landward limit of the tides, encompassing San Francisco Bay, San Pablo Bay, Suisun Bay, and the Sacramento-San Joaquin Delta. The export of large quantities of freshwater from the tidal freshwater Delta is a major concern for management, particularly for the fish species listed under endangered species legislation. In this review I emphasize issues that seem important to management and restoration, in particular the conceptual foundations for our current understanding of estuarine dynamics, and results of recent research. I also examine opportunities and constraints for restoration of the open-water subset of the estuarine ecosystem.

The principal themes running through this paper are: (1) the central role of physical dynamics including freshwater flow in setting the stage for chemical and biological responses; (2) the importance of time scales in determining the degree of interaction between dynamic processes; (3) the key role of introduced species in the estuarine foodweb; and (4) the heterogeneity of scientific information developed by the regional research community.

The importance of physical dynamics in structuring oceanic and estuarine systems has been known for over a century, but we are still learning the details. In the San Francisco Estuary, extensive research has been conducted over the last three decades on physical dynamics and their implications. Patterns of freshwater flow, interacting with strong tidal currents and wind, produce variability on time scales from days to decades. Long-term changes in flow patterns are therefore relevant to understanding estuarine dynamics. These patterns include direct anthropogenic controls, particularly a shift in the seasonal pattern of freshwater inflow to the Delta, and an increase in freshwater exports and concomitant decrease in net outflow from the Delta into Suisun Bay, over the last five decades. An additional temporal change is a continuing trend toward an earlier runoff peak apparently due to warming of the regional climate. At the same time, sediment input to the estuary has been damped, presumably by trapping behind dams, with potential consequences for water clarity and for restoration of wetlands.

Many aspects of estuarine dynamics respond to freshwater flow, and distinguishing cause and effect has proven difficult. High river flow inundates floodplains, increases inputs of nutrients and other materials to the estuary, moves the salinity gradient seaward and compresses it, and reduces residence time of water in most of the estuary. Freshwater flow into the San Francisco Estuary is indexed by ”X2”, the distance from the Golden Gate up the axis of the estuary to where the tidally-averaged near-bottom salinity is 2. This index has proven useful not only as an index of flow, but also as a means of understanding some of the physical dynamics of the estuary. The relationship of annual abundance or survival of several estuarine-dependent species of fish and shrimp to springtime X2 values has led to a salinity standard for the estuary, as well as to an interest in the mechanisms underlying these relationships.

Our understanding of how these freshwater flow patterns play out in the estuary has changed markedly in the last decade with the development of revised conceptual models emphasizing dynamic over static conditions. For example, a previous model of the estuary depicted the Delta as a river-like system of unidirectional flows, with a flow pattern generally westward toward the ocean, and southward toward the export pumping facilities. Through field studies and simulation modeling this view has been sup-

planted by a dynamic model recognizing the key role of tides in moving water; even in the western Delta under most conditions tidal flows exceed net, river-derived flows. These tidal flows are not merely oscillations but result in intense mixing and transport of salt and other substances that can easily exceed transport due to net flows. In addition, fish are more likely to respond to tidal flows than to net flows.

The consequences of the revised view of water movement for the movement of organisms in the Delta, particularly in the vicinity of the export pumping facilities, are now being explored. Several analyses have reexamined previous assumptions about the overwhelming importance of export pumping. For example, the pumping facilities were once blamed for the decline in striped bass, but recent work has shown that the decline more likely resulted from an increase in mortality of adults, possibly due to climate effects. The analyses necessary to determine vulnerability of other fish species to effects of export pumping have not been completed.

Similarly, a lot has been learned about the Low-Salinity Zone, where freshwater and saltwater meet. Previous studies demonstrated that this was an ”entrapment zone” where particles and organisms can became concentrated. The mechanism for this entrapment was believed to be two-layer net flow in Suisun Bay, with tidally-averaged bottom currents moving up-estuary to maintain these particles in this region. However, field, model, and theoretical studies showed that such currents are infrequent in the shallow waters of Suisun Bay. More recent studies have demonstrated how dynamic processes, driven by tidal currents but also dependent on the interplay of salinity and water depth, can retain particles and organisms in various regions of the estuary, and how the behavior of organisms may contribute to their retention in the Low-Salinity Zone. These studies further demonstrated how salinity stratification forms and breaks down tidally, and how the length of the salinity gradient (indexed as X2), strength of the tides, and water depth influence stratification and two-layer flow throughout the estuary.

Similar analyses have shown that salinity stratification in South Bay is a complex response to variation in tidal energy, influenced by lowered salinity in Central Bay due to high Delta outflow, local stream inputs in South Bay, and wind. Field and modeling studies have explored the consequences of stratification in promoting phytoplankton blooms that occur predictably in South Bay during times of low tidal energy. These blooms occur because stratification traps the phytoplankton in surface waters, releasing them from light limitation, and reducing the influence of grazing by clams and other bottom-dwelling organisms. Phytoplankton blooms in South, Central, and San Pablo bays are associated with sharply increased reproduction of zooplankton. Thus, stratification has direct consequences for the estuarine foodweb.

The dynamics of estuarine organisms are generally influenced by both physical and biological interactions. Physical effects tend to dominate when they operate at shorter time scales than biological processes; when the two time scales are similar, interactions can arise between physical and biological variability. For example, the two-week spring-neap variation in tidal energy results in periods of stratification in South Bay that last several days, which is sufficient for the development of phytoplankton blooms and for responses of consumer organisms. Variation in stratification at the tidal time scale is too short to have much influence on bloom formation, but interactions at the tidal time scale may promote phytoplankton blooms in shallow water when low water level coincides with solar noon. Another example of such interaction occurs when organisms migrate vertically in synchrony with tidal currents to be on or near the bottom during the ebb and well off the bottom during the flood, which results in movement toward land. A third example is the interaction between annual cycles of freshwater flow and the reproductive cycles of some fishes, which are timed to take advantage of favorable flows or temperatures.

The San Francisco Estuary has been described as the world’s most invaded estuary. Reasons for this are being debated, although one contributing factor is the large volume of shipping from Asian ports. Introduced species have taken on key roles in a variety of habitats. An introduced aquarium plant is choking waterways of the Delta and altering the habitat to favor introduced over native fishes. Effects of introduced clams are described below. Introduced copepods appear to have altered the estuarine foodweb to become less efficient at transferring energy to fish. Smooth cordgrass, deliberately introduced to the lower estuary, is converting intertidal mudflats to marshes. In addition to the disruptions described above, unpredictable introductions make the estuarine ecosystem a moving target for both researchers and managers.

The monitoring and research results available for this review demonstrate a remarkable variety in terms of depth and breadth of coverage. This variety has arisen through a combination of varying perceptions of needs for research and monitoring, and the expertise and interests of members of the research community. In addition to the topics discussed above, the following have received considerable attention.

- *Phytoplankton Dynamics in Suisun Bay, the Delta, and South Bay.* Phytoplankton in Suisun Bay now appear to be under strong control by benthic grazers, notably the introduced Amur River clam *Potamocorbula amurensis.* Phytoplankton in the Delta are influenced by residence time so that biomass is inversely related to flow, but an unidentified loss term in the phytoplankton budget may be due to grazing by another Asian clam, Corbicula fluminea.
- *Sources of Organic Carbon for the Estuarine Ecosystem.* Recent research has shown that, although land drainage supplies a large quantity of organic carbon, phytoplankton provide most of the organic carbon actually used in the estuarine ecosystem.
- *Key Role of Benthic Grazing.* In addition to controls on phytoplankton, there is evidence that benthic grazing can have direct effects on zooplankton, and indirect effects on at least some species of fish.
- *Contaminants.* The topic of another review paper (Spies et al. in prep.), contaminants cannot be ignored here because they could have subtle effects on the estuarine ecosystem that interfere with the interpretation of other research results.
- *Fishes and Estuarine Habitat.* The Interactions of estuarine fishes with their habitat have been investigated recently, particularly for well-studied species such as striped bass, Chinook salmon, splittail, and delta smelt. The principal finding in this regard has been the importance of detailed life history and behavioral information. Interest in this topic has been amplified by the listing of two fish species under endangered species legislation, and the candidate status of two others.

There is, of course, a great deal still to learn. For example, we do not really understand the controlling factors for some of the important fishes and invertebrates of the estuary. We have almost no information on the dynamics of energy flow in higher trophic levels, or how these levels are limited by productivity at the base of the foodweb. Furthermore, monitoring programs, though extremely valuable, provide incomplete geographic coverage for some taxonomic groups, and omit other groups entirely. Monitoring is not being conducted for such key ecosystem components as bacteria, protozoans, and gelatinous zooplankton. Except for chlorophyll concentration, no programs determine biomass of the target organisms, and monitoring programs for fish provide only indices rather than estimates of abundance. Ecological modeling and synthesis have lagged far behind data-gathering, particularly for higher trophic levels. Thus, the information needed for effective management and restoration is incomplete.

Opportunities for restoration in the open waters of the estuary are more limited than in other regions of the Central Valley. In the rivers and marshes, characteristics of high-quality habitat are visible to a well-trained eye. In the estuary we can see only a few centimeters into the water, and habitat alterations can be evaluated only indirectly. Furthermore, few proposed restoration actions have an adequate scientific basis to suggest that they might be effective. The most effective restoration action in the open waters of the estuary has been the establishment of salinity standards, but these provide a benefit only on average, and the water cost may be high. The response of the system to natural influences is so strong that any benefits of restoration actions may be lost in the ”noise” and be undetectable.

The principal pathways for restoration may not be in the open waters at all. Although it seems unlikely that actions to restore rivers will have a great effect in the estuary, restoration of adjacent wetlands could have beneficial effects. However, there are many pitfalls not only in wetland restoration but also in their likely effects on the open-water system. Restoration of subtidal or freshwater intertidal habitat may not benefit the targeted native species if these habitats are occupied by introduced species. The best prospects for restoration may be on floodplains. Clearly the research on efficacy of marsh restoration should continue, and should be linked with work in open waters.

INTRODUCTION

Estuaries are sites of intense and conflicting human activity. Many of the world's estuaries and their watersheds are urbanized, with heavy demands on estuaries for freshwater, food, transportation, recreation, and waste disposal. Watersheds of many estuaries also support extensive agriculture, which likewise requires water and transportation and must dispose of wastes. Because of the conflicts arising from these and other competing uses, and because of growing awareness of the ecological and economic value of estuaries and the consequences of their many uses, many estuaries are also the subject of intense management interest and activity. Efforts to reverse or mitigate for past damage, restore natural landscapes, and reverse the decline of special-status species have gone hand-in-hand with efforts to understand estuarine ecosystems and their responses to human actions. However, estuaries are also ecologically complex, with often intense seasonal and interannual variability and spatial gradients in many key properties. This complexity makes them difficult to study, so that despite substantial efforts, estuaries remain relatively poorly understood.

The San Francisco Estuary fits all of the general descriptions above. It is highly variable, thoroughly modified, heavily used for a variety of purposes, and intensely studied. The San Francisco Estuary and its watershed are now the subject of one of the most ambitious rehabilitation efforts ever undertaken, the CALFED Bay-Delta Program.

This paper presents my view of the current state of understanding of open-water processes of the San Francisco Estuary. I present this in the context of estuarine science in general, focusing on major gaps in knowledge and on issues that may be important in restoration or rehabilitation. The scope of this paper is limited, and other review papers will address issues not included here. This paper discusses the tidal waters of the estuary, and it does not address marshes or tidal wetlands (see Brown 2003a, 2003b, 2003c; Orr et al. 2003; Davis et al. 2003). Most contaminant issues are not addressed (Spies et al. in prep.), and several fish species are being examined in species-specific reviews (Bennett in prep.; Moyle et al. in prep.; Williams and Yoshiyama in prep.). In addition, the history of human development of the estuary is given only incidental coverage, since the subject has been covered elsewhere (e.g., Skinner 1962; Hedgpeth 1979; Nichols et al. 1986).

The San Francisco Estuary is an extreme case among estuaries in such respects as extent of invasions by introduced species, extent of modification of the watershed and fringing marshes, rather peculiar bathymetry, and large interannual and seasonal variation in freshwater flow. What generalizations can be drawn from such an estuary and, conversely, what information from other estuaries can be brought to bear here? A few examples should suffice to demonstrate that certain principles apply in many estuaries, and that some of these principles may be most readily developed in an estuary where variability is large and therefore the signal-to-noise ratio is high. First, Cloern and colleagues (e.g., Cloern 1996) have developed a detailed conceptual model of phytoplankton production in turbid estuaries, based on work in the San Francisco Estuary but applicable in many locations. Similarly, ideas about benthic control of estuarine phytoplankton were also developed initially by Cloern and have been elaborated by several other researchers in the San Francisco Estuary and elsewhere. Information flow has been equally rich in the opposite direction. For example, early ideas about estuarine circulation (Postma and Kalle 1955; Festa and Hansen 1978) have been extensively applied and modified in the San Francisco Estuary (e.g., Peterson et al. 1975; Arthur and Ball 1979; Cloern et al. 1983; Kimmerer et al. 1998). Concepts about effects of salinity on estuarine zooplankton developed in the Saint

Lawrence Estuary (Laprise and Dodson 1993) have proven very valuable in understanding patterns in the San Francisco Estuary (Kimmerer and Orsi 1996; Kimmerer et al. 1998).

Thus, the San Francisco Estuary can be understood as a particular case of this rather heterogeneous class of environments.

THE SAN FRANCISCO ESTUARY

Descriptions of the geography, hydrology, environmental conditions, and general biology can be obtained from several excellent compendia (e.g., Conomos 1979b; Cloern and Nichols 1985a; Nichols et al. 1986; Hollibaugh 1996). Here I present a brief overview of the environmental setting of the estuary, and summarize some of the key themes that run through those and other descriptions of the estuary.

The San Francisco Estuary (Figure 1) is a drowned, tectonically reshaped river valley. Geology and topography of the region are complex owing to alternating periods of subduction and transform movement at the boundary between the North American and Pacific tectonic plates over the past 100-200 million years, and alternating periods of high and low sea level in the past 1 million years (Atwater 1979). South, Central, and San Pablo bays (Figure 1) were shaped in part by movements of the San Andreas fault to the west and the Hayward fault to the east, which caused the intervening block of crust to be overridden and forced downward, resulting in a broad region of low topography between segments of the coast range (Atwater 1979). Locations where the Bay penetrates the coast range, at the Golden Gate and Carquinez Strait, are constricted and deep, with steep bathymetry. These locations separate the estuary into its major basins (Figure 1, Table 1).

The San Francisco Estuary receives flow from the Sacramento-San Joaquin river system, which drains about 40% of the area of California. Water enters the estuary in the Sacramento-San Joaquin Delta. In contrast to river deltas such as those of the Nile and Mississippi, this Delta formed when sea level rose, forming the present-day estuary, and marshes formed at the landward margin because accumulation of sediment and plant detritus kept pace with submergence (Atwater et al. 1979). The Delta marshes were drained and diked for conversion to farms during and after the Gold Rush. The Delta is now a mosaic of diked islands surrounded by deep channels, as well as smaller sloughs and shallow lakes. The land surfaces on many of the islands have subsided up to 10 m below sea level because of compaction, oxidation, and erosion of the peat soils (Jassby and Cloern 2000). Levees on several of these islands have failed, converting them to tidal lakes with various degrees of connection to the surrounding channels. This habitat type would not have existed in the pre-settlement Delta. Most Delta channels are constrained within the levees, and shallow habitats are limited to backwater sloughs and narrow margins of channels and lakes. Some of the channels have been deepened and straightened by dredging either for shipping or for more efficient water transfer.

Table 1. Size and bathymetry of sub-embayments of the San Francisco Estuary. Data for Suisun Bay to South Bay from Jassby et al. (1993) for mean lower low water, with the boundary between Central and South Bay at the Bay Bridge. Data for the Delta provided by A.D. Jassby (U.C. Davis, pers. comm., June 2000).

		Depth		
Region	***Area km^2***	***Mean m***	***Median m***	***Volume 10^{9}m^3***
Delta	215	5.7	-	1.2
Suisun Bay	100	3.1	1.8	0.3
San Pablo Bay	260	3.3	1.5	0.9
Central Bay	220	11.0	7.7	2.5
South Bay	470	4.0	2.2	1.9
OVERALL	1235	4.6	–	5.8

The remainder of the estuary comprises four broad, shallow basins with one or two deeper channels that were naturally formed but in some locations are dredged for shipping. The northern estuary including San Pablo and Suisun bays and the Delta is a river-dominated estuary, while the South Bay is a weakly-mixed lagoon.

California's Mediterranean climate heavily influences physical and biological conditions in the estuary. Nearly all of the precipitation falls during the winter-spring wet season, mostly due to cold fronts sweeping in off the Pacific Ocean. Most of the freshwater flow

Figure 1. Map of the San Francisco Estuary showing major basins and locations discussed in the text. The darker blue is water deeper than 10 meters. Numbers in blue refer to distance in kilometers up the axis of the estuary from the Golden Gate Bridge. Text and symbols in red refer to barriers in waterways including either permanent with movable openings (open box) or temporary rock barriers (solid box). Text in white indicate major diversions from the Delta.

into the estuary occurs in winter and spring, although extensive water development projects have reduced the winter-spring flow into the estuary and increased flow in summer and early fall. Summers are hot inland of the coast range (i.e., east of Carquinez Strait, Figure 1) and cool and foggy to the west because of cool, southward-flowing coastal currents and coastal upwelling. The summer temperature gradient produces a large-scale east-west pressure gradient across California, resulting in strong westerly afternoon winds across much of the estuary.

Extensive human modifications to the estuary (Nichols et al. 1986 have included: the diking and isolation of about 95% of the estuary's wetlands; introduction of numerous species; reduction or, in a few cases, elimination of stocks of fish and invertebrates; alteration of bathymetry and introduction of contaminated sediment through hydraulic mining in the watershed; reduction in sediment supply due to damming of all of the major rivers in the watershed; disposal of agricultural and urban waste including numerous toxic substances; and alteration of the seasonal pattern and quantity of freshwater flowing into the estuary. The alterations to flow include two large pumping plants in the south Delta and numerous small agricultural diversions throughout the Delta.

Present-day uses of the estuary include extractive uses such as the diversion of freshwater, diversion of salt water into salt ponds, sport and commercial fisheries, and sand dredging. Additional uses with potentially negative impacts include discharge of sewage, industrial waste, and urban runoff, and transportation by ships, ferries, and small boats. Passive uses include recreational uses of the estuary and its margins, and more generally the enjoyment of the estuary's scenic qualities. The economic value of these ecosystem services has not been estimated.

Several features of the estuary shape the functioning of the ecosystem as well as the level of understanding of its function. These features taken together make this estuary unique and could limit the degree to which inferences can be drawn and generalized to broad classes of estuaries. I introduce these features briefly here and discuss them at greater length elsewhere in the paper.

Introduced Species

Introduced species now make up the bulk of both species and individuals in samples taken in various habitats in the estuary. The San Francisco Estuary has been called the most invaded estuary in the world (Cohen and Carlton 1998), and new species are identified continually. Introductions occur through a variety of pathways including discharge of ballast water, inadvertent or deliberate release of aquarium organisms, deliberate introduction for fisheries, and inadvertent release with bait organisms. Studies of the estuarine ecosystem are aiming at a moving target, and conclusions from one study may cease to apply after the next significant introduction. These introductions could limit the extent to which the estuary can be restored to a more desirable state, since in nearly every group of biota introduced species have significantly altered the function of the ecosystem.

Toxic Contaminants

Toxic contaminants continue to pose a difficult problem (e.g., Kuivila and Foe 1995; Flegal et al. 1996; Spies et al. in prep.). Several examples of contaminant effects on local populations have been identified (Hornberger et al. 2000), and contaminants in water and sediments often exceed levels considered detrimental to organisms (Bennett et al. 1995) or humans (Davis et al. 2002). The problem is exacerbated by the large number of different contaminants entering the estuary and the paucity of knowledge about their effects, particularly in the case of agricultural chemicals. Although this paper does not address contaminant effects in any detail, results of experimental or field studies on other ecological issues could be influenced by unseen effects of contaminants.

The Complex Bathymetry

The complex bathymetry of the estuary has had profound effects on circulation patterns, and thereby on the transport of materials and organisms. Only recently have the implications of the peculiar bathymetry of the estuary for its ecology been explored (Monismith et al. 1996, 2002; Burau 1998).

Freshwater Flow

Freshwater flow is highly variable both within and among years, has been heavily altered by dams and diversions, and appears to be changing in seasonal pattern in response to climate change. Principal among the diversions are the federal and state water export facilities in the southern Sacramento-San Joaquin Delta (Figure 1). Because most of the precipitation falls to the north of the Delta and most of the demand is south of the Delta, the river-Delta system during the dry season is essentially a conveyance system for moving water from reservoirs in the north to farms and cities in the south. The Delta itself is a tidal region that is home to a number of species of concern. This situation has led to conflicts over water use and potential harm to endangered species, which provided the major impetus behind the CALFED restoration program.

Availability of Data

Availability of data on the San Francisco Estuary ranges from excellent to none. The conflicts over water use and potential harm to species of concern led federal and state agencies to establish long-term monitoring programs focused mainly on the Delta and Suisun Bay. These have provided an extraordinarily valuable record of changes in the estuarine ecosystem, particularly in abundance and distribution of fish, zooplankton, phytoplankton, and benthos, and in water quality. In addition, a strong research program at the U.S. Geological Survey has produced numerous research articles and greatly enhanced knowledge of the estuary, particularly regarding nutrients, circulation, phytoplankton and benthic ecology, and contaminants. However, major gaps still exist for several topics (e.g., microzooplankton, microbenthos, benthic microalgae), and spatial and temporal coverage is uneven among programs. Data sources are listed in Table 2.

Ecosystem Boundaries

I use "San Francisco Estuary" to mean the entire estuarine ecosystem, extending from some distance outside the Golden Gate to the upstream extent of tidal penetration in the Delta (Figure 1). This is an operational definition of the ecosystem, based on the extent of various studies of the estuary. However, it could be argued that both of these boundaries delineate approximate points where geographic, physical, chemical, and biological properties change qualitatively. Within these boundaries are other locations where conditions change, most notably at the interface between fresh and brackish water. However, these gradients move substantially within and between years, and the Delta and lower estuary are strongly connected through the opposing forces of tide and freshwater, the two-way flux of materials, and the movement of organisms. On the other hand, combining the estuary with either the watershed or the coastal ocean arguably defines a landscape rather than an ecosystem.

The Importance of Scale

Numerous ecologists and oceanographers have discussed the importance of time and space scales in the operation of complex systems (e.g., Levin 1989; Powell 1989). In general, when two processes operate at similar time and space scales in the same location, interactions between them may produce noticeable effects. Many processes operate at diurnal and annual scales, and there are numerous examples of interactions. Several time scales are especially relevant for organisms, including time scales for behavior, growth rate, reproductive cycle, and life span. All of these biological time scales tend to be proportional, so that short-lived organisms do everything faster than others, provided temperature dependence of rate processes is taken into account.

Figure 2 shows estimated time scales for a number of important processes in or influencing the estuary. For example, variability in tidal kinetic energy on scales of days to weeks interacts with the development of phytoplankton blooms on the same scale (Lucas et al. 1999b). Similar interactions can be seen in, for example, interactions at the tidal time scale between current velocity and vertical position of zooplankton and larval fish (Kimmerer et al. 1998), or between the annual timing of reproduction by fish and the hydrologic cycle.

Mismatches in scale can be informative too. For example, the time to double Delta inflow during a storm is on the order of a day to a week; that to halve Delta inflow after a peak is nearly twice as long; and the response time of the estuarine salinity distribution is about two weeks (Figure 2). This implies that the estuary's physical response to changes in flow will generally be at the longer time scale, and the same is probably true for biotic responses to high-flow events. Water residence time in the South Bay is long compared to many of the biological time scales, while residence time in the northern estuary (i.e., the entire tidal reach from the mouth of the estuary through the Delta) can be long or short depending on freshwater flow. When residence time is long we can expect that most of the variability we see in estuarine conditions (relative to the salt field) will be dictated by internal biotic and chemical interactions rather than by large-scale physical forcing.

This theme of temporal scales is addressed in much of the recent research on the estuary, and recurs throughout this paper. However, not all of the research and monitoring conducted in the estuary is on a time and space scale appropriate for the questions being addressed, particularly for questions retrospectively addressed using previous research and monitoring results.

Links to Management and Restoration

Scientific knowledge about the estuary is linked to its management and restoration in two key ways. First, this knowledge (with its complement, uncertainty) is being used to inform management decisions. Second, management needs form a basis for funding and prioritizing research and monitoring, resulting in progress toward understanding. Although numerous government and non-government programs conduct management or restoration activities in the San Francisco Estuary, two programs dominate in terms of scale. The Interagency Ecological Program (IEP), a consortium of nine state and federal agencies, is tasked with assessing the effects of the major water development projects on the estuarine ecosystem. Linkages between the IEP and management groups within the member agencies provide feedback on effects of management activities. IEP established several

Table 2. Sources of data used in this paper.

Data	*Agency*	*URL or source*
Freshwater flow variables	DWR	http://www.iep.water.ca.gov/dayflow/
Unimpaired flow	DWR	DWR 1994 and http://cdec.water.ca.gov/cgi-progs/iodir/wsihist
Tidal height predictions	Standard NOAA predictors	http://tbone.biol.sc.edu/tide/
Tidal height	IEP NOAA	http://iep.water.ca.gov/cgi-bin/dss/ http://co-ops.nos.noaa.gov/
Wind velocity	Integrated Pest Management IEP	http://www.ipm.ucdavis.edu/ http://www.iep.water.ca.gov
Continuous air and water temperature, salinity; tidal flux	IEP	http://iep.water.ca.gov/cgi-bin/dss/
Sediment concentration	USGS	http://sfports.wr.usgs.gov/Fixed_sta/
Chlorophyll concentration	IEP/DWR and DFG	http://www.iep.water.ca.gov
Chlorophyll concentration, oxygen saturation	USGS	http://sfbay.wr.usgs.gov/access/
Zooplankton abundance	IEP/DFG	L. Mecum, DFG, pers. comm.
Fish abundance	IEP/DFG	
SF Bay Study		K. Hieb, DFG, pers. comm.
Fall midwater trawl		http://www.iep.water.ca.gov/data.html
Summer townet survey		http://www.iep.water.ca.gov/data.html
Benthos abundance	IEP/DWR	http://www.iep.water.ca.gov/data.html

Abbreviations: IEP, Interagency Ecological Program for the San Francisco Estuary; USGS, U.S. Geological Survey; DFG, California Department of Fish and Game; DWR, California Department of Water Resources. All agency sampling programs take basic water quality measurements such as salinity and temperature, and most take Secchi depth.

monitoring programs, now 2 to 3 decades old, that provide an invaluable source of information on spatial and temporal trends in abundance of some species, and certain water quality variables.

The CALFED Bay-Delta Program, also a consortium of state and federal agencies, is tasked with restoring or rehabilitating the watershed and estuarine ecosystems, as well as improving the provision of ecosystem services such as a reliable supply of high-quality water

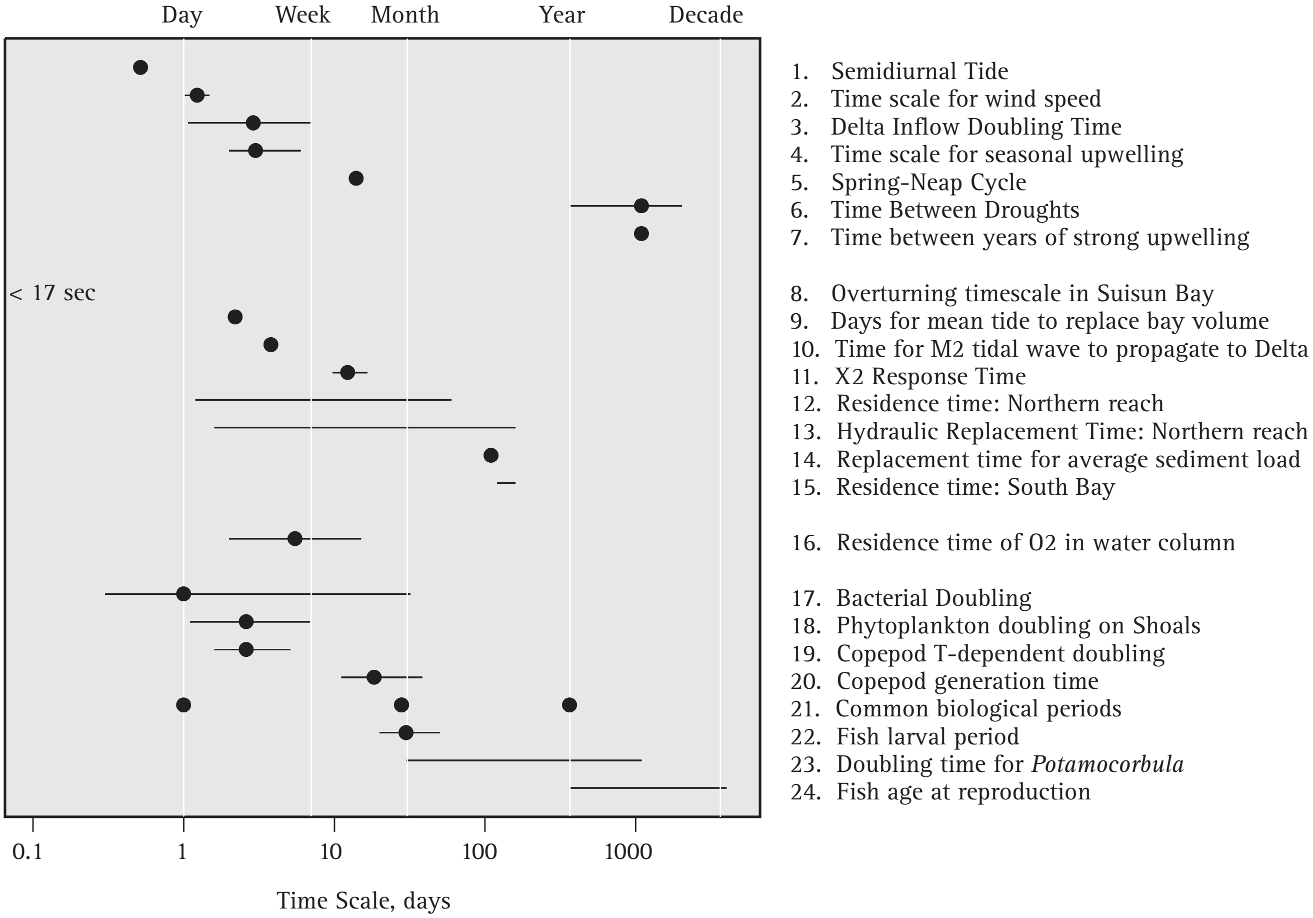


Figure 2. Time scales of selected variables identified by number: 1-7, external forcing; 8-15, physical response; 16, chemical response; 17-24 biological response. Horizontal lines give ranges or similar statistics, while symbols give point estimates.

Sources of data by line number:

1. Lunar semidiurnal tidal period
2. From autoregressive analysis of ocean wind data
3. Annual maximum change in total inflow over 5-day periods
4. Autoregressive analysis of each year's April-Sept upwelling index
5. Lunar cycle
6. Mean time between unimpaired flow < 800 m^3 s^{-1}
7. Autocorrelation peak from upwelling data
8. Burau 1998 Figure 17
9. Conomos et al. 1985 Table 2
10. Walters et al. 1985 Figure 4
11. Jassby et al. Equation 2
12. Walters et al. 1985
13. Walters et al. 1985
14. Krone 1979, Table 1; Buchanan and Schoellhamer 1999, Table 1
15. Walters et al. 1985
16. Hartman and Hammond 1985 for 3.5 m water column
17. Hollibaugh and Wong 1996
18. Cloern et al. 1985 Table 1
19. Huntley and Lopez 1992
20. Huntley and Lopez 1992
21. Diurnal, lunar, annual cycles
22. Houde 1989
23. Doubling time for biomass; J. Thompson, USGS, pers. comm.
24. Emmett et al. 1991

and stability of levees. The CALFED ecosystem restoration program (ERP) is expected to take several decades and to cost several billion dollars, and is therefore one of the most ambitious such programs in existence.

To date most of the focus of restoration has been on the watershed and on tidal wetlands. Restoration of open water, subtidal areas of the estuary is hampered by our poor understanding of how these systems work and what can be done to improve them. Although the knowledge base has improved greatly in the last decade, the opportunities for restoration in open waters remain unclear.

In the following section I focus on the state of the science, and then return to the linkage between scientific knowledge and the restoration of ecosystem functions.

CURRENT SCIENTIFIC UNDERSTANDING

Our understanding of the San Francisco Estuary rests on two pillars: the general science of estuarine ecology, and specific research, monitoring, and model development in this specific estuary. Like any other branch of science, estuarine ecology has certain generally accepted conceptual models that can be useful in placing into context the studies done in a specific estuary. However, complex environments such as estuaries often seem not to obey general rules, but to respond in specific ways for which the general literature on estuaries provides little guidance. For example, much of the literature on estuaries is from temperate zones in eastern North America and Europe, where precipitation and runoff occur year-round, and where the principal concern for the condition of estuaries is generally eutrophication. Neither of these conditions is true in the San Francisco Estuary.

Substantial research and monitoring efforts by USGS, IEP, and numerous academic researchers have led to the development of an estuary-specific body of knowledge and even a revision of some estuarine paradigms. In addition, this work has led to refinement or revision of several key conceptual models which have an important bearing on restoration.

The general theme is the importance of the physical environment in setting the stage for the chemical and biological interactions in the estuary. Tidal flows and freshwater flow affect every aspect of the estuarine ecosystem. A thorough understanding of these flows is therefore essential if we are to make any sense of the ecological patterns we are trying to understand.

THE PHYSICAL ENVIRONMENT

Estuaries in general are strongly influenced by the physical regime. Important influences include variation in freshwater flow (e.g., Postma 1967; Malone et al. 1988; Livingston et al. 1997), tidal stirring (e.g., Ketchum 1954; Wooldridge and Erasmus 1980; Haas et al. 1981), and salinity distribution (Remane 1971).

Conomos et al. (1985) provide a general description of conditions in the estuary, including seasonal weather and flow patterns, tides, and some information on the physical responses of the estuary. Physical conditions in the estuary respond at different time and space scales to a variety of external physical influences or forcing, including freshwater flow, wind, and ocean conditions including tide, mean sea level, and ocean salinity (Cloern and Nichols 1985b; Walters et al. 1985; Walters and Gartner 1985). The response of the estuary to these forcings is strongly influenced by morphology (Monismith et al. 2002), including bathymetry and tidal prism, which can be altered by human activities such as dredging and the construction and removal of levees (Enright et al. 1998).

The principal mechanism of human control over the estuarine ecosystem arises through alteration of freshwater flow. As discussed below, the San Francisco Estuary represents an extreme both in the economic value of freshwater for urban and agricultural use, and the extent to which the estuarine ecosystem responds positively to freshwater flow (Kimmerer 2002b).

Freshwater Flow

Estuaries are defined by the mixing between rivers and oceans. Variability in freshwater flow can influence the physical, chemical, and biological components of estuaries in numerous ways (Drinkwater and Frank 1994; Kimmerer 2002a, 2002b). The response of estuaries to variation in freshwater flow has received considerable attention in the scientific literature (Montagna et al. 2002), particularly with reference to the cessation of flow to some estuaries such as the Nile (e.g., Aleem 1972; Skreslet 1986). With the exception of such extreme cases, the biota of the San Francisco Estuary may have one of the strongest and most consistent responses to flow among large estuaries (Kimmerer 2002a).

Freshwater supply to the San Francisco Estuary depends on highly variable precipitation patterns and the effects of extensive water development projects upstream and within the Delta. These water projects include the federal Central Valley Project (CVP) and the State Water Project (SWP), as well as numerous water diversions spanning a range of sizes throughout the Central Valley. Each includes large reservoirs in the foothills surrounding the Central Valley whose purposes are flood control during the winter and storage and release of water during the rest of the year. The CVP and SWP each have large pumping plants in the southern Delta which export water to the Delta-Mendota Canal and California Aqueduct, respectively, to supply water for farms and cities to the south of the Delta.

Several calculated flow variables are useful in illustrating key patterns. Most of these are presented here on the basis of water year, which begins on October 1 to include most or all of the winter-spring runoff peak in a single year (e.g., water year 2003 began in October 2002).

Monthly unimpaired flow, calculated by DWR for 1921-1992, is the quantity of flow that would enter the Delta with all state and federal dams and diversions removed, but otherwise the current level of development (see Fox et al. 1990). This variable is useful for determining trends in the availability of precipitation to the watershed, although it does not mimic natural flows. To extend the temporal range of this variable I calculated a regression of annual unimpaired flow on the "eight-river index" (DWR 1994), which is unimpaired flow in the Sacramento and San Joaquin rivers and major tributaries for 1906-2002. The annual volume of unimpaired flow has no time trend (Figure 3A). However, the fraction of this flow that occurred in spring-summer has decreased, and that in winter increased, over the period of record (Figure 3B). This trend is apparently related to atmospheric warming resulting in earlier snowmelt in recent decades (See "Climate Change", p35). The capacity of the storage reservoirs in the Central Valley is approximately 29 km^3, close to the median annual unimpaired flow volume of 34 km^3.

Details of flow patterns within the Delta are presented below, but it is useful to highlight some of the key features here for understanding gross patterns of freshwater movement in the estuary. Freshwater enters the Delta via the Sacramento and San Joaquin rivers

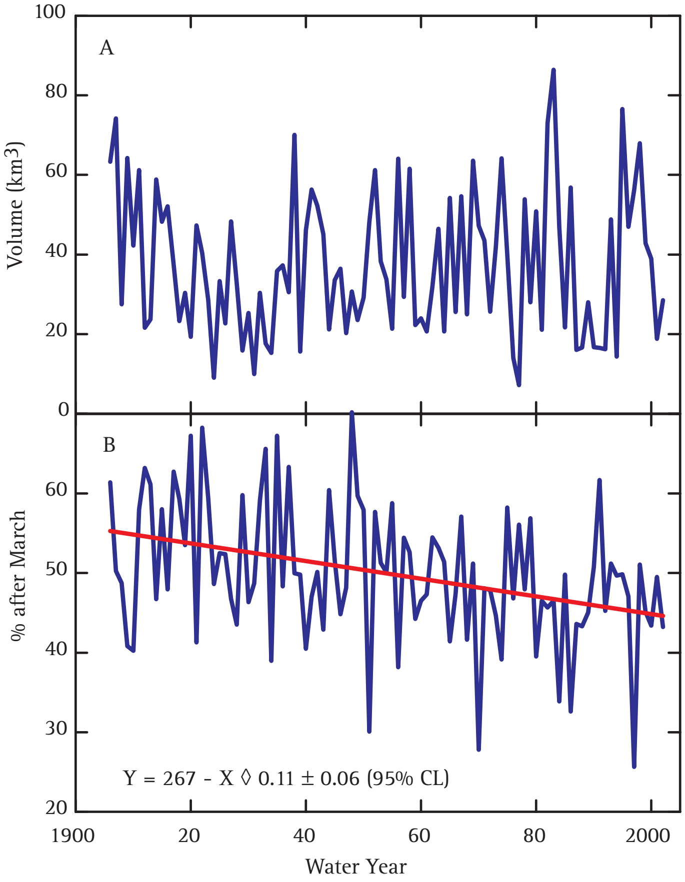


Figure 3. Estimated unimpaired flow for 1906-2002. A., Annual unimpaired flow calculated by regression from the Eight River Index on estimated unimpaired flow for 1921-1992 (DWR 1994): Unimp = - 3.3 + 8River x 1.38 ± 0.016 (95% CL), prediction MSE = 0.84 km^3 . B., Percent of total flow for water year that flowed after March, i.e., April through September. Red line is a significant linear regression ($p < 0.001$).

and several smaller rivers (Figure 1) as well as local precipitation. Freshwater leaves the Delta by advection and dispersion to the lower estuary, through export pumping at the large state and federal pumping plants in the south Delta and the smaller Contra Costa Water District and North Bay Aqueduct diversions (Figure 1), and by consumption within the Delta. The principal flow variables in the Delta are: freshwater inflow, the sum of all the river flows into the Delta; export flow; and net Delta outflow, the difference between inflow and export flow less net consumption in the Delta. The California Department of Water Resources (DWR) calculates these and several related quantities daily in their DAYFLOW water accounting program. River flow data come mainly from gages, and export flows are known accurately; however, at low levels net Delta outflow has considerable uncertainty.

The water projects have clearly affected the seasonal patterns of flow into the estuary (Kimmerer 2002b). Springtime flow has decreased significantly relative to unimpaired flow because of shifts in water project operations each year from flood management in winter, during which reservoirs are kept at relatively low levels, to water storage in spring, when much of the flow is captured for subsequent irrigation. In addition, flow in summer and early fall is higher than unimpaired flow to support demand for irrigation and urban use, much of which is met by releases from reservoirs into the rivers and subsequent recapture and export from the Delta (Arthur et al. 1996). The result is an annual cycle of net storage in spring and net release in summer-fall, with a long-term trend toward increasing amplitude (due to increasing storage capacity) and a shift from storage to release that has occurred progressively earlier in spring (Kimmerer 2002b Figure 4).

Given the extent and magnitude of the water projects, it may seem paradoxical that most of the interannual variability in flow patterns in the estuary is due to variability in precipitation. The correlation between annual unimpaired flow and annual inflow to the Delta was 0.97 for water years 1956-2002, and the annual inflow averaged 80% of the unimpaired flow with no time trend. The close correlation of unimpaired flow and inflow is due to the overwhelming effect of high-flow events (Figure 4), which are largely passed through the reservoirs.

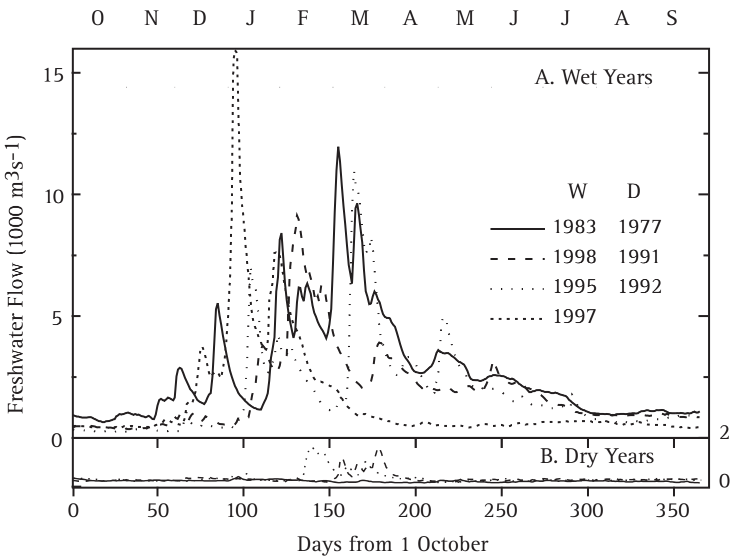


Figure 4. Daily inflow to the Delta for the three wettest and three driest years on record plus 1997. (Kimmerer 2002b)

Delta inflow comes from three main proximate sources: the Sacramento and San Joaquin rivers, and the Yolo Bypass, a managed floodplain of the Sacramento River (Figure 1). The proportions of flow from these sources vary with the total inflow (Figure 5). At very low flows, most of the flow comes from the Sacramento River; this occurs during dry summers when most of the water in the San Joaquin watershed is diverted, and Sacramento River water is being used to support export pumping from the Delta. At higher levels of inflow, the contribution of the San Joaquin can be substantial, and if the Yolo Bypass floods, its contribution can equal that of the two rivers.

Inflow and outflow are closely correlated (Figure 6A, 6B; Correlation coefficients of 0.998 in spring and 0.91 in summer) again reflecting the overriding influence of climate on freshwater flow patterns. Export flows increased up to the early 1970s after which export flows have fluctuated between broad limits, although the highest historical values occurred in summer 1999 (Figure 6C, 6D). In summer the ratio of export flow to inflow has consistently exceeded 50%, but daily export flow still comprises less than 3% of the volume of the Delta, and in spring averages about 1% (Figure 6C, 6D). The ratio of outflow to inflow has an overall mean of about 70%, but varies by season and has a declining time trend (Figure 7A, 7B).

An additional flow-related variable is X2, the distance from the mouth at the Golden Gate up the axis of the estuary to where tidally-averaged bottom salinity is 2 practical salinity units (psu) (Jassby et al. 1995). [Note regarding salinity units: strictly speaking salinity on the Practical Salinity Scale (UNESCO 1981) is a ratio and therefore unitless, but many authors use psu or practical salinity units where needed for clarity]. This variable, used to index the physical response of the estuary to changes in freshwater flow, is closely and inversely related to outflow with a time lag of about two weeks (Figure 8). The response of X2 to flow is discussed below.

Much has been written on seasonal and interannual patterns of freshwater flow and the influence of the water projects on these patterns (Nichols et al. 1986; Peterson et al 1989; Fox et al. 1990). Oddly, there is not general agreement on the nature of these influences, partly because the water projects were developed concurrently with trends in regional climate and patterns of precipitation (Dettinger and Cayan 1995; Arthur et al. 1996). However, there are also clear differences in perception of the roles of the water projects in altering the rate of freshwater flow into the estuary (e.g., Fox et al. 1990; Peterson et al. 1995).

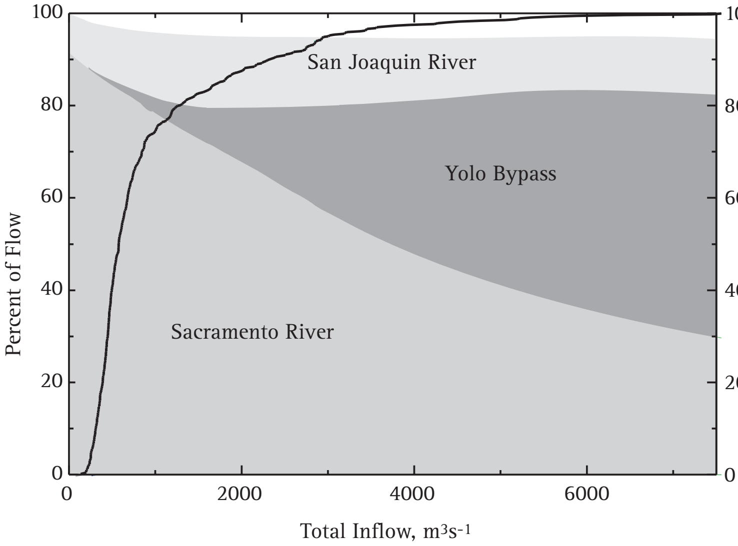


Figure 5. Proportion of inflow to the Delta from different sources based on monthly flow from water years 1956-2002 from the Dayflow program (http://iep.water.ca.gov/Dayflow). Remaining inflow is from small tributaries on the east side of the Delta (e.g., Mokelumne, Cosumnes). The black line is the cumulative percent frequency, i.e. the percent of inflow less than or equal to that value.

It is tautological that exports of freshwater from the basin reduce the quantity of water that would otherwise flow into the estuary on an annual basis, under the current level of development in the Central Valley. Prehistoric salinity records suggest an annual average inflow to the estuary over the last two millennia of ~1250 $m^3 s^{-1}$ (Ingram et al. 1996a), similar to the current unimpaired flow of about 1195 $m^3 s^{-1}$ (mean of estimated values from 1906 through 2002). Export flow averaged 185 $m^3 s^{-1}$ from 1975 through 1999, or about 16% of unimpaired flow during that period.

Some confusion also exists in the literature regarding the relationship between export flow and Delta outflow. For example, Peterson et al. (1996) implied that exported water would otherwise have flowed into the estuary, i.e., there should be an inverse relationship between export flow and outflow. In fact, export flow is weakly and nonlinearly related to inflow (Figure 9), decreasing when inflow is either very high, presumably because of lack of demand, or very low, because of lack of water, or to meet outflow or salinity standards in the Delta. There is no inverse relationship between outflow and export flow at the lower end of the outflow range.

The ratio of export flow to inflow, or E:I ratio, has been used in management as a measure of the relative magnitude of pumping. Analyses of the combined effects of flow conditions on salinity (Peterson et al. 1995) and survival of striped bass (Jassby et al. 1995) and salmon (Newman and Rice 2003) have used the E:I ratio as a covariate with outflow. The rationale for using export:inflow ratios for these analyses is that export flow should be scaled to the quantity of water flowing into the Delta. However, this scaling implicitly assumes an advective environment in which river-derived net flows dominate, which is not the case when freshwater inflow is low. Furthermore, since export flow is weakly related to inflow, the ratio of export flow to inflow is strongly correlated with inflow and therefore outflow (Figure 6 C, 6D). Thus putting both variables in a statistical model can make results difficult to interpret. Both salinity (Peterson et al. 1975, 1989; Jassby et al. 1995) and striped bass

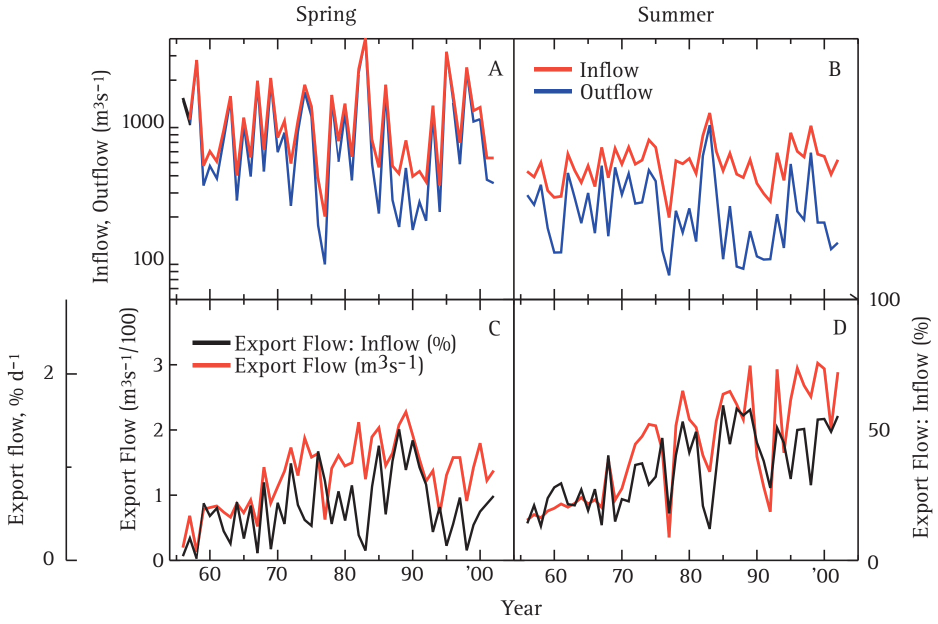


Figure 6. Time courses of flow variables averaged over spring (April-June, left panel) or summer (July-October, right panel) of each year: A, B delta inflow (narrow red line) and outflow (heavy blue line); C, D Export flow (heavy red line) and export:inflow or E:I ratio (narrow black line). Export flow is also given as a daily percentage of the volume of the Delta (far left axis).

survival (Stevens et al. 1985; Kimmerer et al. 2000) are strongly related to outflow. Analyses of effects of outflow (or X2) together with export flow (not export: inflow ratio) have revealed nonexistent (salinity; Kimmerer unpublished) or very weak (striped bass survival, Kimmerer et al. 2001) effects of export flow.

Tidal Effects

Tides in the San Francisco Estuary are mixed semidiurnal, with a median daily tidal range of 1.8 meters. Additional short-term effects as well as subtidal variation in sea level (i.e., variation with a longer period than the tidal cycle) in the coastal ocean are produced by variation in atmospheric pressure and wind setup along the coast, particularly in the variation in wind conditions that causes upwelling and relaxation (Wang et al. 1997). These variations in sea level have measurable effects on tidal height in the estuary and can be important in exchange between the estuary and the coastal ocean (Walters and Gartner 1985). The spring-neap tidal cycle, resulting from the interference pattern between tidal components of similar period, causes variation in tidal energy and filling and draining of the estuary on a two-week time scale (Walters and Gartner 1985). This cycle has important consequences for stratification and for measurement and interpretation of net flows in the Delta.

The tide moves as a seiche or standing wave in the South Bay, and as a combination standing and progressive wave in the northern estuary (Walters et al. 1985). This means that the tidal currents are in phase with tidal height in the northern estuary (Figure 9A) but not in South Bay (Figure 9B); correlation coefficients between tidal height and current for predicted tides in 2003 were 0.86 for Carquinez Strait and 0.37 for the San Mateo Bridge (Figure 1). The seiching action in the South Bay means that tidal heights generally increase, and timing does not change much, with distance from the Golden Gate south to the Dumbarton Bridge (Figure 10). In the northern estuary the time of high tide lags that at the Golden Gate by up to 8 hours, and the height of the high tide decreases with distance, particularly through Carquinez Strait (Figure 10).

At any point in the estuary the water level is a function of tidal forces due to the fluctuation in sea level at the mouth of the estuary, and to effects internal to the estuary, mainly freshwater flow. These effects can be seen in tidal predictions and records for Port Chicago (Figure 1), filtered to remove the daily and shorter periods, from wet and dry years (Figure 11). In dry years predicted fortnightly spring-neap cycles fluctuate between large ranges around December and June and smaller ranges in March and September. These cycles result in filling and draining of the estuary at that time scale and are the source of substantial variability in currents. In addition, there is an annual cycle by which tidal elevation overall is highest in February and August. The measured tide roughly follows the predicted tide during dry periods, with additional variability probably due to month-scale variation in sea level and local wind effects (Walters and Gartner 1985). During wet periods the astronomical signal is swamped by the effect of increased river stage.

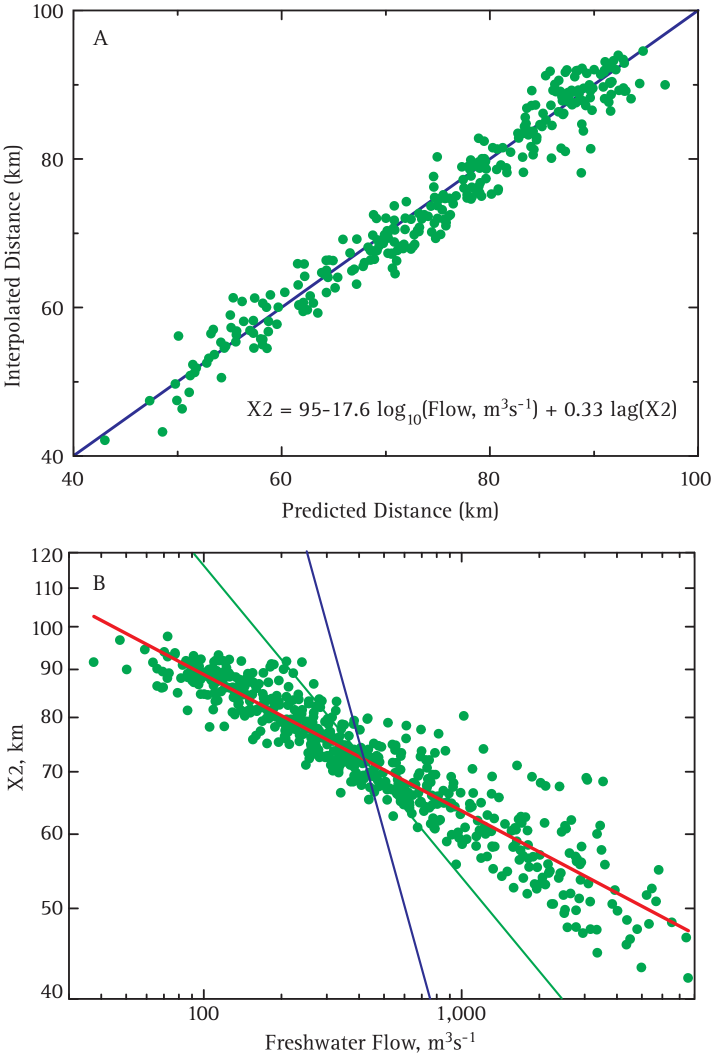


Figure 7. Relationship of X2 to freshwater outflow, monthly means. A., Predicted vs. interpolated X2, the distance in kilometers from the Golden Gate up the axis of the estuary to where tidally-averaged near-bottom salinity is 2. Monthly time series model from Jassby et al. (1995). B., Power function relationship of X2 to freshwater outflow with regression line; note that this relationship ignores the lag shown in the upper panel. Additional lines indicate theoretical relationships with slopes of –1/3 (green) and –1 (blue).

Tidal height at the mouth of the estuary also responds to freshwater flow, and also to subtidal variation in ocean surface elevation indexed by upwelling and atmospheric pressure (Figure 12). Since the flow signal originates in the estuary, its presence in the residual tide at the Fort Point tidal station suggests that this station does not truly mark the entrance to the estuary, which is more likely at the semicircular sill about 10 km outside the entrance.

The importance of river flow relative to ocean tide increases going landward in the estuary. At Sacramento (river kilometer 155) water level is controlled almost entirely by river stage, which depends on freshwater flow, although a tidal signal appears at lower freshwater flows (Figure 13). At the Golden Gate Bridge, tidal height is dominant with only a slight increase in height at high Delta outflow. At Rio Vista, at river kilometer 101 on the Sacramento River below the discharge of Yolo Bypass, water level has both a strong tidal signal and a progressively rising stage with river and Bypass discharge.

Flow volumes similarly change with distance up the axis of the estuary. Under conditions of low net Delta outflow (~200 m^3 s^{-1}), spring and neap tidal volume fluxes based on a modeled tidal prism (Cheng et al. 1993a) were 42,000 to 95,000 m^3 s^{-1} at the Golden Gate, 5,000 to 13,000 m^3 s^{-1} at Martinez, and 1,800 to 5,900 m^3 s^{-1} at Chipps Island. Tidal flows west of the Delta therefore exceed typical freshwater flow rates, which are less than 2,200 m^3 s^{-1} 90% of the time year-round based on monthly means (Figure 14).

Tides are also responsible for most of the mixing in the estuary (Cheng and Smith 1985). Although gravitational circulation plays an important role at some times and places, tides provide the energy for most movement of salt and other substances, including pas-

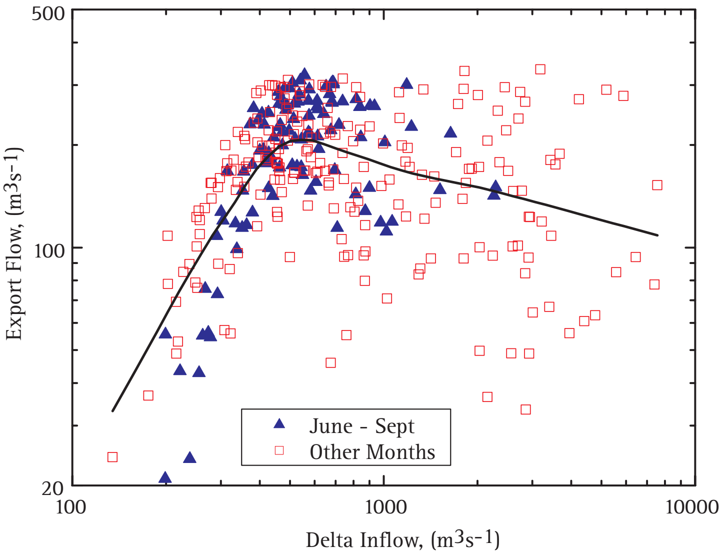


Figure 8. Delta inflow vs. Delta export flow, monthly means for 1972-1998. The line is a locally-weighted regression fit to all the data.

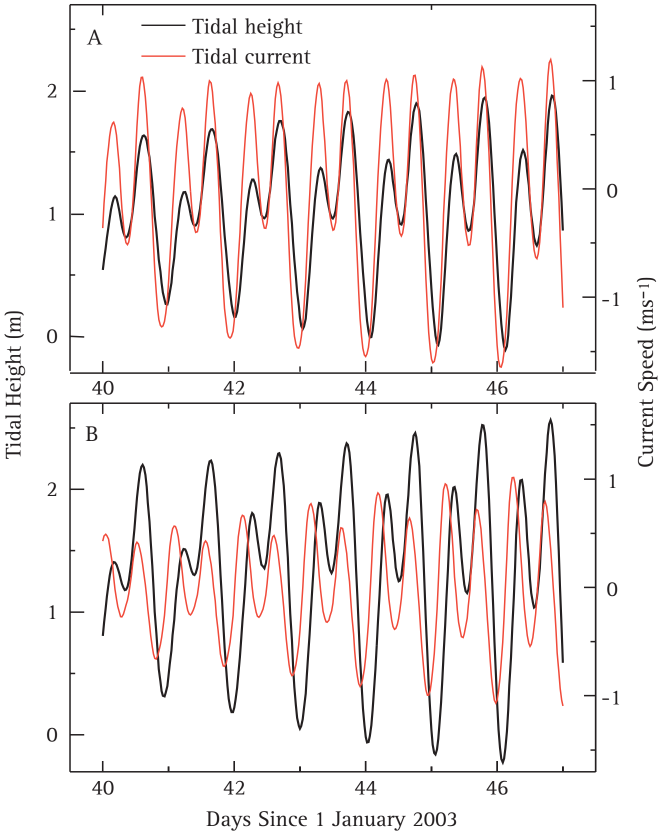


Figure 9. Example of tidal height (black lines, left axis) and tidal currents (red, right axis) for a single week. A., Carquinez Strait in the northern estuary; B., San Mateo Bridge in South Bay.

sively drifting particles, throughout the estuary. Mixing or exchange processes, discussed below, depend mainly on tidal movements that are far more complex than a simple oscillation.

Effects of Regional Climate

Wind patterns over the San Francisco Estuary are spatially variable and have a pronounced seasonal component. Winter winds are dominated by the passage of cold fronts through the area, preceded by strong southerly winds and followed by strong northwesterlies. Summer wind patterns are dominated by the onshore flow due to the pressure gradient set up by cooling of air over the ocean and heating inland. This results in strong westerly winds, particularly in the afternoons, modified by the complex topography of the region. For example, summer wind at Antioch is westerly with a mean speed of about $7 m s^{-1}$, about twice that at Davis, where summer wind tends to be from the south (Figure 15). Wind can exert an important effect on estuarine dynamics, particularly by driving currents in shallow areas (Huzzey et al. 1990; Warner et al. 1996; Lacy 1999) or vertical mixing and resuspension of sediments (Krone 1979). Although wind is not usually important in mixing in the channels (McDonald and Cheng 1994, 1997), strong wind can occasionally destratify the water column in the channels (Koseff et al. 1993).

Temperature is a fundamental variable for biological processes, and temperature changes can stimulate biological responses such as spawning (Turner 1976) and movement (Radovich 1963). Water temperature in the estuary is measured by continuous monitoring stations, and by several shipboard monitoring programs that visit fixed stations monthly or more frequently. Temperature in the estuary depends mainly on air temperature, which is relatively predictable. Air temperature east of the Coast Range varies between seasonal means of 8* and 22°C (Figure 16A), and is more variable than that west

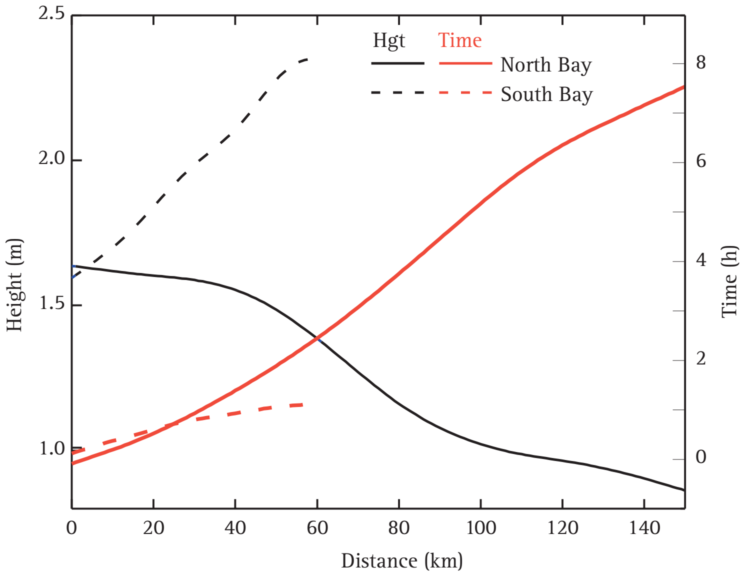


Figure 10. Timing and height of high tide as a function of location, expressed as distance along the channels from the Golden Gate north and east into the Delta (solid lines), or south through South Bay (dashed lines). Black lines, height of high tide. Red lines, lag in hours of high tide after the high tide at the Golden Gate. Lines are generalized additive models with smoothing function, fit to published timing of high tide by location.

of the Coast Range. Water temperature in the Delta follows a similar pattern but with much less diurnal variability (Figure 16B). Water temperature at the Golden Gate (Figure 16C) varies much less on a seasonal basis but more diurnally, because of tidal transport of heat, and interannually, possibly because of upwelling conditions.

Freshwater flow is an important influence on water temperature in rivers, but much less so in the estuary. Even in the Delta, the relationship between air and water temperature is only slightly affected by freshwater flow (Figure 17). At Freeport, high flow reduces temperature on warm days, presumably because water arrives in the Delta before its temperature can equilibrate with air temperature. At Antioch low flow increases water temperature on cool days, probably because of the moderating effect of the less-variable water from down estuary (Figure 16).

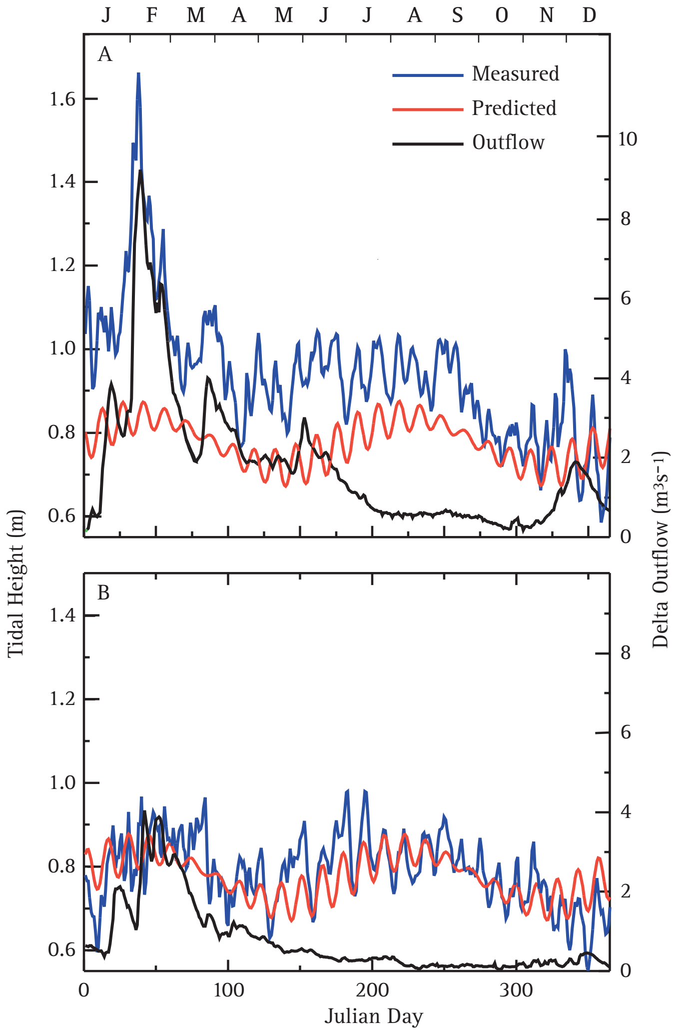


Figure 11. Filtered tidal heights at Port Chicago and net Delta outflow for: A, 1998 and B, 1999. Blue line, predicted (astronomical) tide; red line, measured tide; green line, flow (right axis).

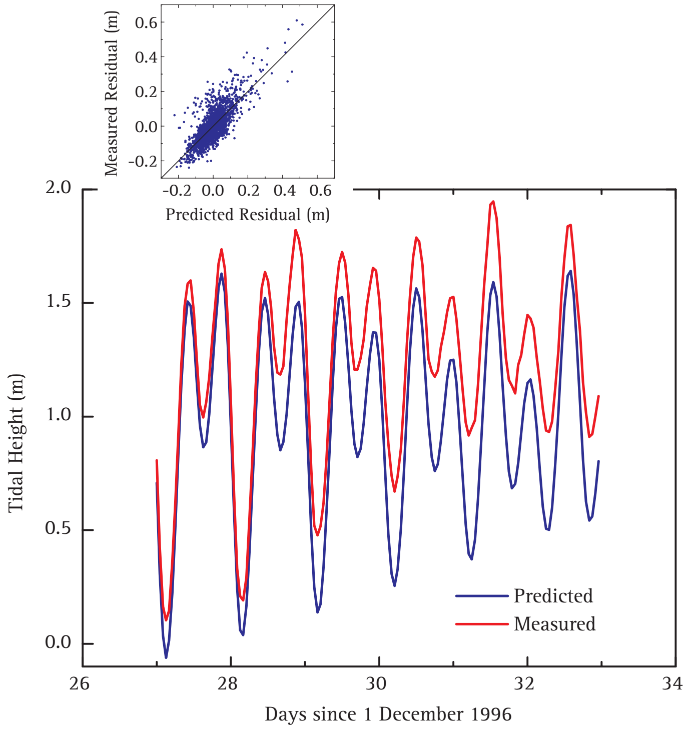


Figure 12. A short example of predicted and measured tidal height at the Golden Gate, with an inset showing the fit of a model of the residual tide (measured - predicted). The model includes three parameters (N=2087, confidence limits uncorrected for serial autocorrelation): freshwater outflow (m^3s^{-1}, 2.7 ± 0.2 x 10^{-5}), upwelling index (Bakun Index Values from NOAA/PFEG for: 36°N 122°W, -2.0 x ±0.3 x 10^{-4}), and atmospheric pressure at sea level (from PFEL web site, Mb, -0.013 x ± 0.0006).

The various sources of temperature data give similar seasonal patterns but differ somewhat in interannual patterns (Figure 18). These differences are likely due to differences between these spatially-intensive and temporally-intensive approaches. None of these data had time trends over the period of record. Spatial patterns of temperature are best exemplified by summer data from one or more of the shipboard monitoring programs; for example, both the fall midwater trawl data (Figure 19) and the zooplankton monitoring data (not shown) indicate a gradient of increasing temperature from northwest to southeast through the Delta, presumably reflecting differences in source water and residence time.

Flow Patterns and Net Transport in the Delta

The Sacramento-San Joaquin Delta is the keystone of water management in the Central Valley. Because of its central role in the movement of water, and use of the Delta by fish and other species of concern, particular attention has been paid to water movement in the Delta and its influence on biota. Recent research using modern hydrodynamic instruments and models has led to a greatly improved understanding of how the Delta functions.

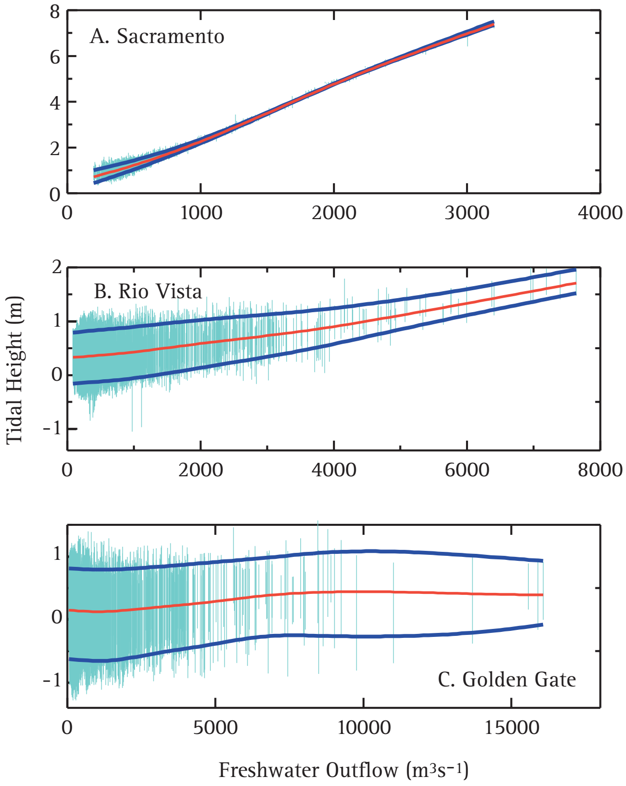


Figure 13. Effect of freshwater flow on water level and tidal range for three locations in the estuary. Vertical bars represent 10th and 90th percentiles of the daily tidal range, calculated as the residuals after tidal filtering, plus the daily mean filtered value. A., Sacramento River at Freeport (river kilometer 155) vs. Sacramento River flow. B., Sacramento River at Rio Vista (river kilometer 101) vs. flow at Rio Vista. C., San Francisco Bay at the Golden Gate vs. net Delta outflow. Flow data from the DAYFLOW program and water level data from continuous monitoring sites maintained by DWR and USGS (http://iep.water.ca.gov/Data).

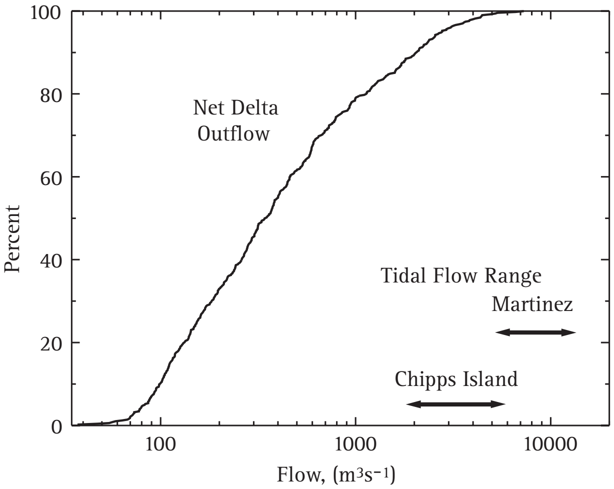


Figure 14. Frequency distribution of monthly net Delta outflow from DWR DAYFLOW program (line), with tidal volume fluxes for two locations shown as arrows connecting modeled values for spring and neap tides.

Flow in the Delta is an amalgam of net, river-derived flow and tidal oscillation. Effects of stratification come into play when salinity intrudes into deeper channels in the western Delta (Nichol 1996), and possibly due to surface warming in the Stockton Ship Channel. Otherwise, the water column can be considered vertically well-mixed throughout the Delta.

Delta channels have been widened, dredged, and straightened to improve flow and allow for passage of ships. In addition, barriers have been installed in some parts of the Delta to control water movement. The Delta Cross Channel (DCC, Figure 1) was constructed in 1953 to increase water flow from the Sacramento River into the interior Delta. This channel connects the Sacramento River to the lower Mokelumne River so that water can flow through the central Delta to the pumping plants. The DCC has two gates that can be operated independently, and are usually closed when high flow in the Sacramento River threatens flooding in the central Delta, or when needed to protect emigrating juvenile salmon. Keeping the gates closed for extended periods when pumping is high, however, can result in salinity intrusion, increasing salt content of the diverted water. Gates are generally open in July-October, and historically have been either open or closed during other months. Starting in 1993, DCC gates have been held closed for all of February-April and most of May for salmon protection (DWR data).

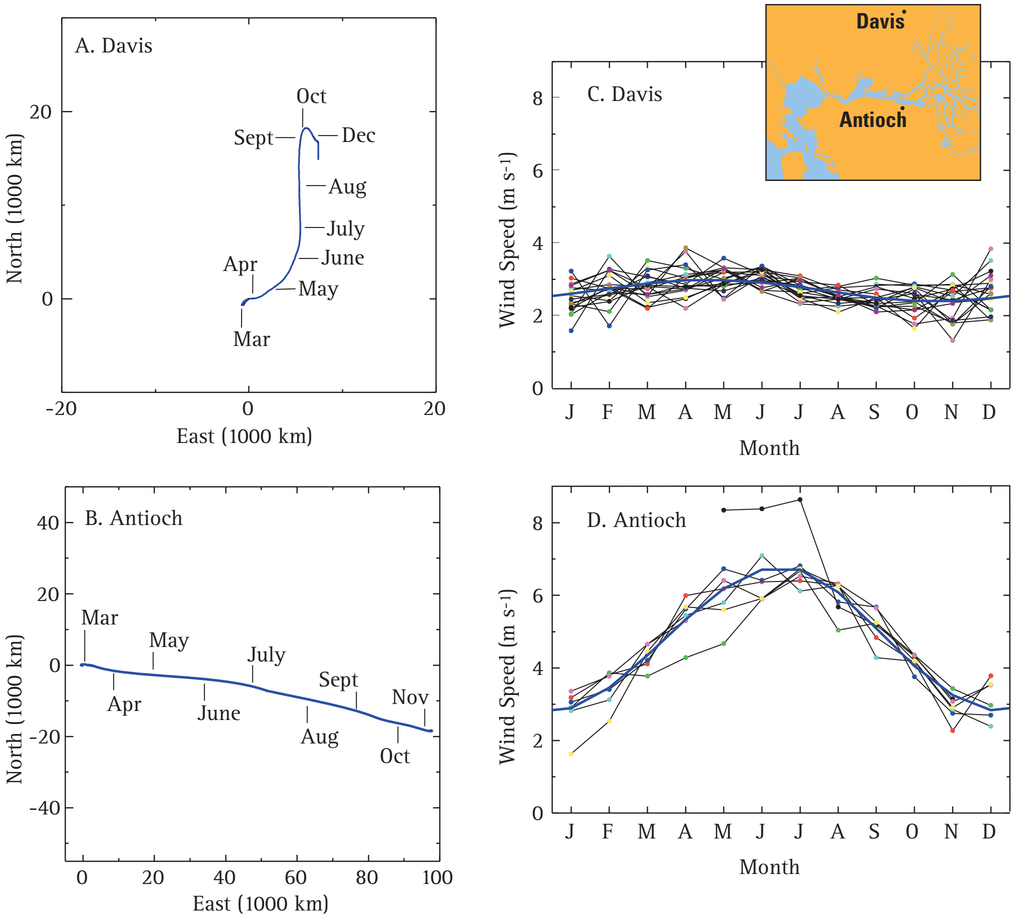


Figure 15. Wind conditions at Davis (16 years, data from Integrated Pest Management web site) and Antioch (7 years, DWR continuous monitoring site). A, B, progressive vector diagrams illustrate the mean daily wind at each location as a series of vectors resulting in the trajectory of a particle influenced by that wind speed and direction for one year. Letters indicate months. C, D, annual cycle of monthly mean wind speed at each location, with the grand mean shown by a heavy line.

An additional barrier in Montezuma Slough (Figure 1) is operated tidally to reduce salinity in Suisun Marsh.

Temporary rock barriers have also been installed in the south Delta (Figure 1). The principal purpose of these barriers is to increase water level and improve water quality for farms that use south Delta water for irrigation, and to prevent fish from migrating close to the export pumps. The head of Old River barrier (HORB) is installed in spring and fall of each year to prevent migration of young San Joaquin salmon down Old River toward the pumping plants. This barrier is installed with culverts and flap gates to allow some circulation, but to reduce the movements of salmon. Hydrodynamic effects of these barriers have not been worked out, but they do seem to have the desired benefit for water level and quality.

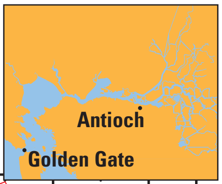
During high-flow conditions much of the Sacramento River discharge enters the Delta through the Yolo Bypass, an engineered floodplain designed to protect Sacramento from flooding. The Yolo Bypass connects the Sacramento River upstream of Sacramento with the lower river in the Delta below Rio Vista (Figure 1). The fraction of Delta inflow carried by the Yolo Bypass varies from 0 at flows below the long-term median, and can be as much as 50% at high flow (Figure 5). Water discharging from the Yolo Bypass can be warmer and higher in chlorophyll concentration, sediment, and particulate organic matter than Sacramento River water (Schemel et al. 1996; Sommer et al. 2001a). This water may reach Suisun Bay before mixing thoroughly with estuarine water (Monsen 2000).

Net flow in Delta channels and tidal lakes occurs through river input, water diversions and drains, and tidal asymmetries. The Department of Water Resources' DAYFLOW program calculates daily net flows at several locations in the Delta, neglecting tidal effects and time lags from one part of the Delta to another. Inputs include gaged river flows, estimated flows in several smaller ungaged rivers, export flow in the South Delta including the CVP and SWP facilities as well as the smaller Contra Costa Water District facility, and net consumption within the Delta. This latter term includes monthly estimates of precipitation less consumption on Delta islands, to represent the net effects of roughly 2,200 unmonitored pumps and siphons that take water for irrigation throughout the Delta (Herren and

Kawasaki 2001). In addition to total inflow and net Delta outflow, the DAYFLOW program calculates several variables representing non-tidal net flows within the Delta, e.g., at Rio Vista on the Sacramento River and Jersey Point on the San Joaquin River.

The CVP export pumps remove water directly from the southern Delta, whereas the SWP pumps water from Clifton Court Forebay, a lagoon that is filled during high tide by opening radial gates on Old River. These differences do not come into play in the DAYFLOW program, but affect instantaneous velocities in the nearby channels, and may be important in the effects of export pumping on fishes in the Delta.

During the dry season, export pumping and within-Delta consumption can remove a substantial fraction of Delta inflow. The proportion of freshwater entering the Delta that is subsequently exported during June to September has a median of 38% over the last 30 years, with 90th percentiles of 20% and 54%. Net consumption within the Delta has a median value of 18% of total inflow in the same period, with 90th percentiles of 10% and 35%. Gross consumption, the actual amount removed from the estuary by farms in the Delta, has been estimated as about one-third higher than net consumption (DWR 1995).



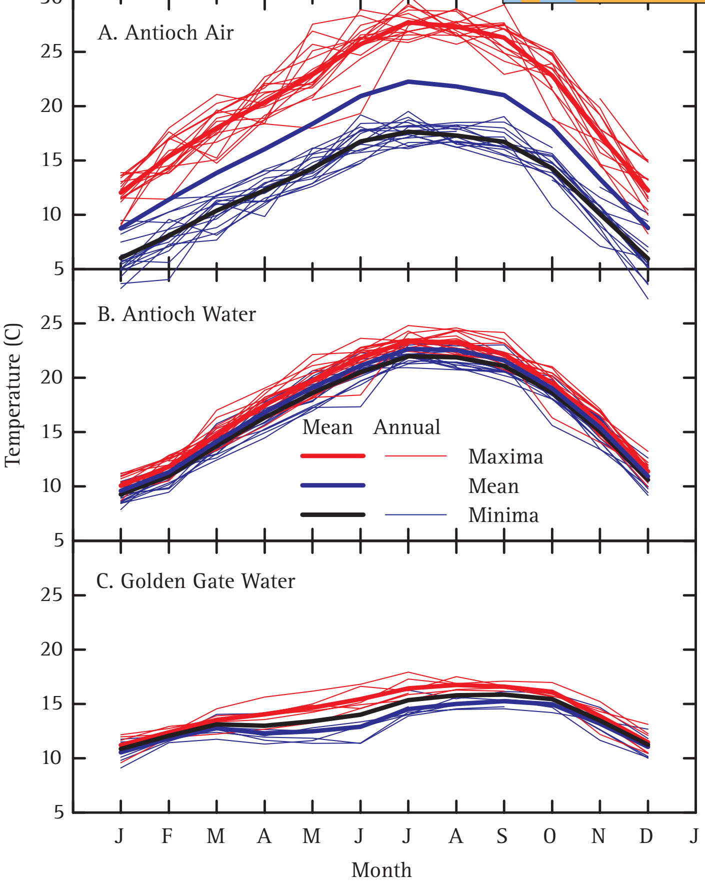


Figure 16. Monthly mean temperature from IEP monitoring sites: A., Air temperature at Antioch (17 years during 1983 to 2002); B., Surface water temperature at Antioch (same years); C., Surface water temperature at the Golden Gate (1990 to 1996). In each panel the thin lines are monthly maxima (pink) or minima (green) for a single year, while the heavy lines are grand means (blue) or means of maxima (red) or minima (black).

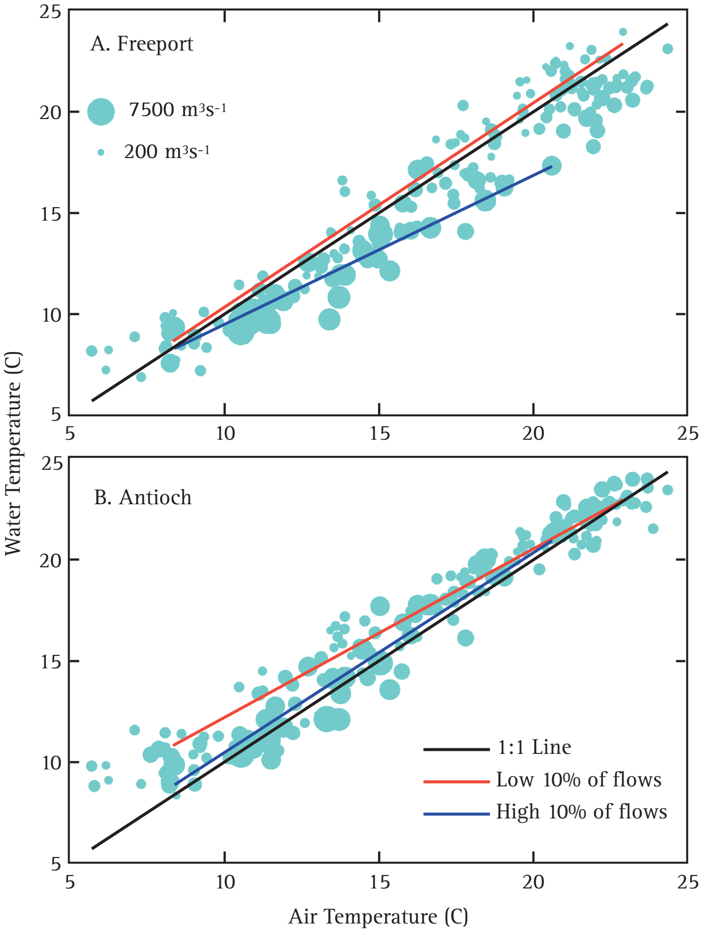


Figure 17. Monthly mean temperature at Freeport and Antioch vs. air temperature at Antioch. Size of symbols indicates freshwater flow. Lines are: Black = 1:1; Red: regression line for the lower 10th percentile of flow; Blue: regression line for upper 10th percentile of flow.

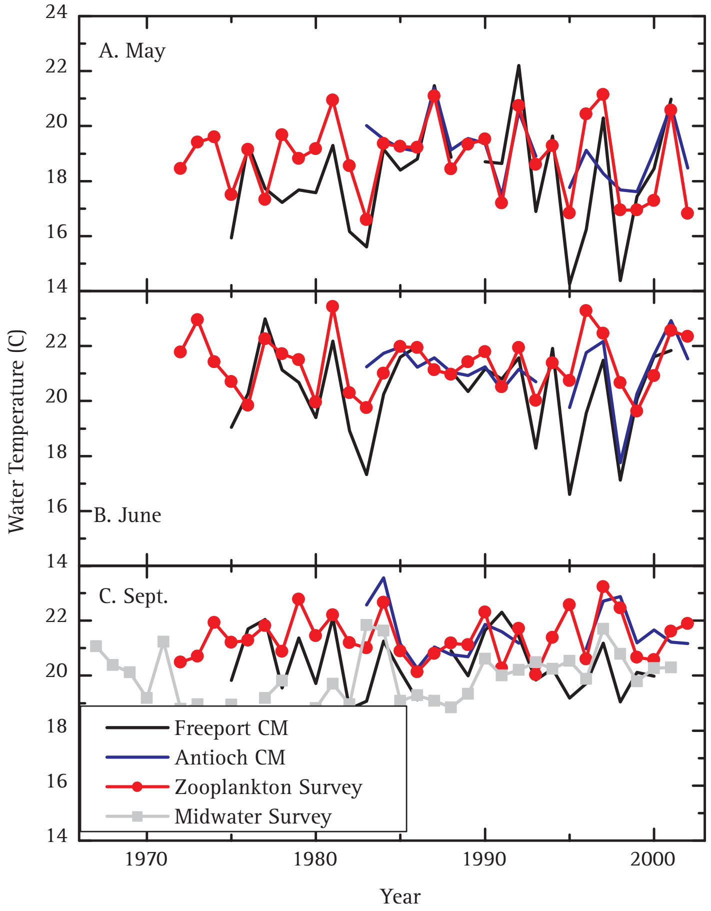


Figure 18. Monthly mean temperature in the Delta for selected months from two continuous monitoring (CM) sites (Freeport and Antioch) and two grab-sample sources (IEP zooplankton surveys and fall midwater trawl surveys for all Delta stations). Data from IEP web site.

The above comparison of export flow to inflow may be inappropriate, since during low-flow periods the Delta is largely a dispersive environment in which tidal motions greatly exceed motions due to river flow. A more appropriate comparison may be between export flows and total Delta volume, which would be related to the daily risk of a particle being exported if the Delta were well-mixed. Daily export flows range up to 2.8% of Delta volume in summer (Figure 6D), but most of the time in summer the fraction of Delta volume exported daily amounts to less than 2%. Export and diversion flows may have a considerable cumulative effect on slowly-growing biota but are unlikely to affect populations with high turnover rates such as phytoplankton.

The above comparison highlights differences among alternative conceptual models of flow patterns in the Delta (Figure 20). The earlier view (Figure 20A) held that calculated net flows such as QWEST (net flow in the San Joaquin River at Jersey Point) were important in determining the movement of substances and organisms. According to this perspective, the pattern of net flows in the Delta moves substances and guides the movement of fish. A commonly-used figure (e.g., Ball and Arthur 1979, Figure 2) shows net flow directions calculated for each major channel in the Delta. The more recent view (Figure 20B) sees the Delta as a region of transition between unidirectional riverine flows and reversing tidal flows. The relative importance of each depends on location in the Delta and the magnitude of freshwater flow (Figure 13).

The two conceptual models described in Figures 20A and 20B differ sharply in the consequences for fish

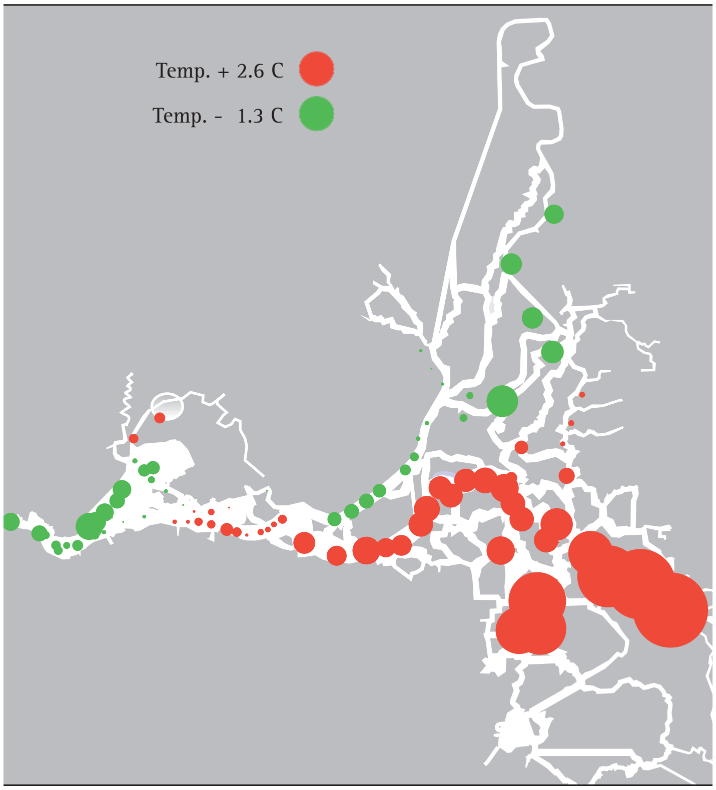


Figure 19. Spatial distribution of temperature in September in the Delta and Suisun Bay based on fall midwater trawl sample data. Each symbol represents the deviation from the spatially-averaged temperature for all years from 1990 to 2001 and for all stations sampled at least 7 times during that period.

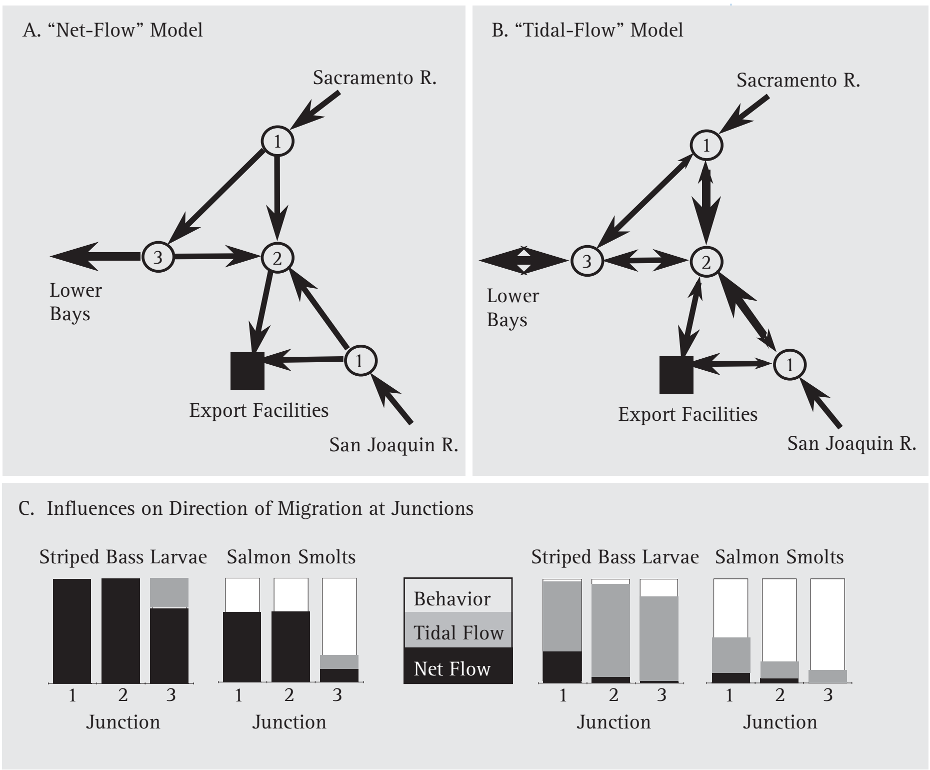


Figure 20. Conceptual models of flow patterns in the Delta and their consequences for movements of fish. A and B, schematic diagrams of the Delta with representative channels and nodes: 1, points of entry of Sacramento and San Joaquin Rivers into Delta; 2, lower San Joaquin River at junction with Old and Middle Rivers; 3, western Delta at confluence of rivers. A, "Net-flow" model showing directions of calculated net flows; B, "Tidal-flow" model in which double-ended arrows indicate tidal flows, with the relative sizes of arrowheads indicating relative magnitudes of flows in each direction; C, Qualitative depiction of influence of these alternative models on expected movements of early striped bass larvae and salmon smolts. Each bar shows the relative importance of fish behavior, net flow, and tidal flow in moving fish past each of the numbered junctions.

movement depicted in Figure 20C. If the "net-flow" model is assumed, then relatively passive organisms such as early striped bass larvae should move largely with net flows, with an increasing behavioral component of motion as the fish develop. Larger, strongly-swimming salmon smolts are more capable of moving independently, but they too would be affected to some degree by net flow. According to the "tidal-flow" model, striped bass larvae would be influenced most by the interaction of their behavior with tidal flows, and only slightly by net flows, once they were in the Delta. Salmon smolts would be under control of their behavior, but with a strong influence by tidal flow; net flow would probably affect them indirectly by setting up cues for finding the ocean. The difference in the consequences for movement of these fish through the Delta are clear (Figure 20C).

The shift of perspectives on flow in the Delta has arisen mainly through the development of two tools: particle-tracking computer models of the Delta, and direct measurement of flow velocities and volume transport at various locations in the Delta. The development and use of hydrodynamic models is discussed in greater detail below, but results of some modeling exercises are useful in understanding flow patterns in the Delta. Several particle-tracking and transport models of the Delta have been developed, most using a simplified one-dimensional representation of Delta channels, although two-dimensional models are becoming more widely used (e.g., Lucas et al. 2002).

The general trend of model results seems to be that a patch of particles released in the Delta will move in the direction of net flow, but with extensive spreading of the patch due to tidal pumping and trapping and shear flow dispersion (Fischer et al. 1979). The export pumps in the south Delta impose a risk that a particle will be lost from the system. This risk increases with export flow, initial proximity of the particle to the pumps, and duration of the model run. A model study of the suitability of QWEST as an indicator of flow conditions for management showed that computed reverse flows (negative QWEST) had at most a minor effect on the entrainment of neutrally-buoyant particles, which was better predicted by the absolute magnitude of export flows. Thus, the earlier concept that salmon smolts and other fish were "sucked" up this part of the Delta and pulled toward the pumps did not match the reality of flow in this region, which is dominated by tides under low-flow conditions; this net-flow concept never matched the behavior of fish.

Using acoustic doppler current profilers (ADCPs) and ultrasonic velocity meters, Oltmann (1995, 1998) began a program to monitor tidal flow in the Delta accurately enough to allow the calculation of tidally-averaged net flows. Results of these measurements show how important tidal effects are in net transport. For example, net flows in the various pathways toward the export pumping plants were not greatly affected by the sign of net flow in the lower San Joaquin River, although they responded to the installation of a barrier at the head of Old River (Oltmann 1995). In addition, net flow through Threemile Slough in the western Delta was generally from the Sacramento River to the San Joaquin River because of differences in tidal phase, except during very high flow in the San Joaquin. Net seaward flow in the Sacramento River was higher upstream and decreased downstream of the Delta cross-channel when the gates were open compared to when they were closed. Net Delta outflow, estimated as the sum of net flows at four stations in the western Delta, was close to that calculated by mass balance at high freshwater flow, but diverged substantially at low flow as spring-neap filling and draining and meteorological effects on water level became apparent (Oltmann 1998). A study using a spatially-detailed two-dimensional model has also shown that under low-flow conditions net Delta outflow is a crude measure of flow patterns in the western Delta, which are strongly affected by the spring-neap tidal cycle (Monsen 2000), although net Delta outflow is reasonably accurate when averaged over weeks to months. Dye studies showed that longitudinal dispersion was of similar importance to net flow in the movement of dye patches (Oltmann 1999).

The importance of tidal flows in the Delta is illustrated using UVM data from two locations, Jersey Point and Middle River, during a time of near-maximum changes in export flow (Figure 21). At both locations the instantaneous velocity is dominated by tides. At Jersey Point, the measured net flow declined early in the year as river flow declined. After March 20, net Delta outflow had a median value of 331 $m^3 s^{-1}$, close to the grand median for this time period in all years. The measured net flow was always positive, and inversely related to export flow (slope ± 95% CL = -0.42 ± 0.16, 83 df, $r^2 = 0.24$, $p < 0.001$ uncorrected for autocorrelation). Based on this slope, over the normal range of available export flow (50 to 400 $m^3 s^{-1}$) net flow at Jersey Point would vary only between 176 and 30 $m^3 s^{-1}$. During the same period, calculated flow at this point (QWEST) was sometimes negative, strongly correlated with export flow (slope = -1.0 ± 0.14, 83 df, $r^2 = 0.70$, $p < 0.001$), and would vary between +182 and -160 $m^3 s^{-1}$ over the same range of export flows.

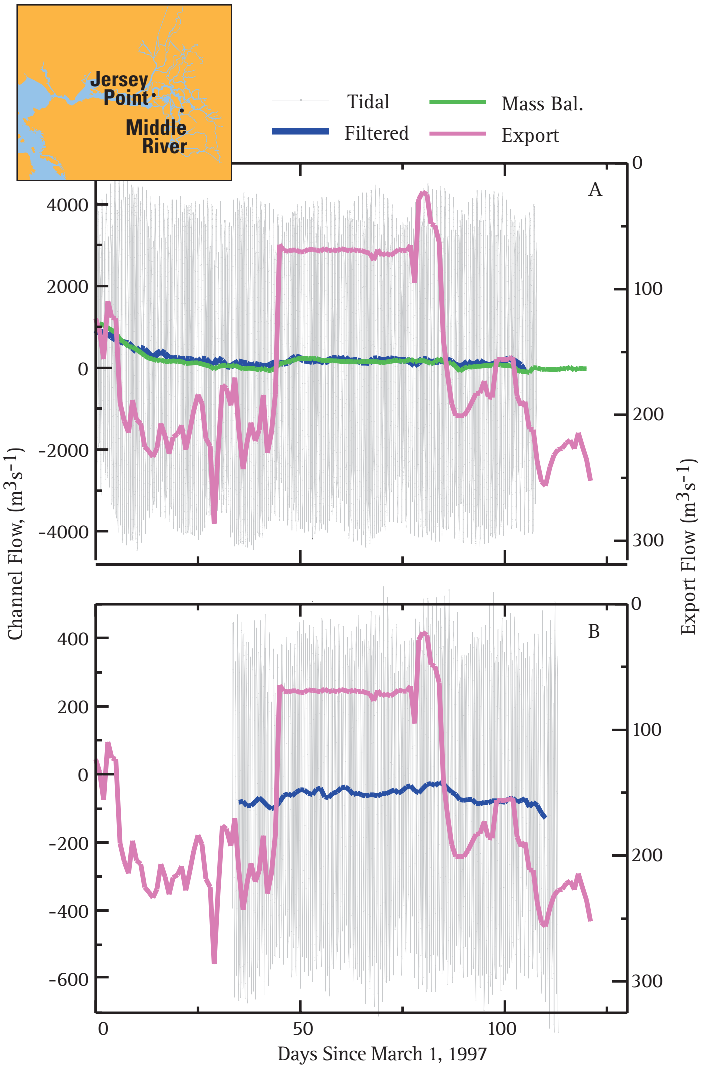


Figure 21. Flow patterns at two locations in the Delta in 1997 from USGS continuous montoring stations using ultrasonic velocity meters (Oltmann 1995, see Table 2). A, Jersey Point on the San Joaquin River; B, Middle River. Gray line, tidal flow data; blue line, tidally filtered data; green line, flow calculated by mass balance in the DWR Dayflow program (Jersey Point only, coded as QWEST); magenta line, export flow on a reversed scale.

Net flows were negative (southward) in Middle River because of the influence of net flows toward the export pumps. Even here, however, tidal flows were many times larger than net flows. This means that tidal dispersion effects are likely to be important.

The functioning of the tidal lakes in the Delta has received attention recently. These areas may have long or short residence times depending on the peculiarities of configuration such as number, size, and orientation of breaches in their levees (Lucas et al. 2002). These differences have implications not only for conditions within the tidal lakes, but for their influence on surrounding channels and on movement of salt and other constituents. These tidal lakes are less able to retain the sediments that generally cause shallowing in normal lakes.

In spite of efforts to ensure that Delta levees can withstand variations in water level, storms, and earthquakes without failure, it seems likely that one or more Delta levees will ultimately fail because of seismic activity. Levee failure within the Delta would result in significant salinity intrusion because of the increase in area of the Delta and volume of the tidal prism (Enright et al. 1998).

The Interaction of Freshwater Flow with Tides and Salt

One of the greatest challenges in estuarine physics is to understand and model the interaction among tidal flows, buoyancy, stratification, and transport. These factors are the focus of active research in the San Francisco Estuary, at least partly because of the perceived importance of physical conditions to the estuarine ecosystem. As with flow in the Delta, our views of the physical dynamics of brackish regions of the estuary have changed substantially in the last ten years. Again, the major shift appears to be from a static view dominated by consideration of net flows to a dynamic view in which the tides play a major role.

Movement of the Salt Field

Freshwater flow entering any estuary increases the mean slope of the water's surface, resulting in a barotropic residual flow toward the sea (e.g., Officer 1976). An opposite density gradient due to the salinity gradient results in a tendency for landward density-driven or baroclinic flow. The position of the salt field can be thought of as the net result of these opposing forces, though greatly modified by the tides and by the complex bathymetry of the estuary (Lacy et al. 2003).

In the San Francisco Estuary, the tidally-averaged mean penetration of salinity up the estuary depends primarily on freshwater flow, and to a lesser extent on spring-neap tidal oscillations and meteorological variation (Peterson et al. 1975, 1989, 1996; Knowles and Cayan 2002; Knowles 2000). The degree of penetration can be indexed by X2 (Jassby et al. 1995; Monismith et al. 2002), a convenient index of the physical response of the estuary to freshwater flow. The 2 psu isohaline is most often found in Suisun Bay, and in spring is constrained by regulations to be west of the confluence of the Sacramento and San Joaquin rivers.

Several features of X2 are important here. First, the value 2 psu is not arbitrary but has a physical basis. It is high enough to unambiguously result from dilution of ocean water, and is higher than salinities in the southern Delta elevated by agricultural drainage (Schemel and Hager 1986). It is low enough to mark the landward limit of salinity stratification. Thus, X2 represents the approximate landward end of the salt field and the longitudinal density gradient.

Second, X2 responds to freshwater flow with a time constant of about two weeks (Peterson et al 1975; 1989, Jassby et al. 1995), which may differ somewhat between rising and falling hydrographs (Peterson et al. 1989). This lag can be seen in the response to salinity that occurred during the 1997 flood event (Knowles et al. 1997). It is also consistent with models in which salinity at a point is related to flow with a lagged term to account for antecedent conditions (Denton 1993).

Third, salinity at any point in the northern estuary is related to X2 (Figure 22). This relationship is most nearly linear in mid-estuary where salinity is far from its limits (e.g., USGS station 11 in central San Pablo Bay). At both the low- and high-salinity ends of the distribution there is a noticeable flattening as the relationship approaches its limits. This means that the steepest salinity gradient, and the greatest tidal variability in salinity, will usually be where salinity is near 15 psu. Note, however, that these relationships are time-averaged, whereas on any given transect up the

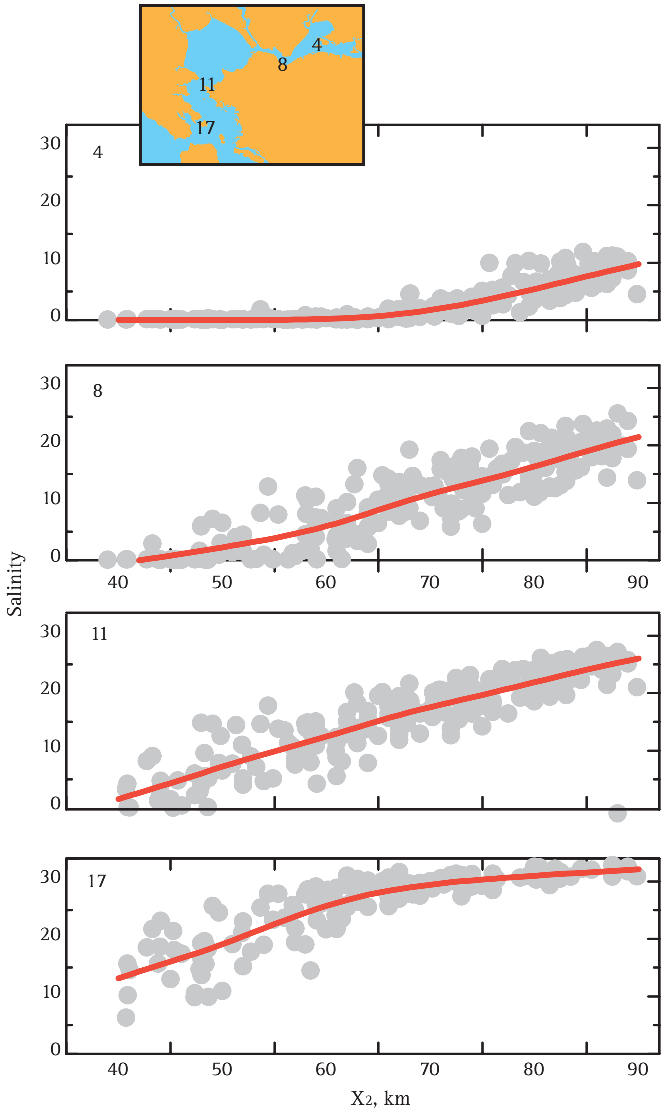


Figure 22. Salinity (practical salinity units) at four locations in the northern estuary plotted against X2. Data are from USGS monitoring stations shown on inset (Table 2). Data points are water column means of individual samples, and corresponding X2 value is for the same day. No tidal correction has been applied. Lines are from generalized additive models with smoothing splines fit to the data.

estuary salinity is highly variable, with obvious fronts and even reversals of the trend (Figure 23).

The mid-salinity range is also where the greatest potential for stratification exists (Figure 24), although salinity stratification throughout the estuary is usually small (<1 psu in 66% of samples in this data set). Although the relationship between salinity and X2 appears complex, that between salinity and the ratio X/X2 (i.e., the ratio of the position of the point in kilometers up the estuary to X2) is more consistent, indicating that the salt field changes in steepness but not in shape as X2 moves seaward (Monismith et al. 1996, 2002).

Fourth, X2 can be modeled either as a function of the log of flow (Jassby et al. 1995), or as a power function of flow with an exponent of about -0.14, smaller than expected by theory (Figure 7B, Monismith et al. 2002). If longitudinal dispersion did not depend on compression of the salinity and density field, an exponent of –1 would result. In a uniform estuary in which gravitational circulation moved salt up-estuary, X2 would respond to flow with an exponent of –1/3 (Festa and Hansen 1976). The exponent determined by Monismith et al. 2002 was much smaller, apparently because of landward salt flux due to gravitational circulation in deeper parts of the estuary.

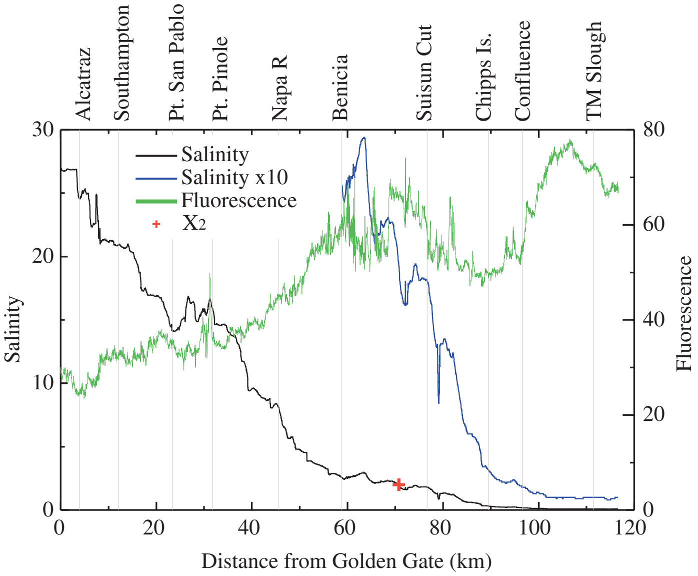


Figure 23. Salinity and chlorophyll fluorescence from a transect up the northern estuary on 26 February 2001. Salinity (black line) has been rescaled by x10 (blue line) for better visibility. Chlorophyll fluorescence (green line) in arbitrary units. The transect went from near Alcatraz through the northern channel in Suisun Bay up the Sacramento River to Rio Vista. USGS data. From a transect up the northern estuary on 26 February 2001. Salinity (black line) has been rescaled by x10 (blue line) for better visibility. Chlorophyll fluorescence (green line) in arbitrary units. The transect went from near Alcatraz through the northern channel in Suisun Bay up the Sacramento River to Rio Vista. USGS data.

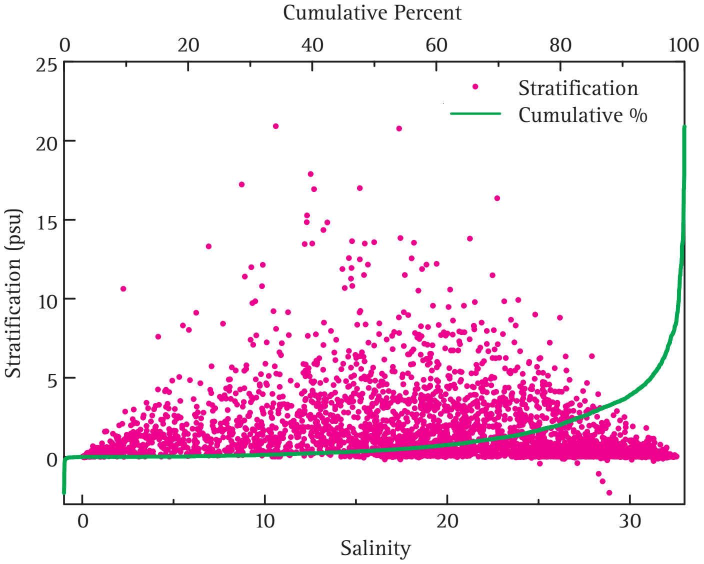


Figure 24. Salinity stratification vs. salinity from USGS monitoring data. Data are from 1988-2002 for 29 stations west of the Delta with at least 100 dates sampled. Water column mean salinity is averaged over all 1-m depth bins reported. Stratification is measured as the difference in salinity between 1 and 10 meters depth, or at least a 7-m depth range. The green line gives cumulative percent frequency of stratification.

At the seaward end of the estuary, plumes of low-salinity surface water can propagate out to sea a considerable distance (Peterson et al. 1996). However, bottom salinity is constrained to be near oceanic values at the mouth of the estuary, because the ocean is effectively an infinite source of saline water for dilution with an infinite cross-sectional area. This means that the average salinity gradient is effectively represented by X2. Since most of the density variation in the estuary is related to salinity rather than temperature, X2 is an index of the length and steepness of the density gradient.

The degree of human impact on the distribution of salt is comparable to that on flow, discussed above. Generally human activities raise salinity in the winter-spring wet season, and lower it in summer, relative to pre-development conditions (Knowles 2000). However, natural interannual variability greatly exceeds the range of human effects (Knowles and Cayan 2002).

Stratification and Gravitational Circulation

In the absence of stratification, turbulent mixing throughout the water column results in an approximately logarithmic vertical profile of tidal velocity, with most of the water column at the same mean velocity (Cheng et al. 1998a). Typically a benthic boundary layer develops, where velocity changes sharply near the bottom (Cheng et al. 1997). In addition, if a substance is being released (e.g., by sediment resuspension) or taken up (e.g., by bivalve filtration) at the bottom, a steep concentration gradient can develop because vertical mixing becomes limited near the bottom.

Salinity stratification uncouples surface from deep waters, reducing vertical movement of substances and momentum. The most energetic turbulence is confined to a bottom mixed layer, and vertical momentum transfer is suppressed by the difference in buoyancy between the surface and near-bottom layers (Stacey et al. 1999b). The resulting suppression of vertical transfer allows the two water layers to move in different directions and to have different properties. One result of a stratified water column is that longitudinal transport is greatly enhanced (Nunes Vaz et al. 1989; Geyer 1993). In addition, stratification and gravitational circulation can have a substantial effect on biota.

Stratification arises ultimately because of the buoyancy difference between river and ocean water, but the proximate cause of stratification is rarely related directly to freshwater flow (Monismith et al. 1996). Rather, stratification can arise through several mechanisms. First, tidally-varying vertical gradients in velocity can interact with longitudinal gradients in density to produce a tidal cycle of stratification and destratification known as Strain-Induced Periodic Stratification ("SIPS," Simpson et al. 1990). Any tidal current is sheared by bottom friction. On an ebb, the baroclinic or density gradient acts in the same direction as bottom friction to retard bottom flow and enhance shear throughout the water column, so that low-salinity water flows over higher-salinity water, stratifying the water column. On the succeeding flood, friction and the baroclinic gradient oppose each other, so that the shear through the water column is reduced, near-bed flow and shear are enhanced, strengthening turbulence and erasing the stratification. SIPS has been observed in field studies (Monismith et al. 1996) and in 3D model simulations of San Francisco Estuary (Cheng and Casulli 1996).

Because stratification impedes the vertical transport of momentum, when sufficiently well-developed it can suppress the destratification part of the SIPS cycle, resulting in “runaway” or persistent stratification. This positive feedback cycle occurs when the tendency for baroclinic flows overcomes the tendency for vertical mixing by the tidal shear stresses. This mode of stratification depends on the steepness of the baroclinic density gradient (related to X2), and the strength of turbulence, which is related to tidal velocity and water depth. Monismith et al. (1996, Eq. 18) proposed the use of a “horizontal Richardson number” to identify the transition between periodically and persistently stratified conditions. This dimensionless number is the ratio of the potential energy of the longitudinal density gradient to the tidal kinetic energy that drives mixing. A high value indicates a tendency for stratification to persist. This ratio increases linearly with increasing density gradient and the square of water depth, and decreases with the square of tidal velocity. In contrast with the estuarine Richardson number (Fischer et al. 1979), which explicitly includes freshwater flow, the horizontal Richardson number varies with the steepness of the salinity gradient. Thus, we expect persistent stratification in deep locations with a strong salinity gradient and weak (i.e., neap) tides. Persistent stratification has been observed in 3D model studies (Cheng and Casulli 1996) and in field investigations of deeper channel areas in both the northern and southern estuary during neap tides (Huzzey et al. 1990; Monismith et al. 1996). Strong wind can also eliminate stratification by enhancing vertical mixing (Koseff et al. 1993; May et al. 2003).

Stratification may also be found in association with fronts formed by the joining of different water masses, e.g., saltier channel water with fresher water from shoals. The resulting interaction can have complex influences on stratification (Lacy et al. 2003).

Strong stratification is associated with the development of gravitational circulation, in which net (tidally-averaged) flow is up-estuary near the bottom and down-estuary near the surface. Although gravitational circulation may be possible in unstratified conditions, it generally occurs in the presence of stratification (Hansen and Rattray 1966; Festa and Hansen 1976; Geyer 1993; Monismith et al. 1996; Cheng and Casulli 1996). Gravitational circulation is an important mechanism for upstream salt penetration, thereby providing a negative feedback that limits the seaward movement of the salt field (Hansen and Rattray 1966; Monismith et al. 2002, see ”Movement of the Salt Field”, p. 27). It is also an important mechanism for the transport of organisms and materials, particularly negatively buoyant particles. Gravitational circulation has been observed in deeper locations, particularly under neap tidal conditions, e.g., in the Central Bay and Golden Gate (Conomos et al., 1970; Conomos 1979a; Petzrick et al. 1996), Carquinez Strait (Smith et al. 1995), and the lower Sacramento River in summer (Nichol 1996).

The Entrapment Zone

The landward limit of gravitational circulation, or null zone (Peterson et al. 1975), has been the subject of considerable interest in the San Francisco Estuary because of its potential role in entrapment of particles (Arthur and Ball 1979). The conceptual model of the entrapment zone (Postma and Kalle 1955; Festa and Hansen 1976, 1978; Peterson et al. 1975, Figure 14 in Arthur and Ball 1979; Figure 25A) holds that gravitational circulation produces a net seaward (barotropic) current at the surface and a net landward (baroclinic) current at the bottom. Through continuity these currents must result in an upward net current near the null zone, which is the landward limit of gravitational circulation. This net flow pattern traps negatively-buoyant particles and downward-swimming organisms near the null zone. The null zone was believed to occur consistently at around 2 psu salinity, which is frequently in Suisun Bay (Peterson et al. 1975; Arthur and Ball 1979).

This appealing idea seemed to match observations of maxima in turbidity and abundance of some planktonic organisms. However, recent analyses from a variety of estuaries suggest mechanisms may be more complex and dynamic than suggested in these earlier studies (e.g., Jay and Musiak 1994; Grabemann et al. 1997; Guezennec et al. 1999). A recent series of studies in Suisun Bay using modern oceanographic sensors failed to support the entrapment zone model. The key finding was that gravitational circulation was rare in Suisun Bay except in fall (Burau 1998; Kimmerer et al. 1998; see also Figure 3 in Peterson et al. 1975) because of the shallow depth and consequently low horizontal Richardson number. Furthermore, vertical turbulent motions are much larger than the upward

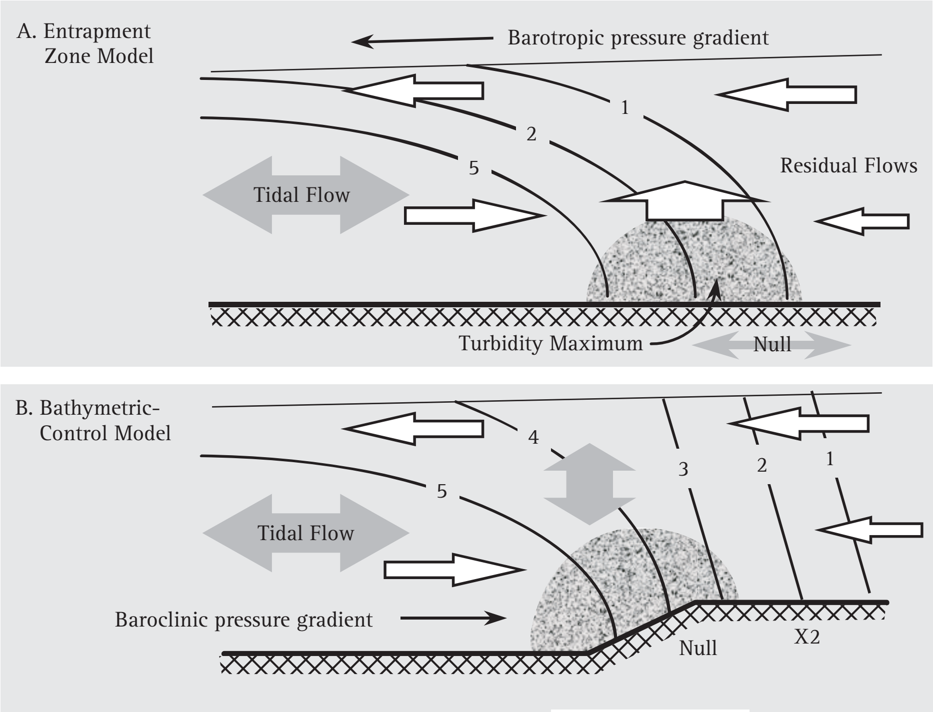


Figure 25. Alternative models of dynamics of the Low-Salinity Zone. Tidal motions are depicted as solid gray arrows, and residual motions as open arrows. In both models, seaward residual currents result from the barotropic pressure gradient, and landward residual currents result from the baroclinic pressure gradient. A., Entrapment-zone model: a null zone exists at approximately 2 psu salinity, representing the landward limit of stratification and gravitational circulation. Residual currents are unidirectional landward, and bidirectional seaward of the null zone, where bottom currents move particles landward. A vertical residual current in the vicinity of the null zone is responsible for maintaining particles in suspension, resulting in a turbidity maximum. B., Bathymetric-control model: gravitational circulation depends on water depth and steepness of the baroclinic pressure gradient. When the LSZ is in Suisun Bay, the baroclinic pressure gradient is insufficient to stratify the water column because of strong turbulent mixing. Stratification and gravitational circulation are strong in deeper areas such as Carquinez Strait. The landward limit of this circulation occurs at the shoal, resulting in a bathymetrically-fixed null zone and turbidity maximum.

current calculated from continuity and believed responsible for maintaining particles in suspension (Peterson et al. 1975; Arthur and Ball 1979). When the salt field moves further up the estuary, it produces a steeper longitudinal salinity gradient in Suisun Bay, since the gradient begins to flatten out below about 2 psu (see Figure 2B in Jassby et al. 1995). This can result in gravitational circulation in Suisun Bay in fall, but only when the 2 psu isohaline is further landward, which is not consistent with the entrapment zone model.

Because the putative entrapment mechanism has not been observed in Suisun Bay, a less ambiguous or misleading term for this hydrologic zone of the estuary may be the Low-Salinity Zone (LSZ), essentially the same as the oligohaline zone of the Venice classification system (Cowardin et al. 1979). The revised conceptual model for this region (Figure 25B) shows that stratification and gravitational circulation in the LSZ persist only in deeper waters, e.g., in Carquinez Strait. There is no null zone associated with the LSZ in Suisun Bay, although a persistent, spatially fixed null zone with a turbidity maximum has been noted where Carquinez Strait abruptly shoals into Suisun Bay at Benicia (Schoellhamer 2001).

The relationship between X2 (i.e., the location of the LSZ) or flow and the abundance of various biota in the estuary is discussed below. Two important physical features of the estuary bear on how those relationships can be considered and how they might work. The first is the lag time in the response of the estuary to changes in flow discussed above, which means that pulse flows must be large and long-lasting to affect the estuary. The second is that except under very high-flow conditions, the LSZ is vertically well-mixed. This means that there is no way for river flow per se to penetrate the estuary west of Suisun Bay; the degree of stratification and gravitational circulation is directly related to the longitudinal density gradient but only indirectly related to river flow. The implication for biota is that river flow usually does not disperse organisms into seaward areas as previously hypothesized (e.g., Armor and Herrgesell 1985). This may happen under extremely high-flow conditions, however, when much of the area of the estuary is fresh.

Conceptual Model

The physical responses of the estuary to freshwater flow are summarized in Figure 26. Flow has direct influences only within the freshwater Delta, where it affects the inputs of various substances (sediment, organic matter, contaminants), inundation of flood plains, and travel time of water, particles, and fish down the rivers to the Delta. Inflow and export flows (including within-Delta diversions) determine Delta outflow and the overall pattern of flows determines residence time in the Delta. In addition, export flow together with the position of the salt field (which influences the position of populations of organisms) affects the rate of entrainment of organisms. Freshwater flow influences the brackish estuary by establishing a tidally-averaged barotropic (i.e., water level) pressure gradient that forces the depth-averaged residual flow and transports salt seaward. The salinity gradient resulting from the mixing of salt up into the estuary produces the baroclinic (i.e., density-driven) pressure gradient, which opposes the barotropic pressure gradient. The baroclinic gradient promotes stratification and gravitational flow, which are both opposed by turbulence produced by tidal shear. The three principal longitudinal flow patterns (depth-averaged residual, tidal, and gravitational) together determine the residence time for water, substances, and particles, and influence the retention of organisms.

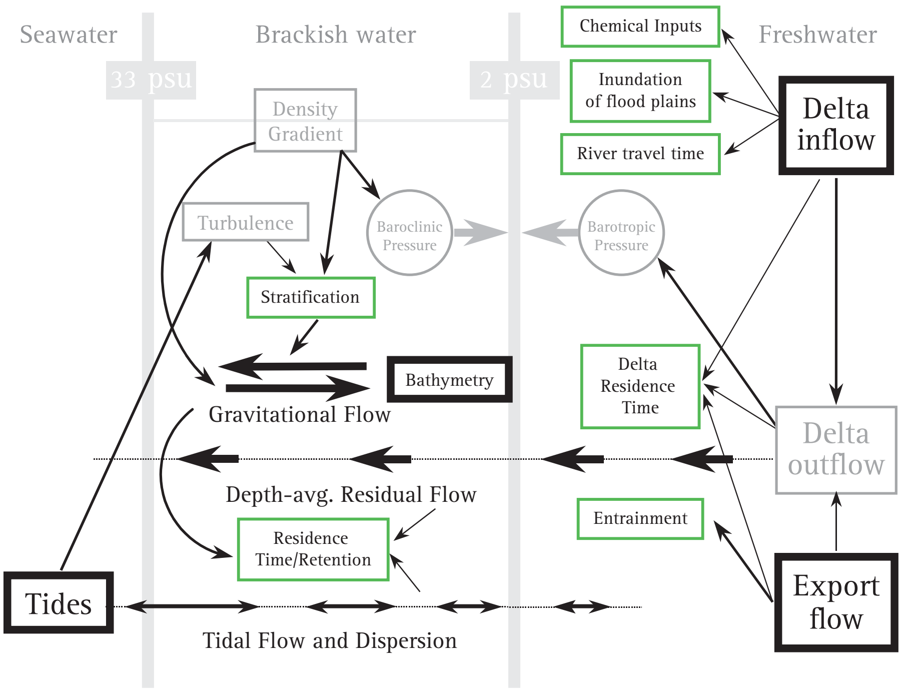


Figure 26. Conceptual model of effects of tide and freshwater flow on physical habitat in the estuary. Boxes with heavy lines are major forcing factors; those with lighter lines are intermediate responses; and those with double lines are responses that potentially influence habitat. Heavy arrows indicate various components of flow; intermediate arrows indicate positive influences; and thin arrows indicate negative influences. See text for further explanation.

Exchange Processes

Understanding exchange or movement of water, salt and other dissolved substances, sediment, and organisms between and within regions of the estuary is key to understanding how physical conditions in the estuary affect chemical conditions and how these together influence estuarine life. Exchange occurs through advection by the mean (river-derived) flow, and through longitudinal dispersion, which is predominantly a function of tides. Dispersion requires energy for mixing, and a concentration gradient: for example, dispersion can move salt up-estuary from high toward low salinity, but net down-estuary movement of salt can only occur through advection by the mean flow.

Exchange can be calculated as the product of instantaneous water velocity and scalars such as concentration, integrated over appropriate realms of time and space. Any process resulting in correlations between velocity and concentration provides a mode of exchange (Walters et al. 1985; Jay et al. 1997; Kimmerer et al. 1998). Although theoretically well-developed, measurements of exchange have proved difficult because variations in water velocity and scalars occur across a range of space and time scales, any of which could be involved in a predominant mode of exchange (Jay et al. 1997). Exchange of particles, particularly those that sink (sediment) or swim (organisms) is especially challenging. It is usually helpful to decompose the mathematical description of exchange into terms having known meanings and modes of variation (e.g., mean flow, gravitational circulation) and focus on those likely to be important. For example, longitudinal movement of organisms in the Low Salinity Zone was found to depend on the interaction between vertical movement of organisms and vertical variability in flow velocity at the tidal time scale (Kimmerer et al. 1998).

In the absence of persistent stratification, longitudinal dispersion occurs through tidal pumping and trapping and shear flow dispersion (Fischer et al. 1979). The tidal wave propagates up the estuary by alternative pathways that result in differences in phase because the wave propagation speed increases with increasing depth, and the time of travel depends on speed and the distance traveled. In the case where two channels branch off the main channel and then rejoin, as in Suisun Bay, phase differences may arise because of differences in both depth and distance, so that water masses that initially split apart at the branch will rejoin some distance from each other. Similarly, a wave will propagate up a shoal more slowly than in the nearby channel, resulting in phase differences. Propagation of the tidal wave up a side channel on a flood tide can result in a phase difference at the junction on the subsequent ebb. These phase shifts cause stretching and distortion of the water masses, resulting in longitudinal mixing. This mixing can be strongly affected by changes in the tidal wave speed or excursion due to modification of channel geometry, e.g., by dredging or alteration of estuarine area (Enright et al. 1998).

Another mechanism for exchange depends on the configuration of flood and ebb flows. For example, in both the Golden Gate (M. Stacey, UC Berkeley, pers. comm.) and Franks Tract (J. Burau, USGS, pers. comm.) in the Delta, flood flows occur as a jet resulting in strong mixing of the flooding water with the water in the wider basin just inside the entrance. On the subsequent ebb, the water moves out across the entire basin. The net result is a stronger exchange than would occur without the jet.

Stratification in the channels can have a profound effect on longitudinal transport by uncoupling the surface and bottom layers and promoting gravitational circulation, as discussed above. When stratification is strong, the effective longitudinal eddy dispersion coefficient can increase by an order of magnitude over that seen under unstratified conditions (Monismith et al. 1996; compare to values in Cheng and Casulli 1992). This leads to the paradox that turbulence in an estuary can actually impede longitudinal exchange by eliminating stratification (Nunes Vaz et al. 1989).

Vertical stratification in salinity can appear at the surface as a front. Analogous to meteorological fronts (but upside down), estuarine fronts mark the surface boundaries between water masses of different density (Bowman and Esaias 1978; Largier 1992, 1993; O'Donnell 1993). As with vertical density gradients, fronts impede the exchange of materials, and are often locations of strong downward movement resulting in visible accumulation of foam and debris at the surface and differences in turbidity in the adjoining water masses (Largier 1992). In the San Francisco Estuary, ephemeral shear fronts typically form and dissipate on a tidal cycle because of differences in tidal velocity in shoals and channels (O'Donnell 1993). Because these fronts are ephemeral, they probably contribute little to exchange over subtidal time scales or between embayments, although they are important to exchange within embayments. Numerous fronts are visible in salinity data from an example transect through the northern estuary (Figure 23).

An important mode of exchange in many shallow estuaries is Stokes' drift. This is a net transport of water, salt, and particles up-estuary due to the phase between the tidal height and velocity as the tidal wave progresses up the estuary. This phasing can result in a positive correlation during the tidal cycle between water depth and water velocity, such that particles and water are moved up-estuary. Although this is unimportant in the channels of Suisun Bay (Burau 1998), its importance in other areas of the estuary has yet to be determined. Stokes' drift may be important over shoals, implying that it could be a significant mechanism for longitudinal exchange in most basins of the estuary.

Exchange processes can be conceptualized in terms of residence time, defined as the average time that a particle of water, salt, sediment, or other material spends within a region (Monsen et al. 2002). Residence time of a conservative property (i.e., one that is not produced or consumed within the water body) is the total quantity of that property (e.g., amount of water or salt in a body of water) divided by the rate of input or output of that property across all boundaries. This concept is most useful when applied to regions of the estuary that are well-defined and have relatively few points of exchange with other regions. Residence time in various basins of the estuary varies inversely with exchange rate, and with the mode of exchange and therefore the nature of the property. Thus, residence time of water in the northern estuary decreases sharply as freshwater flow increases, but residence time of certain kinds of particles may actually increase because of gravitational circulation.

Smith and Hollibaugh (2000) estimated residence times using a salt mass-balance approach. Residence times for the northern estuary, including only part of the Delta, ranged from 2 to 14 days in the wet season and 19 to 29 days in the dry season, while residence times in the South Bay were 8 to 51 days in the wet season and effectively infinite in the dry season. Walters et al. (1985) reported hydraulic replacement times, i.e., volume divided by freshwater inflow, for different regions of the estuary. Unlike residence times, hydraulic replacement times neglect tidal mixing, but are much easier to calculate. Hydraulic replacement times for Suisun and San Pablo bays were 1.2 days under high flow conditions and 60 days under low flow, while corresponding values for the South Bay were 120 and 160 days.

Exchange between the estuary and the coastal ocean is important because the ocean is the source of salt, some organisms, and possibly nutrients and organic matter, and the sink for materials produced in or transported through the Bay including freshwater, sediment, contaminants, organic matter, and organisms. Several analyses have estimated exchange at the Golden Gate; however, the seaward boundary of the estuary from a hydrodynamic perspective may be the sill west of the Golden Gate (Largier 1996), for which relatively little information exists about exchange processes. Exchange through the Golden Gate is complex, with strong vertical stratification and lateral variability in current velocities and tidal phase (Petzrick et al. 1996; Largier 1996). Exchange occurs through tidal flow, gravitational and lateral circulation (Conomos 1979a; Walters et al. 1985), changes in sea level due to the spring-neap tidal cycle, wind stress, and large-scale atmospheric pressure gradients (Walters and Gartner 1985; Largier 1996). Circulation is ebb-dominated on the northern side and flood-dominated on the southern side of the main channel (Petzrick et al. 1996). Gravitational circulation is controlled largely by the salinity gradient due to freshwater flow in winter and spring, and by variation in density due to upwelling of cold, salty water in the adjacent ocean when freshwater flow is low and the estuarine salinity gradient has moved landward (Largier 1996).

Exchange between South and Central Bay is strongly affected by the salt field in the northern estuary. When Delta outflow is high and X2 is seaward, salinity in the Central Bay is reduced. Under these conditions an inverse estuarine circulation cell can be set up in South Bay with residual circulation to the south at the surface and north at the bottom (McCulloch et al. 1970; Schemel 1998). This increases stratification and decreases residence time in the South Bay.

Another area of active research is exchange between shoals and channels, an important mechanism for longitudinal mixing (Walters et al. 1985), and in phytoplankton production (Cloern et al. 1983; Lucas et al. 1999b), sediment transport (McDonald and Cheng 1997), and possibly recruitment of fish and macroinvertebrates. Exchange between shoals and channels is strongly affected by tides and also by longer-scale processes such as spring-neap oscillations, wind, and intrusions of low-salinity water (Huzzey et al. 1990). Recent work in Honker Bay showed that exchange between shoals and channels was very rapid, and that wind and the orientation of the channels resulted in up-estuary residual currents (Warner et al. 1996; Lacy 1999).

Exchange can be estimated using one of three general approaches. The most straightforward conceptually is also the most difficult in practice: measuring velocity and concentration at sufficient temporal and spatial resolution to allow the net flux to be calculated. The principal difficulty is the high degree of variation in velocity, although Acoustic Doppler Current Profilers (ADCPs) permit a much higher resolution of the velocity and turbulence field than was possible with current meters (e.g., Stacey et al. 1999a). The high variability remains when the tidal oscillation is subtracted out, resulting in a small net flux value with high variation. In addition, determining concentration with sufficient resolution for flux measurements takes a lot of sampling, and is particularly laborious for organisms (e.g., Kimmerer et al. 1998). The second approach is numerical modeling, using hydrodynamic models coupled with models of concentration or particle movement. This approach allows for much finer resolution than field measurements, but has disadvantages in both the hydrodynamic description itself (see "Modeling"p.36) and the accuracy of algorithms used to model particle movement (e.g., McDonald and Cheng 1997). The third approach is to use mass-balance to estimate either exchanges or "non-conservative" terms (local consumption or production), generally with salt as a tracer of mixing (e.g., Smith 1991, Peterson et al. 1985, Smith and Hollibaugh 2000). This approach is simple and straightforward, and is often useful for determining large-scale patterns of exchange. However, it is a relatively coarse measurement, lacking spatial and temporal resolution needed to answer some biological questions. In addition, this approach usually requires an assumption of steady state which is not often met in the San Francisco Estuary, particularly during times of high outflow.

Two key features of exchange processes need to be considered. First, most of the data used as input to models or analytical programs are measured at fixed stations, referred to by oceanographers as an Eulerian frame of reference. However, substances, particles, and organisms move in a Lagrangian frame of reference, following the water. Calculations or observations made in one frame cannot readily be transposed into the other. Second, estimates of exchange require the integration over time of processes that change rapidly (e.g., tides, turbulence, vertical movement, sediment concentration) to determine the much smaller net exchange rates. Small errors in measurements can readily accumulate into large errors in the results (Kjerfve and Proehl 1979). To minimize these errors requires a high frequency of measurements in time and space, particularly for the more rapidly-varying properties. Multiple independent approaches can be helpful in uncovering biases and missing source or sink terms.

Climate Change

Interest in long-term climate effects on the estuary has grown recently owing to concerns over global warming and sea-level rise, as well as recent discoveries about decadal-scale and interannual variability in regional climate and oceanography (e.g., Ebbesmeyer et al. 1991; Mantua et al. 1997; Dettinger et al. in prep.). Larger-scale influences on the estuary arise predominantly from meteorological effects, although upwelling and other oceanographic conditions can affect exchange between the Bay and the ocean. The principal meteorological effect on the estuary occurs through the timing and quantity of precipitation and freshwater flow, which has seasonal, interannual, inter-decadal, and longer-term patterns, although the shorter-term patterns have been altered by dams and diversions. The seasonal pattern of winter precipitation, spring snowmelt and runoff, and dry summer and fall is altered by variations in large-scale climate. Winter precipitation is related to the position of the Aleutian low-pressure system (Cayan and Peterson 1989, Wang et al. 1997), but modified by regional atmospheric pressure effects described as the "California Pressure Anomaly" (Peterson et al. 1989, 1995). The timing and amount of spring runoff, however, is a function of spring temperature which depends on the distribution of regional high- and low-pressure centers in the northern Pacific (Cayan and Peterson 1993). Snowmelt runoff, which supplies most of the water for human use in the Central Valley, has occurred in earlier months of recent years owing to a trend toward higher spring temperature (Roos 1989; Dettinger and Cayan 1995; Dettinger et al. 1998; Figure 3).

El Niño-Southern Oscillation (ENSO) events cause increases in precipitation in the southern United States, and decreases to the north (Dettinger et al. 1998; Cayan et al. 1999). The location of the San Francisco Estuary on the boundary between these regions can produce both wet (1983, 1998) and dry (1977) conditions during El Niños. The phasing of the ENSO event determines the frequency of heavy precipitation, particularly in coastal regions (Cayan et al. 1999). The frequency of ENSO events appears to vary on a decadal time scale (Pacific Decadal Oscillation, Mantua et al. 1997), with higher frequencies of ENSO events between 1977 and the mid-1990s (Ebbesmeyer et al. 1991; Chavez et al. 2003). Studies of palaeo-climate in the region and of millennial-scale variations in salinity in the San Francisco Estuary show larger variation than is seen in the historical record (Ingram et al. 1996a, 1996b; Ingram and Ingle 1996; Goman and Wells 2000), and evidence from tree rings shows periods of extreme precipitation for various intervals (Stine 1994). Thus, regional climate is highly variable at all time scales. Trends of less than a century's duration are difficult to distinguish from longer-scale variation and may not provide good estimates of the long-term mean.

Global climate can influence ecosystems through various regional manifestations (Stenseth et al. 2001). The future trend in global climate is almost certainly toward warmer conditions (IPCC 2001), which should result in a continuing trend toward earlier runoff (Dettinger et al. 1998, in prep.). Forecasts differ on the trend of total precipitation (IPCC 2001), so at present the expectation is for no change in total runoff in the Central Valley's watershed, but a continuing shift to an earlier runoff peak and therefore reduced availability of water during the dry season. These anticipated changes should be seen in the context of other regional activities including changes in patterns of demand for water due to population growth (Vörösmarty et al. 2000), as well as to economic, technological, and political developments.

Modeling Considerations

Substantial effort has been expended in developing and applying models of estuarine circulation and exchange processes. Models of circulation and exchange can be useful in testing theories, teaching about circulation, interpolating among sparse field data, and ultimately predicting physical responses to new conditions.

Before the 1990s much modeling effort centered on the US Army Corps of Engineers' Bay Model in Sausalito, a physical scale model of the estuary. This model has been made nearly obsolete by developments in computer simulations, although it still has considerable heuristic value. The principal disadvantage of a physical scale model is that scaling down from the estuary distorts the relationships among key forces acting on the water.

Several one-dimensional models of the Delta have been developed and applied (e.g., Enright et al. 1996, 1998). These models are widely used for regulatory and other purposes, and have great value for illustrating the relative influence of tidal and net flows in the Delta. The most recent version of the Delta Simulation Model (DSM-2) accurately depicted the phasing of tides at several key locations in the Delta and has been extensively validated against field data for stage and salinity (C. Enright, DWR, pers. comm.). However, these models may be limited in their depiction of the movement of particles and substances. Since momentum is not conserved at nodes connecting Delta channels, the influence of inertia on mixing and phasing of tidal transport cannot be represented. Furthermore, the interactions between channel geometry (both cross-sectional and plan view) and mixing are unlikely to be depicted very accurately. The movement of particles that sink or otherwise violate the assumption of neutral buoyancy can only be crudely parameterized. Of course, any model attempting to depict the movements of "particles" with complex behavior, such as zooplankton or fish, would have additional sources of error.

A two-dimensional model has been used to investigate tidal and residual circulation in Suisun Bay (Smith and Cheng 1987). An extension of that model (Casulli and Cheng 1992; Cheng and Casulli 1992; Cheng et al. 1993a) called TRIM2D (Tidal, Residual, Intertidal Mudflat) is capable of modeling the entire estuary. More recently this model has been developed into TRIM3D (Casulli and Cheng 1992; Cheng et al. 1993b). Both TRIM2D and TRIM3D have been applied to various problems in the estuary (Gross et al. 1999a, 1999b; Monsen 2000; Lucas et al. 2002; Monsen et al. 2002). An additional three-dimensional model has been developed by P. Smith (Smith and Larock 1993; Smith et al. 1995). One issue that needs to be addressed, however, is the turbulence closure scheme, the algorithm used to describe vertical turbulent mixing at a spatial scale smaller than that resolved by the model. In strongly stratified flows in Suisun Bay, the most commonly used turbulence closure scheme was found to underestimate the turbulent kinetic energy, thereby potentially misrepresenting the interaction between shear stress and stratification (Stacey et al. 1999b). New approaches may be needed to depict accurately the effects of stratification and destratification on exchange processes.

Preliminary results using TRIM2D show the potential importance of inertial effects at channel boundaries (Monsen 2000), but this model has not been subjected to intensive validation against field data. Furthermore, evaluations have been made (e.g., Figure 3 in Monsen and Monismith 1999) without stated criteria for deciding whether a model's representation of flow or salinity patterns is adequate, and without comparisons to the existing, simpler models.

Numerous models of physical dynamics in the San Francisco Estuary have been developed and applied for specific purposes. For example, a one-dimensional model of phytoplankton growth (Cloern 1991) has been extended by Koseff et al. (1993) and Lucas et al. (1998) to examine effects of stratification and benthic grazing on phytoplankton blooms. A tidally-averaged multiple-box model has been developed to investigate patterns of salinity distribution in the estuary (Uncles and Peterson 1995, 1996; Peterson et al. 1996; Knowles 2000). Finally, simulation models of wind and tidal heights and currents, with data-assimilation capabilities, have been developed into a real-time display system (SFPORTS; Cheng and Smith 1998; Cheng et al. 1998b; http://sfports.wr.usgs.gov/).

Key Findings and Uncertainties

Significant advances have been made in our understanding of circulation patterns in the estuary. Still, the details of physical processes governing mixing and circulation in the estuary remain poorly understood. Subjects of some recent advances, or research needs, include:

- *Climate*. The most likely influence of climate change is through a shift of the runoff peak from spring to winter caused by warming. Models do not agree on the trajectory of annual precipitation, frequency of storm events, upwelling, or wind.
- *Freshwater Flow*. Unimpaired freshwater flow has no time trend in annual amount during the last century, but a long-term trend toward an earlier runoff peak probably due to climate change. Delta inflow is about 80% of unimpaired flow, and closely correlated to unimpaired flow. Delta outflow has averaged about 70% of inflow since 1956, with a trend for lower outflow as export flows have increased.
- *Importance of Tides*. Tidal flows are far stronger than net freshwater flows in most of the estuary except under extreme high-flow conditions. Even in much of the Delta the tidal flows dominate over net flows, and tidal dispersion is a key mechanism for moving materials. The model of flow in the Delta by which net flow are calculated from mass balance has been replaced by one in which tidal and net flows both play a role. Nevertheless, further research is needed, e.g. on particle and fish movement in the upper estuary, and on the influence of physical configuration on exchange processes throughout the estuary.
- *Stratification and Gravitational Circulation*. Results of theoretical, modeling, and field studies show how the density gradient interacts with bathymetry at the tidal time scale to produce stratification and gravitational circulation. Although the salt field is relatively unresponsive to increasing freshwater flow, the up-estuary salt flux and therefore potentially the flux of materials and organisms should be stronger when flow is strong. This potential retention mechanism needs further investigation.
- *The Entrapment Zone*. Gravitational circulation is rare in Suisun Bay because it is shallow, so the early models of entrapment mechanisms do not apply there. Furthermore, the lack of stratification in the low-salinity zone except during high flow means that particles and organisms are not washed through Suisun Bay in the surface flow as previously believed. Instead, diffuse net seaward flow and circulation patterns at the tidal timescale must be responsible for transport.
- *Shoal-Channel Exchange*. The estuary's shoals differ fundamentally from the channels in many respects, including their response to wind, sediment composition, phytoplankton productivity, and movement and residence patterns of fish. Exchange between shoals and channels determines how these differences are maintained and the importance of processes on shoals to those in the channels. Field studies are resolving these uncertainties, but more progress needs to be made.
- *Exchange with the Ocean*. Although studies have been conducted and are in progress on the movement of water and salt through the Golden Gate, we know little about how that exchange varies with flow and oceanographic conditions, or the impor-

tance of that variation to recruitment of organisms into the estuary.

- *Modeling.* A variety of models is now available to simulate physical circulation and particle movement in the estuary. One-dimensional models have been most useful for modeling flow patterns in the Delta and for making predictions about flows and the movement of particles. Two- and three-dimensional models have been applied mainly as research tools to investigate flows in relatively small regions. As computer power continues to improve, more complex models with finer grids and richer internal dynamics become feasible. Nevertheless, the various models should be compared and their domains of applicability identified.

ESTUARINE CHEMISTRY AND GEOCHEMISTRY

This section examines sources, transport, and retention of substances, some of which are important to "water quality." Organic carbon and oxygen are discussed in the next section, and contaminants are covered in a separate paper (Spies et al. in prep.). Most of this discussion focuses on sediments and nutrients.

In general, the concentration and movement of a conservative property or substance can be described in terms of a balance between sources and sinks (i.e., processes or places where the material is added to or removed from the system). For example, the principal source of salt in the estuary is the ocean, although agricultural drainage provides a locally important source in the southern Delta (Schemel and Hager 1986). Salt enters the estuary from the ocean by a combination of tidal mixing and gravitational circulation, and is removed from the Bay by advective transport in the mean (net or river-derived) flow. The position of the salt field, including X2, reflects the recent history of the balance between these two fluxes. In the South Bay, net evaporation over precipitation in summer also results in a southward advective transport of salt and a northward dispersive transport due to the elevated salinity in the South Bay. Movement of salt provides a useful way of tracing the movement of water.

Most properties of interest in the estuary are non-conservative, i.e., they have sources or sinks internal to the estuary. The same principles as for conservative properties govern their movement, but non-conservative properties have one or more sources or sinks internal to the estuary. Principal non-conservative substances discussed here are sediments, nutrients, organic matter, and dissolved oxygen. Because the latter three are intimately involved in the dynamics of phytoplankton blooms, some of the information in the next two sections may be useful in understanding these dynamics.

Much of our understanding of the dynamics of non-conservative properties and substances in estuaries is achieved through the development of box models or other simplified models of chemical mass balance (e.g., Smith and Jokiel 1975; Officer 1980; Smith and Atkinson 1983; Smith and Hollibaugh 1997). These models often use salinity as a tracer to obtain the mass balance terms due to water movement, with the remaining imbalance ascribed to non-conservative terms including internal uptake, release, and transformation. In particular, graphs of some substances plotted against salinity (e.g., Figure 3 in Peterson et al. 1978) may be linear, indicating approximately conservative behavior, or nonlinear indicating either net uptake (concave up) or net release (convex up). Steady state is usually assumed to exist over a suitable time scale, generally the residence time for the region of interest. However, when inputs vary widely at time scales close to the residence time, steady-state assumptions do not hold and alternative analytical methods are required, such as time-varying models (e.g., Cifuentes et al. 1990).

Alternatively, individual nonconservative terms can be measured and mass balance calculated (e.g., Caffrey et al. 1996). Although this may be less accurate in determining long-term mass balance than more broad-based approaches described above, it provides information about mechanisms by which this balance is achieved and does not require an assumption of steady state. In some estuaries several alternative approaches have yielded information about both the mass balance and the source of imbalance in the estimate (e.g., Kemp et al. 1997).

Different "pools" or forms of a substance of interest may turn over at vastly different rates, resulting in variable behaviors of the substances on different time scales or during different seasons. For example, the residence time of dissolved heavy metals in the waters of the estuary is probably similar to the water residence time; however, heavy metals tend to be bound up in sediments and therefore to enter the sediment pool, which has a much longer residence time. The entire sediment budget of the estuary is out of steady-state over a time scale of decades (Jaffe et al. 1998), which must be considered in interpreting long-term mass-balance of heavy metals or other substances with an affinity for sediments.

Sources and pathways of biologically and chemically active materials differ between the northern estuary and South Bay. The northern estuary is more immediately affected by freshwater flow and agricultural drainage, while South Bay is more heavily affected by industrial and urban sources of various materials, and has much less rapid turnover of water especially during the dry season (see Exchange Processes).

Sediment Supplies and Budgets

Characteristics of bottom sediments vary estuary-wide mainly in response to variability in tidal and wind-driven currents. Larger channels have sandy bottoms because of tidal scouring (Rubin and McCulloch 1979; Nichols and Pamatmat 1988), whereas shoal sediments are generally finer because of lower tidal energy. Much of the sediment in South Bay is clay (<4µm) or silt (4 to 63 µm), with up to 30% sand (Regional Monitoring Program data). In other regions of the estuary, sandy sediments prevail in deeper channels, with fine sediments in shoal areas of Honker, Grizzly, and San Pablo bays (RMP data). Sandy sediments are particularly abundant in deeper parts of Central Bay, where sand waves due to strong tidal currents are visible on depth-sounder traces and on multibeam sonar composites. Sand is sufficiently abundant in parts of the estuary to be mined for use in construction.

The source of sediments to an estuary is ultimately erosion in the watershed followed by river transport and deposition in the estuary (Krone 1979). The supply of sediment to the estuary is approximately balanced in the long term by export to the coastal ocean and burial. A similar quasi-equilibrium exists between local deposition and resuspension such that the short-term movement of sediment vastly exceeds the longer-term rates of net accretion or erosion (McManus 1998; Postma 1967, 1980). Over a time scale of centuries, sediment accumulation rate has varied substantially, probably because of changes in patterns of precipitation and therefore erosion and runoff (Ingram et al. 1996a, 1996b; Ingram and Ingle 1996; Goman and Wells 2000). Trapping of sediment by marshes (Patrick and DeLaune 1990) may be less important to sediment budgets in the San Francisco Estuary than it once was because of the small remaining area of tidal marsh compared to the area of open water (Atwater et al. 1979).

The long-term sediment trend was disturbed by a huge influx of sediments due to hydraulic mining in the watershed in 1850 to 1884 (Krone 1979). This sediment source caused an accretion of about 1 meter averaged over San Pablo Bay, with much larger local accretion (Jaffe et al. 1998). Net sediment accumulation in San Pablo Bay continued until the mid-20th century, forming extensive mudflats and fringing marshes, after which net erosion occurred. In Suisun Bay, erosion over the last 130 years has exceeded accumulation due to hydraulic mining, and the extent of intertidal mud flat has decreased from a maximum of about 52 square kilometers at the end of the mining period to about 12 km^2 by 1990 (Cappiella et al. 2000).

Sediment now enters the estuary predominantly during floods which inundate the Yolo Bypass and other flood plains (Oltmann 1999). Although some sediment leaves the estuary directly, producing visible turbid plumes in the coastal ocean during floods (Ruhl et al. 2001), most is deposited and retained within the estuary for a long time before being dispersed to the coastal ocean (Krone 1979, 1996). The supply rate from the Sacramento River may be decreasing because of trapping behind dams (Oltmann 1996; Oltmann et al. 1999). This decline can be seen most clearly in the trend in concentration with the effect of flow removed (Figure 27A), which occurred over a time period when river flow had no trend. A decrease in sediment supply rate is also indicated by the net erosion referred to above, which is a more robust indicator of long-term sediment supply than the short-term measurements of sediment loading rate.

Reduced sediment supply is likely to continue, and combined with sea-level rise it should result in loss of shallow areas and an increase in the sediment needed to construct and maintain marshes. In San Pablo through South Bay a loss of sediment may result in erosion and loss of mudflats. These mudflats may also be captured through the aggressive growth of the invasive smooth cordgrass, *Spartina alterniflora* (Callaway and Josselyn 1992). These mudflats are important habitat for large populations of migratory birds (Warnock and Takekawa 1995; Poulton et al. 2002).

Movement of sediment is a complex phenomenon that depends on sediment characteristics such as grain size and cohesiveness; turbulence, which maintains sediment particles in suspension; and shear stress across the bottom, which can erode bottom sediments and prevent settlement (Rubin and McCulloch 1979; Ruhl et al. 2001). Sediment movement can influence the distributions of contaminants (Bergamaschi et al. 2001) and biota, and can have short-term (Cheng et al. 1999) and long-term (Jaffe et al. 1998) effects on bathymetry and bottom roughness, which in turn affect tidal flow patterns and gravitational circulation. The sediment balance within the Bay is also affected by dredging of channels, which is required to offset the tendency of sediments to accumulate in low-energy environments. Dredging can affect not only the distribution of sediments and their associated contaminants and biota, but also the bathymetry of the estuary and thereby the extent of gravitational circulation, possibly affecting the salt field (Burau 1998). On the other hand, dredging appears to have only local effects on turbidity in the water column, owing to the dynamic natural processes that keep sediments in suspension (Schoellhamer 2002a).

Sediment resuspension and movement is a strongly nonlinear function of movement of the overlying water. Movement occurs predominantly at the tidal time scale because of short-term deposition and resuspension (McDonald and Cheng 1994, 1997; Schoellhamer 1996, 2001, 2002b), although the brief period of slack water does not permit much deposition (Schoellhamer 2001). Spring-neap cycles have a strong effect on suspended sediment concentrations through their influence on tidal current velocities and shear stress (Schoellhamer 1996, 2001). Wind-driven resuspension can also be strong in shoal areas (Schoellhamer 1996; Warner et al. 1996) and resuspended sediments can be conveyed to channels (Gartner et al. 1997). Because of these short-term, localized processes, patterns of suspended sediment concentration tend not to be closely related to salinity patterns (Powell et al. 1989).

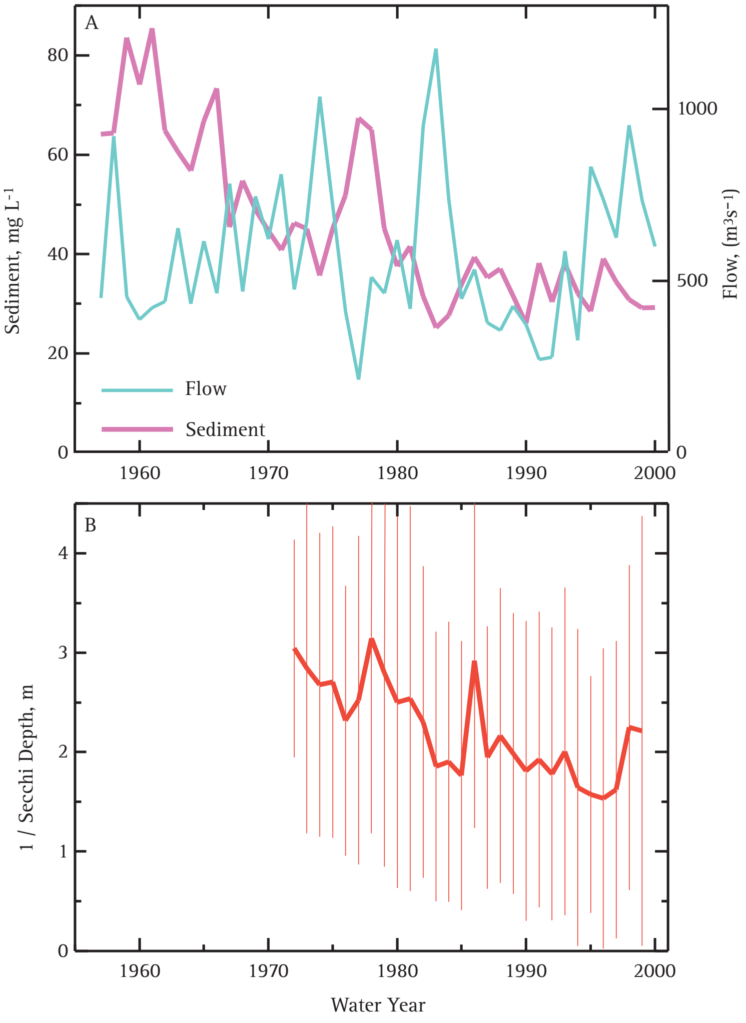


Figure 27. A, sediment concentration with effect of interannual variation in flow removed (magenta line) and freshwater flow (blue line) for stations near Sacramento. Sediment concentration was modeled using a generalized additive model (gam) of log concentration as a smoothed function of log flow (Venables and Ripley 1997). Annual mean residuals from this relationship were then added to the long-term mean log concentration, and antilogs calculated. The gam regression explained 97% of the variance in log concentration. Sediment data from USGS, flow from Dayflow. B, Water column turbidity estimated as 1/Secchi depth for the delta during summer months (June to October) with 95% confidence limits of the raw data. Data, from IEP water quality monitoring, include all stations with a record extending through most of the time period.

Seasonal patterns of sediment movement occur in response to seasonal patterns of both runoff (Krone 1979) and wind (Schoellhamer 1996). Fine sediments are winnowed from the bed and the bed sediment becomes coarser and less erodible through summer in San Pablo Bay (Krone 1979; Nichols and Thompson 1985a). Suspended sediment concentration tends to decrease during late summer and fall as the supply of erodible sediment decreases (Schoellhamer 1997, 2002b).

Tidal and wind-driven resuspension of fine particulate matter makes the San Francisco Estuary highly turbid (Conomos and Peterson 1977; Krone 1979). Concentrations of suspended particles are generally highest in Suisun and San Pablo Bays, moderate in the Delta and South Bay, and lowest in Central Bay (Conomos and Peterson 1977; Cloern 1987). Mean values of SPM (suspended particulate matter) ranged from 10 mg L^{-1} in Central Bay to nearly 100 mg L^{-1} in Suisun Bay (Conomos and Peterson 1977). In most of the estuary, values were higher in summer than winter presumably because of wind-driven resuspension; values in the western Delta and Suisun Bay tended to be higher in winter, probably because of riverine input (Conomos and Peterson 1977). Continuous measurements made since 1992 with optical backscatter sensors at locations throughout the estuary (e.g., Buchanan and Schoellhamer 1995,1996; Schoellhamer 2002b) show very strong tidal variability superimposed on more slowly-varying signals presumably due to seasonal effects of wind and freshwater flow.

An estuarine turbidity maximum or ETM is a prominent feature of many estuaries (e.g., Postma and Kalle 1955; Festa and Hansen 1978). Flocculation due to electrostatic charge may result in increasing turbidity in the low-salinity regions of estuaries (Postma 1967), but ETMs are probably caused more by dynamic processes than flocculation (Postma and Kalle 1955; Postma 1967; Schoellhamer 1998). These processes include tidal resuspension and deposition, gravitational circulation, and ebb-flood asymmetries in vertical velocity profiles (Postma 1967; Jay and Musiak 1994; Grabemann 1997; Guezennec et al. 1999).

Trapping of suspended sediment by gravitational circulation cells in Suisun Bay has been extensively discussed and interpreted using terminology and conceptual models based on the assumption of gravitational circulation in the ETM , "entrapment zone", or "null zone" (Peterson et al. 1975; Arthur and Ball 1979; see Kimmerer 1998 for a discussion of these terms). However, recent research has revealed that gravitational circulation is uncommon in Suisun Bay. Gravitational circulation near a sill at Benicia on the eastern margin of Carquinez Strait produces an intense turbidity maximum that is geographically fixed (Schoellhamer 2001) rather than moving with a particular salinity range as predicted by earlier models (Peterson et al. 1975; Arthur and Ball 1979).

A near-surface turbidity maximum in the Low-Salinity Zone consistently observed by monitoring programs (Kimmerer et al. 1998, Schoellhamer 2001) may be an artifact of sampling most often near the end of the flood, when short-term resuspension at the leading edge of the salt field results in ephemeral maxima in turbidity (Schoellhamer 2001). In addition, flocculation appears not to be a major mechanism for increasing turbidity in this region (Schoellhamer 1998), as it can be in other estuaries (Postma 1967).

Trends in turbidity are not apparent in the data from continuous monitoring sites, mainly because of their relatively short duration and the high variability in the data. However, Secchi disk data from the Delta and Suisun Bay show a trend of increasing clarity over the period of record (Figure 27B). This could be due to the decrease in sediment supply (Figure 27A), but a potential alternative cause is an increase in submerged aquatic vegetation, particularly the water weed *Egeria densa*, which may have increased trapping of fine sediments (Grimaldo and Hymanson 1999). The total estimated area of *E. densa* coverage in 2000 was 2400 ha or 11% of the area of the Delta (P. Foschi, SFSU, pers. comm.). Geographic variation in the rate of change of Secchi disk depth (Figure 28), however, does not match very well with the known distribution of *E. densa*, which is concentrated in shallow areas such as tidal lakes and small slough. Furthermore, the rate of change of water clarity was similar for all months from June to October, whereas *E. densa* develops seasonally with highest coverage in late summer to fall.

Contaminants, particularly heavy metals, are commonly associated with fine sediments. Water column trace element concentrations were closely correlated to suspended-solids concentrations in samples from the Regional Monitoring Program (B. Thompson et al. 2000), allowing the (much more expensive) metal analyses to be supplemented with estimates based on suspended solids concentrations (Schoellhamer 1997). Toxicity of sediments to test organisms is frequent throughout the estuary, most often associated with metal contamination (B. Thompson et al. 1999; Spies et al. in prep.).

Relatively little work has been done on the biogeochemical transformations in the sediments of the San Francisco Estuary of substances other than contaminants (e.g., van Geen and Luoma 1999). General patterns of sediment chemistry are a well-established function of oxidation-reduction potential (Heip et al. 1995). Nichols and Pamatmat (1988, Figure 30) present a diagram of the major processes and relative depths in the sediment at which they occur. In general, sediment chemistry depends on the degree of irrigation of sediments with the overlying water, and the supply of organic matter. Irrigation increases with increasing grain size, increasing water velocity, and increasing degrees of bioturbation, or disturbance of sediments by benthic organisms (Officer and Lynch 1989). Strong disturbance of sediments was observed in a core from Richardson Bay due to bioturbation and shear, but much less in a core from San Pablo Bay (Fuller et al. 1999). Higher organic matter deposition, frequently associated with fine sediments, can increase the rate of benthic respiration resulting in anoxic conditions near the sediment surface. The top centimeter or so of sediment is usually oxygenated (Nichols and Thompson 1985a), but sediments below that layer can be anoxic, releasing sulfide to the overlying water column (Kuwabara and Luther 1993). Denitrification in the shoals (Hammond et al. 1985) also indicates anoxia in shallow sediments.

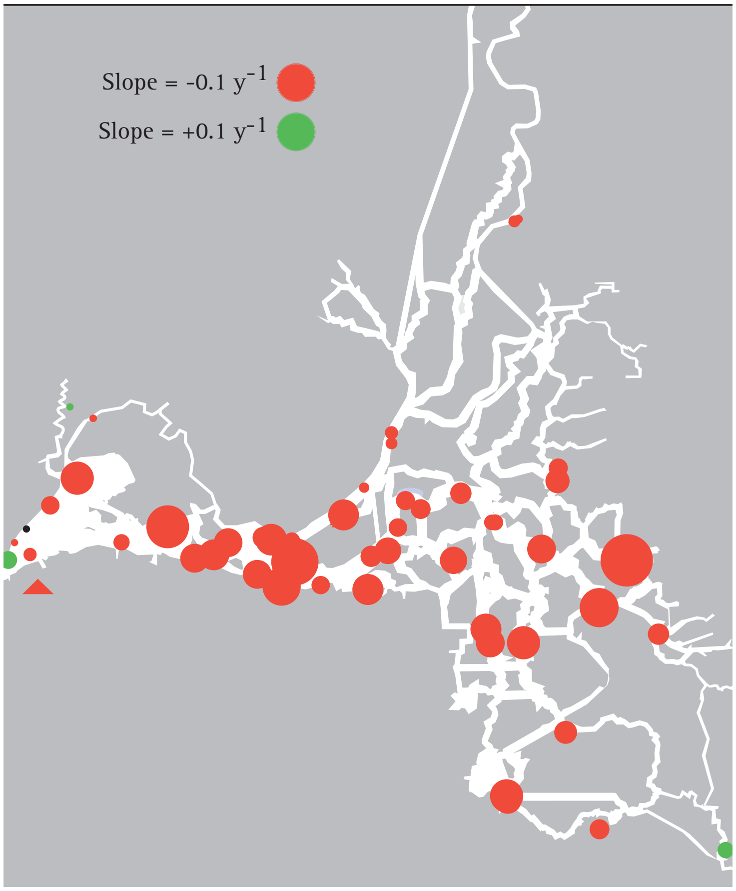


Figure 28. Spatial distribution of long-term change in turbidity. Data as in Figure 27B for individual stations, except that slopes of the long-term trends were calculated for each station by linear regression against year. Sizes of symbols indicate relative magnitude of the trend, and color indicates sign of trends significant at $p< 0.05$. Black symbols indicate no trend.

Nutrients

Dissolved inorganic macronutrients include the nitrogen forms nitrate, nitrite, and ammonium (together, dissolved inorganic nitrogen or DIN), soluble reactive phosphorus (SRP, often called phosphate), and silicate. Organic nutrients include dissolved organic N and P. Micronutrients such as iron (Martin et al. 1994) are unlikely to limit plant production in the estuary since concentrations tend to be high in sediments (Thomson-Becker and Luoma 1985) and the water column (Flegal et al. 1991). Here I discuss nutrient sources and sinks; the next section covers nutrient uptake by phytoplankton and nutrient limitation.

The general sources, modes of cycling, and behavior of nutrients in estuaries are discussed by Pritchard and Schubel (1981) and Nixon (1981). The chemistry of the major nutrients differs in some important aspects. First, all plants require nitrogen and phosphorus, whereas use of silicate is restricted to a few taxonomic groups, most notably diatoms (Officer and Ryther 1980). Thus, low silicate can limit diatom production even when other nutrients are plentiful. Second, the principal macronutrients have very different geochemistry, and that of nitrogen is particularly complex: fixed nitrogen occurs principally as nitrate, most often supplied by rivers, and ammonium, available from sewage and local recycling, and fixed nitrogen can be added by nitrogen fixation and removed by denitrification. Phosphorus has simpler chemistry than nitrogen but, at typical pH values in ocean and estuarine water, it can become tightly bound to sediments and therefore unavailable as a nutrient. Both nitrogen and phosphorus can be rapidly recycled when organic matter is consumed and respired by microbes and animals, but silicate has a much longer regeneration time. Third, sources of nitrogen and phosphorus include land drainage, agricultural drainage, and sewage, whereas silicate comes almost entirely from weathering of silicate minerals and subsequent runoff. Oceanic upwelling can supply all three macronutrients.

The principal environmental concern for many estuaries is that excessive nutrient loading promotes eutrophication, in which high plant production and subsequent microbial respiration deplete oxygen, producing anoxia in subsurface waters and sediments (e.g., Ketchum 1967; Ryther and Dunstan 1971; Jaworski 1981; Nixon 1981; Boynton et al. 1982; Baird and Ulanowicz 1989; Smetacek et al. 1991; Fisher et al. 1992; Rabalais and Nixon 2002; NRC 2000). Eutrophication is no longer widespread in the San Francisco Estuary. Until passage of the Clean Water Act and resulting improvements of sewage treatment in the 1960s - 1970s, waters of the San Francisco Estuary were often depleted in oxygen because of excessive loading of organic matter (Nichols et al. 1986). Since that time, depressed water column oxygen concentrations in the San Francisco Estuary have been confined to a region of the Stockton Ship Channel (See "Dissolved Oxygen" p. 62) and local conditions or uncommon events (e.g., Cloern and Oremland 1983).

The principal reason for the current lack of widespread eutrophication in the San Francisco Estuary is the turbidity of the estuary, which results in light limitation of phytoplankton most of the time (Cole and Cloern 1984). This condition is typical of estuaries with high turbidity (e.g., Hudson Estuary, Cole et al. 1992; Gironde Estuary, Irigoien and Castel 1997).

Nutrients are supplied to the estuary mainly from wastewater treatment plants (WWTPs; Hager and Schemel 1992, 1996; Smith and Hollibaugh 2000), but also from rivers, urban and agricultural drainage, and the ocean. WWTPs also supply much of the nutrient content of river waters entering the Delta, with agricultural sources contributing a smaller amount (Hager and Schemel 1992). The oceanic source may be important during the summer upwelling season when oceanic nutrient concentrations are elevated (Peterson et al.1985); nearby Tomales Bay receives much of its nutrient supply as organic matter from the coastal ocean (Smith and Hollibaugh 1997). The flux of nutrients from the sediment to the water column is often considered a source term but is more accurately described as a recycling term.

Silicate is particularly amenable to geochemical model analysis. It has no dissolved organic form, and most of the non-conservative processes, including exchange with mineral particles and recycling from organic particles, are slow relative to water residence time in the San Francisco Estuary, so that they can be neglected. The one major exception is uptake by phytoplankton. Since silicate is recycled slowly once it has been incorporated in phytoplankton cells, uptake approximately equals removal of dissolved silicate, at least on a seasonal or shorter time scale (Conley et al. 1993). During winter, with low temperature (thus low metabolic activity) and high runoff, silicate behaves nearly conservatively, whereas during dry periods silicate is substantially reduced by uptake (Conomos et al. 1979; Peterson 1979; Peterson et al. 1978, 1985). Nitrate, ammonium, and phosphate have substantial estuarine source terms in winter, presumably from WWTPs (Figure 5 in Peterson et al. 1985), and unknown exchange with dissolved organic forms making calculations of mass balance difficult (Smith and Hollibaugh 2000).

Peterson et al. (1978) observed depressions in silicate concentrations at intermediate salinity in Suisun and San Pablo bays during dry summers, and related the depressions to a silicate uptake rate of about 1µg-at l^{-1} d^{-1}, corresponding approximately to a primary production rate of 350 mgC m^{-2} d^{-1}, similar to observed rates (Peterson et al. 1985). This suggests that most of the production was by diatoms. Reduced silicate depletion in 1976-1977 may have been due to increased benthic grazing on phytoplankton (Peterson et al. 1985). Depletion of other nutrients, particularly ammonium, is also observed in summer, but the extent of the depletion is difficult to evaluate because of the multiple sources and sinks of these nutrients (Peterson et al. 1985).

Nutrient sources and sinks vary by region. Nitrogen in the Sacramento River behaved roughly conservatively, but soluble reactive phosphorus (SRP) decreased slightly because of its reaction with inorganic sediments (Hager and Schemel 1992). Because the nutrient output of a WWTP does not vary strongly among seasons, the nutrient concentration of the riverine source to the Delta was inversely related to freshwater flow (Hager and Schemel 1992).

A nutrient box model for Suisun Bay showed that about 40% of the nutrient input to that region was from a local WWTP, with the rest coming from the Delta (Hager and Schemel 1992). In addition, the estimated non-conservative mass balance term was strongly, negatively related to chlorophyll, indicating that this term was due to uptake. Slight negative intercepts of relationships of non-conservative terms for DIN and SRP to chlorophyll were interpreted as possibly indicating denitrification and sediment adsorption (Hager and Schemel 1992). Concentrations of DIN (20 to 30 µM) are equivalent to chlorophyll concentrations of 53 to 79 µg Chl l^{-1} assuming complete conversion, a C:Chl ratio of 30 (Cloern et al. 1995), and a C:N molar ratio of 6.6. However, the uptake rate implied by Hager and Schemel's (1992) Figure 8 amounts to only about 0.14 d^{-1}, which implies slow net phytoplankton growth and the potential for nutrients to leave the Bay before they are taken up.

The nutrient picture in South Bay is quite different. DIN and SRP inputs primarily come from WWTPs in the south (Hager and Schemel 1996). Exchange with waters from the Central Bay, driven primarily by tides or by inverse estuarine circulation during high-flow periods (McCulloch et al. 1970), is the principal sink for SRP and also the principal source of silicate (Hager and Schemel 1996), while most DIN is apparently denitrified within South Bay (Smith and Hollibaugh 2000).

Benthic remineralization of nutrients co-occurs with benthic respiration, which depends on sediment characteristics, the previous deposition of organic matter, and the degree of physical disturbance or bioturbation. On short time scales, sediment nutrient fluxes respond rapidly to phytoplankton blooms in the overlying water column, both through the drawdown of water column nutrients which enhances upward flux, and the supply of nutrient-rich detritus to the bottom, providing substrate for remineralization (Grenz et al. 2000). Generally over a long time scale the sediments should be a sink because of net burial of nutrients, but in the San Francisco Estuary net erosion may release buried nutrients. Exchange of substances (including nutrients) between the bottom and the water column did not vary with wind speed, but appeared to depend on sediment movement by currents and, for silicate and ammonium, on the degree of bioturbation (Hammond and Fuller 1979; Hammond et al. 1985). Nutrient fluxes out of the sediment in South Bay were seasonally variable, responding on relatively short time scales to variability in temperature and organic deposition rate, particularly during the spring bloom (Hammond et al. 1985, Caffrey et al. 1998). Furthermore, denitrification was strong in shoal areas, resulting in a substantial removal of fixed nitrogen from the system (Hammond et al. 1985).

Dissolved inorganic carbon (DIC) is not generally considered a nutrient since it is usually available in excess in seawater and river water. In the South Bay DIC is supplied in excess by WWTPs, resulting in release of CO^2 to the atmosphere (Spiker and Schemel 1979). However, an inverse relationship between chlorophyll during blooms in the South Bay and the carbon isotope ratio of the particulate matter was used to infer carbon limitation during the blooms (Canuel et al. 1995). In Suisun Bay the isotopic composition of DIC indicated mixing between the freshwater and seawater sources with no apparent internal sources or sinks (Spiker and Schemel 1979; Canuel et al. 1995).

Key Findings and Uncertainties

Several prominent issues stand out for estuarine chemistry, geochemistry, and sediment movement, particularly over the long term.

- *Sediment Supply.* The rate of sediment supply to the estuary has declined, with an apparently related increase in water clarity in the upper estuary and net erosion in much of the estuary. If this trend continues it will lead to deepening of at least parts of the estuary, and sea level rise will accelerate that trend. The result of these changes may be a loss of valuable mudflat habitat, retreat of shorelines, and erosion of existing wetlands and those to be constructed. The construction of extensive marshes may lead to trapping of some amount of the existing sediment load. These effects may increase water clarity and enhance phytoplankton growth with an attendant risk of eutrophication. If allowed to expand unchecked, the invasion of mudflats by the cordgrass *Spartina alterniflora* may accelerate this trapping. All of these changes will need to be taken into account in designing and constructing new or restored wetlands.

- *Sediment Movement.* Sediment resuspension and settlement at the tidal time scale has been shown to be important to understanding both short- and long-term movement of sediments. Wind- and tide-driven resuspension on shoals mobilizes sediments that then move to other parts of the estuary. Improved models of sediment movement at various time scales would be useful for understanding patterns of water clarity and predicting the effects of long-term declines in sediment input.
- *Nutrient Budgets.* Previous work has shown that mineral nutrients are supplied by WWTPs and the watershed, and are plentiful most of the time. However, attempts to determine estuary-wide nutrient budgets have been limited by the availability of nutrient concentration data and a lack of knowledge about denitrification and adsorption of phosphate onto sediments. Although nutrients do not often limit the development of plant biomass in the estuary, this could change in the future, in which case accurate nutrient budgets and measurements of budget components (especially benthic regeneration) would be helpful.

PRIMARY PRODUCTION

An estuarine food web obtains its energy from organic carbon fixed by primary production either within or outside the estuary. This section considers only the portion fixed within the estuary.

Primary producers within the estuary include phytoplankton, benthic microalgae, attached microalgae (seaweed), sea grasses and other submerged macrophytes, and floating vascular plants (e.g., water hyacinth, *Eicchornia crassipes*). All have essentially the same role in the ecosystem's carbon budget, which is to take up inorganic (sometimes organic) nutrients and carbon dioxide, absorb light, and produce organic matter. A key difference between the attached plants and phytoplankton is that plankton move with the water, and therefore are not subject to salinity variation at the tidal time scale (Laprise and Dodson 1993). In addition, geographic variation in abundance of phytoplankton can be confounded with variation due to salinity or other water properties. Phytoplankton are also subject to losses from the system, or movement out of favorable areas, by advection and dispersion. Some of these points are elaborated below.

Seagrass (Zimmerman et al. 1991) and macroalgae (Josselyn and West 1985) are minor producers owing to high turbidity and lack of suitable attachment sites for macroalgae, which are generally confined to Central Bay (Silva 1979; Josselyn and West 1985). However, Zimmerman et al. (1995) reported persistence of transplanted seagrass in Central Bay, and found light levels to be adequate. Seagrasses are of particular interest since extensive seagrass beds are often considered to indicate pristine conditions, and have declined in extent in many estuaries (e.g., Nixon 1997; Fourqurean and Robblee 1999). Submerged macrophytes in the Delta, including the aquatic nuisance weed *Egeria densa*, are addressed by Brown (2003b).

Phytoplankton

Phytoplankton form the base of the pelagic food web throughout most water bodies, and play a key role in biogeochemical cycling of nutrients and trace metals in estuaries (Luoma et al. 1998). Production by phytoplankton is the major source of fixed carbon in the South Bay and an important source in Suisun Bay and the Delta (Jassby et al. 1993, 2002; Jassby and Cloern 2000). Cloern (1996) provided an excellent review of the role of phytoplankton in estuaries using the San Francisco Estuary as an example. In general, phytoplankton biomass and production in the San Francisco Estuary are near the low end of the range for large estuaries (Boynton et al. 1982; Cole and Cloern 1984, 1987, Jassby et al. 2002). For example, average annual surface chlorophyll concentration in Chesapeake Bay during 1982-2000 was 8 to 18 µg L^{-1} depending on region (Harding et al. 2002), compared to 2 to 8 µg L^{-1} for the San Francisco Estuary (means of data from regions of the estuary).

In general, phytoplankton production can be limited by temperature (i.e., by thermal limits on the maximum growth rate), light, nutrients including micronutrients, inorganic carbon, or grazing, and high levels of contaminants such as copper can inhibit phytoplankton production. Below I explore aspects of phytoplankton that may apply to all parts of the estuary, then examine some key regional differences in physical and chemical influences on phytoplankton.

Phytoplankton biomass is generally expressed as chlorophyll concentration, related to organic carbon through the carbon:chlorophyll ratio. This ratio varies among taxonomic groups and with growth conditions (Hunter and Laws 1981; Cloern et al. 1995), but is generally on the order of 30 to 50 (Cloern et al. 1985, 1995). Most of the measurements of chlorophyll in the estuary have actually been estimates based on in vivo fluorescence of untreated water samples, calibrated to chlorophyll measured by fluorescence of filtered and extracted samples. However, the relationship of in vivo fluorescence to chlorophyll varies with growth rate and species composition, and suspended matter and fluorescent dissolved organic matter can interfere with the measurement, so the calibration incorporates a moderate and variable amount of error. An example trace of fluorescence from a transect up the estuary shows numerous peaks and a general upward trend from Central Bay to the Delta (Figure 23).

Patterns of phytoplankton biomass differ substantially among regions of the estuary (Figure 29). Generally chlorophyll concentration in the northern estuary is characterized by declines either throughout the 1970s-80s in the interior Delta or as a step change in 1987-88 in the western Delta and Suisun Bay (see also Lehman 1996; Jassby et al. 2002; Kimmerer 2002a, 2002b). Chlorophyll in San Pablo Bay appears to have declined slightly in the late 1980s, and in South Bay and Central Bay chlorophyll concentrations have not changed substantially. Chlorophyll is highest in the southeastern Delta, presumably because of long residence time. Seasonal patterns also differ among the regions of the estuary: in Suisun Bay before 1988 there was a summer-long period of high biomass, which has since been replaced by a shorter, smaller

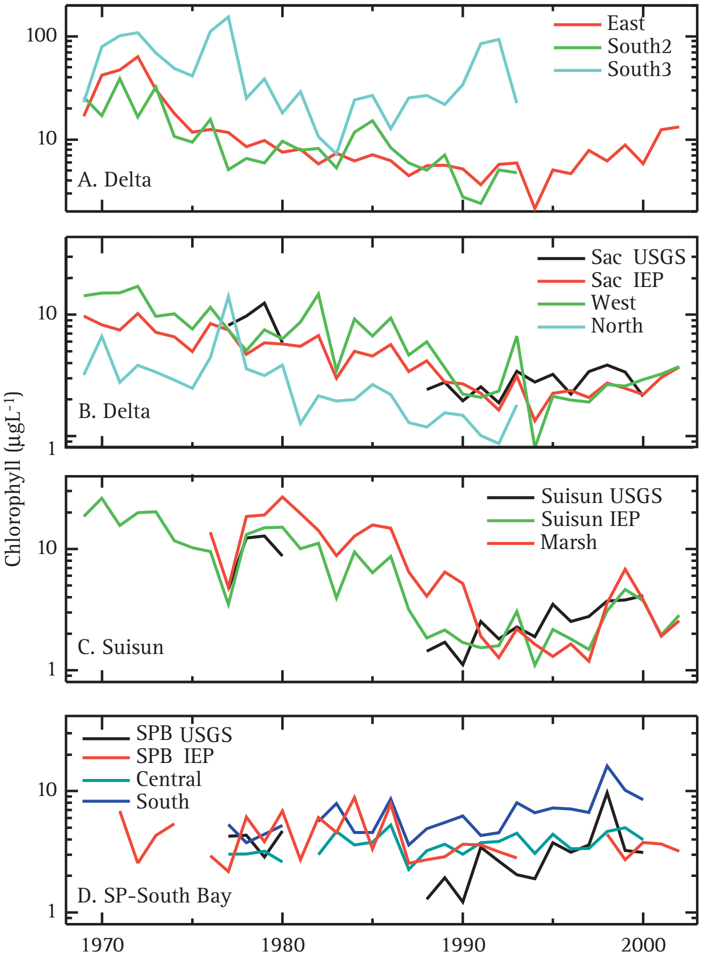


Figure 29. Time course of annual mean of monthly mean chlorophyll concentration for March-October from IEP and USGS monitoring programs, and for different regions of the estuary. Note scale change between panel A and the other panels; relative variation is the same throughout. The top two panels refer to regions of the Delta identified by Jassby et al. (2002):
A., two regions of the southern Delta and the eastern Delta;
B., the lower Sacramento River (below Rio Vista), the western Delta, and the northern Delta (at Hood on the Sacramento River);
C., Suisun Bay and channels of Suisun Marsh;
D., San Pablo, Central, and South bays. Although most of the data were from stations sampled consistently, the monitoring programs have had numerous additions and deletions of stations throughout the time period.

spring bloom (Figure 30). Seasonal patterns of chlorophyll concentration in South Bay (Figure 30C) are characterized by a single spring bloom, and seasonality in San Pablo Bay appears to be somewhere between these other bays (Figure 30B).

Primary production is the product of biomass and specific growth rate (i.e., growth expressed as a fraction of biomass per day), which generally depends on temperature and light and less on ambient nutrient concentrations (e.g., Laws et al. 1984). Primary production generally responds to variation in the physical environment (e.g., stratification, residence time) on a time scale related to that for phytoplankton biomass to double (Figure 2). It is usually measured by the incorporation of radioactively-labeled inorganic carbon into particulate organic matter during incubations of up to a day under light conditions that approximate natural light. Cole and Cloern (1984, 1987) developed an empirical model of phytoplankton production under light-limited conditions by which production is estimated from chlorophyll, incident light, and water transparency. This model predicted production reasonably well, explaining 82% of the variation in production in the San Francisco Estuary and similarly high values for other estuaries, although no estimate of the prediction error was given (Cole and Cloern 1984, 1987). The model was recently updated for use in the Delta (Jassby and Cloern 2000).

Phytoplankton Composition

Although many studies have included microscopic examination of phytoplankton, nearly all reports from these studies have been qualitative, reporting on the identities of common or bloom taxa. This probably emphasizes taxa that preserve well and are readily seen and identified, such as diatoms. Most of the bloom organisms in the northern estuary have been diatoms (Ball 1975; Ball and Arthur 1979; Cloern et al. 1983, 1985; Cole et al. 1986; Lehman 1996), and the percentage that was diatoms increased during blooms in Suisun Bay (Cloern et al. 1983). Most of the blooms in the brackish regions of San Pablo and Suisun bays were of the diatom *Skeletonema costatum* (Cloern 1979; Cloern and Cheng 1981), possibly seeded by populations from the coastal ocean (Cloern 1979). A decline in the last two decades in the proportion of phytoplankton biomass in diatoms in the Delta and Suisun Bay was attributed to changes in climate influencing the estuary through river flow (Lehman 1996, 2000a). Although the decline in total biomass in Suisun Bay was attributed to increased benthic grazing (Alpine and Cloern 1992), the possible influence of grazing on taxonomic or size composition has not been investigated.

Cloern et al. (1985) compared abundance of dominant phytoplankton in the major basins of the estuary for different seasons in 1978-1981. Bloom organisms in South Bay tended to be microflagellates rather than diatoms, and species composition of the blooms there often differed between shoals and channels.

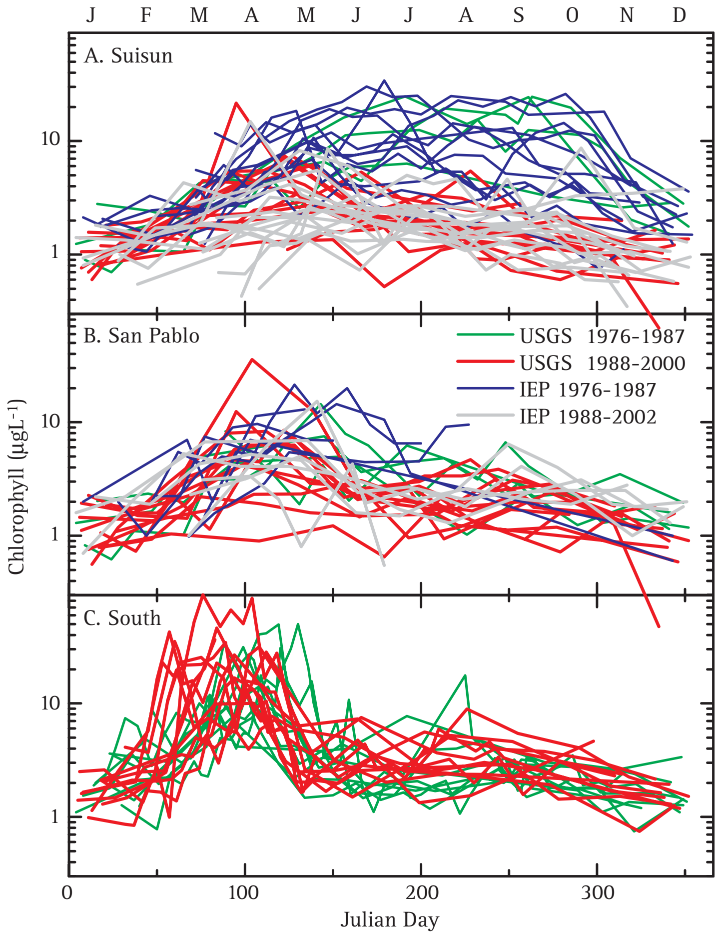


Figure 30. Seasonal variability of chlorophyll concentration from 2 sources and 3 locations and 2 time periods. A, Suisun Bay, B, San Pablo Bay; C, South Bay (USGS only). Each line is the seasonal pattern of monthly mean values for a single year from a single data source.

Blooms of nuisance algae cause various problems in many estuaries around the world (Anderson et al. 1993). The San Francisco Estuary has been affected only infrequently by these blooms, although red tides are occasionally reported in coastal waters. In 2002 a very dense bloom of *Heterosigma akashiwo*, a small flagellate sometimes associated with fish kills, appeared in waters of the Central Bay and coastal ocean (Herndon et al. 2003), although no fish kills were noted. A bloom of a dinoflagellate in the Berkeley marina was previously reported by Cole and Cohen (1998). The pigmented ciliate *Mesodinium rubrum*, a motile protozoan that functions essentially as a phytoplankton cell, occasionally occurs as visible streaks of red water at the surface in South Bay (Cloern et al. 1994) and has been observed in San Pablo Bay (F. Wilkerson, SFSU, pers. comm.). The diatom *Pseudonitzschia australis*, common in Monterey Bay, produces domoic acid which has been associated with mortalities of pelican and closure of shellfish beds there (Buck et al. 1992). This may enter the San Francisco Estuary, and may have already been collected here (Jassby et al. 1996). Blooms of *Microcystis* have occurred in the southern Delta (Lehman and Waller 2003).

No explicit analysis has been published of the distribution of species with regard to salinity. As shown below, species composition of both zooplankton and fish is strongly affected by salinity, with a suite of freshwater species that are uncommon in brackish to saline water. Freshwater phytoplankton are sensitive to osmotic stress and can quickly lyse on exposure to brackish water (Morris et al. 1978). Taxonomic composition of phytoplankton counts in freshwater regions of the Delta is dominated by diatoms including the large, bloom-forming diatom *Aulacoseira* (formerly *Melosira*) *granulata* (Ball 1987). Its high abundance in blooms often interferes with scientific sampling, and it may not be very nutritious for zooplankton (Orsi 1995).

Size distributions of chlorophyll have also been determined relatively rarely. Biomass by size class has been determined by several workers (Table 3), although with differences in methods, mesh sizes used, and scale of the measurements. Although these data do not allow for a test of the hypothesis that the size distribution of phytoplankton has changed, such a change would be consistent with the increase in benthic grazing in San Pablo and Suisun bays, particularly at higher salinities.

The cyanobacteria *Synechococcus* sp., is notable for its small size (ca. 1 µm) and importance to total phytoplankton biomass in the world oceans. Recent analyses have revealed that it made up 2% to 19% of the total chlorophyll in the San Francisco Estuary during spring-summer 1998, with higher values in the northern and southern reaches and lower values in the Central Bay and during the spring bloom (Ning et al. 2000).

Light Limitation

Light penetration into the water column depends on the concentration of fine particles which absorb and scatter the light. High turbidity in the San Francisco Estuary is due almost entirely to inorganic particles rather than to phytoplankton, as is the case in ocean

Table 3. Percentages of total chlorophyll in various size fractions by region of the estuary and year.

Time period	*Statistic*	*Location*	*>5*µm	*>10*µm	*>22*µm
1980 (Cloern et al. 1985, Cole et al. 1986)	Annual Mean	Suisun	96%		54%
		San Pablo	80%		35%
		South	78%		26%
Spring 1994 (Kimmerer et al. 1998, unpublished)	Grand median from 3 cruises	Suisun: S=0.5		41%	
		Suisun: S=1.6		25%	
		Suisun: S=3.3		22%	
Nov. 1999- Apr. 2000 (F. Wilkerson, SFSU, pers. comm.)	Median of up to 8 cruises	Suisun	59%	32%	
		San Pablo	39%	22%	
		Central	55%	47%	

Data from 1994 are presented for 3 salinity values during three 30-hour cruises in Suisun Bay to the western Delta.

waters and lakes as well as in many other estuaries (Riley 1967; Tyler 1975). Because of the high turbidity, phytoplankton production in the San Francisco Estuary is predominantly a function of light (Cole and Cloern 1984, 1987; Cloern 1987). An index of relative importance of light limitation to nutrient limitation showed that on some occasions nutrient limitation appeared important in South Bay but not in Suisun Bay (Cloern 1999).

The light level at a given depth in the water column has an inverse exponential relationship with the concentration of suspended particulate matter (SPM), and the depth at which 1% of the incident light remains depends inversely on SPM (Cloern 1987). The light level decreases exponentially with depth when the concentration of particles is uniform. The effect on phytoplankton is that net growth (i.e., photosynthesis minus respiration) in turbid water is possible only near the surface. This has great implications not only for total production but also for the dynamics of this production, which in turn influence the entire food web.

The depth of the 1% light level, which roughly defines the photic zone, is a useful index of how much of the water column can be used for photosynthesis. With a few exceptions, phytoplankton are passively drifting particles, so their vertical movements are governed by turbulence, and they move more or less randomly within the water column. When most of the water column is below the photic zone, respiration on average exceeds photosynthesis, and phytoplankton populations do not bloom. By contrast, blooms can develop when the photic zone is deep (because of clear water), the water column is shallow (i.e. over shoals), or the phytoplankton are trapped in the surface layer by stratification.

The critical depth (Sverdrup 1953), the depth to which integrated net production is exactly zero, is directly related to the depth of the photic zone and therefore inversely related to turbidity. If the critical depth is deeper than either the water column or the surface mixed layer in a stratified water column, a bloom should develop. In shallow estuaries phytoplankton are subjected to a number of loss factors that were not included in Sverdrup's original model, discussed further below. Cloern (1987) estimated the effective critical depth (i.e. the greatest depth at which blooms can develop including all loss terms) to be about 5 times the depth of the 1% light level; thus, blooms can develop when the photic zone depth exceeds 20% of the water column or mixed layer depth. Based on the relationship between light extinction coefficient and suspended particulate matter in the San Francisco Estuary in 1980 (Figure 2 in Cloern 1987), a uniform SPM concentration of 10 mg L^{-1} results in a critical depth of about 17 meters, deeper than about 90% of the area of the estuary (Conomos and Peterson 1977). Values of SPM often exceed about 200 mg L^{-1} (Buchanan and Schoellhamer 1999), corresponding to a critical depth of 1.8 meters; thus under turbid conditions (e.g., summer afternoons) net production appears possible only in the shallowest areas of the estuary.

In regions of the estuary where the mean depth is greater than the critical depth, net production can only occur if the water column is stratified at a depth shallower than the critical depth. This mechanism is responsible for the triggering of the annual spring bloom in the North Atlantic and other regions of the ocean (Sverdrup 1953). It has been inferred as a mechanism partially responsible for triggering blooms in the South Bay, with an added advantage that stratification insulates the phytoplankton from benthic grazing, which can be a major loss term (Cloern 1991; Koseff et al. 1993). However, a model analysis revealed some complications in the mechanisms working in South Bay, including the effects of sinking of phytoplankton cells and vertical (downward) mixing, both of which add loss terms not considered in the original model (Lucas et al. 1998). In addition, the relative importance of light limitation and benthic grazing can vary between channels and shoals, such that either can be source regions for phytoplankton blooms (Lucas et al. 1999a, 1999b), discussed further below.

Most studies of the response of phytoplankton to light levels have considered only spatial variation in water depth. However, in many parts of the estuary tidal range may exceed, or be a substantial fraction of, water depth. Lucas and Cloern (2002) modeled the response of phytoplankton to tidal fluctuations in tidal lakes in the Delta, concluding that the interaction between phytoplankton growth and changes in depth at the tidal time scale could be an important determinant of phytoplankton dynamics. In most parts of the estuary similar patterns would presumably be obscured by tidal advection.

Nutrient Limitation

For most of the year in most of the estuary, nutrient concentrations are sufficient to supply the requirements of phytoplankton. However, at certain times and places, nutrients can reach levels that may limit the further development of biomass. This most often occurs during and after strong phytoplankton blooms, when other conditions (e.g., clarity, stratification) are conducive to rapid growth. Such depletion has been noted in the Delta (Ball 1975; Ball and Arthur 1979) and in the South Bay (Hager and Schemel 1996). In particular, silicate can be depleted in the South Bay even though it is usually present before the blooms in about a 2:1 molar ratio to DIN, and its uptake by diatoms is approximately in a 1:1 molar ratio. The reason seems to be that DIN is rapidly recycled in the water column and benthos (Caffrey et al. 1996), while silicate has a much slower regeneration rate (Conley and Malone 1992). In particular, blooms of the ciliate *Mesodinium rubrum* may occur after diatom blooms when silicate has been depleted (Cloern et al. 1994). Thus, either DIN or Si could be the limiting nutrient, depending primarily on the extent to which freshwater flow from the north delivers Si to the South Bay. Phosphorus limitation is also becoming more likely in the South Bay with reductions in phosphate content of waste discharge (Hager and Schemel 1997).

This situation contrasts with frequent nutrient limitation of phytoplankton in many other estuaries (Fisher et al. 1992), where either nutrient loading is low (rarely the case in developed regions), hydrodynamic residence time long, or light limitation infrequent. The nutrient most often limiting is nitrogen (Fisher et al. 1992), although silicon can limit diatom production, and phosphorus can limit total production in some cases (Harrison et al. 1990). From a geochemical perspective nitrogen should not be the limiting nutrient in estuarine waters because the combined feedback loops of denitrification and nitrogen fixation should adjust the supply of fixed N to the availability of other nutrients such as P (Smith 1984, Smith and Hollibaugh 1989). However, this adjustment depends on residence time, which may be too short for the feedbacks to adjust the N supply (Kimmerer et al. 1993).

The role of ammonium in bloom dynamics is being investigated. Generally a high ammonium concentration suppresses uptake of nitrate (MacIsaac and Dugdale 1969). Dugdale et al. (2003) reported that estuarine phytoplankton may grow more rapidly on nitrate than on ammonium, leading to more rapid bloom formation after ammonium has been drawn down by phytoplankton uptake. This concept requires further investigation, and integration into the existing conceptual models of bloom formation in the San Francisco Estuary.

Grazing

Benthic grazing is considered a major influence on phytoplankton in many estuaries (e.g., Officer et al. 1982; Cloern 1982; Cohen et al. 1984; Nichols 1985; Alpine and Cloern 1992; Phelps 1994; Caraco et al. 1997). Shallow depth and large populations of benthic filter-feeders combine to maximize the influence of benthic grazing on phytoplankton in these systems. It is believed to be a major influence on bloom dynamics in the South Bay (Cloern 1991; Lucas et al. 1998, 1999a, 1999b). Grazing by benthic organisms, notably the Amur River clam *Potamocorbula amurensis*, may be responsible for significant interannual and longer-term variations in phytoplankton in Suisun and San Pablo bays (Nichols 1985; Alpine and Cloern 1992). The annual cycle of abundance of this clam may result in low abundance during the spring, such that the annual phytoplankton bloom in South Bay has not been affected but the summer high-biomass period in Suisun Bay has been eliminated (J. Thompson 2000).

Abundance of the clam *Corbicula fluminea* is associated with low chlorophyll in tidal lakes in the Delta (Lucas et al. 2002). Unfortunately data on the abundance of this clam do not predate the chlorophyll time series, so in contrast with *P. amurensis* there is no way to assess its effects directly. Routine monitoring does not cover enough stations to permit Delta-wide grazing rate estimates.

Grazing by zooplankton is generally considered a minor sink for primary production. However, Cloern et al. (1983) calculated that zooplankton grazing was an important pathway for losses of phytoplankton in San Pablo Bay.

Hydrodynamic Effects

Principal hydrodynamic effects on phytoplankton include horizontal transport (advection and dispersion), and vertical effects including changes in tidal height, stratification, vertical mixing, and boundary layer formation. Aggregation in the "entrapment zone" is discussed below.

Horizontal transport can move phytoplankton from an area of net production to an area of net loss. Thus phytoplankton can be supplied from a source region to other regions, enhancing biomass over what could be produced under local conditions, and depleting biomass in the source region. For example, phytoplankton in the Central Bay are often similar in species composition to the open coast, implying transport into the Bay (Cloern 1979). Similarly, transport of phytoplankton in the Delta to the export pumps is a major loss term that could limit phytoplankton biomass and therefore production, at least in the southern Delta (Jassby and Powell 1994; Jassby and Cloern 2000). Pulses of residual flow due to density gradients and wind resulted in large fluctuations in chlorophyll over shoals in the South Bay (Huzzey et al. 1990). Model studies showed horizontal advection or exchange to be important in allowing blooms in Suisun and San Pablo bays (Cloern and Cheng 1981) and in the South Bay (Lucas et al. 1999a, 1999b).

Advection and dispersion also affect the residence time of a region and can exert a controlling influence on bloom formation. Short residence time is commonly associated with breakdown of blooms or lack of bloom formation. For example, termination of blooms in the South Bay in 1982 may have resulted from strong advection due to density and wind effects (Huzzey et al. 1990). Model studies of South Bay indicate that local, short-term conditions can be important in bloom development, and that circulation patterns in and between shoals and channels can control development and location of a bloom (Lucas et al. 1999a). Subtle interactions between water movement and phytoplankton growth at the tidal time scale can affect the formation and propagation of a bloom (Lucas et al. 2002), and can effectively override local conditions that would otherwise result in a bloom (Lucas et al. 1999b). Phytoplankton in the Delta may bloom primarily when freshwater flow rates are low, resulting in long residence time (Ball 1987; Jassby et al. 2002). A time-series analysis of chlorophyll in the Delta and Suisun Bay showed that freshwater flow, water clarity, and temperature were all important (Lehman 1992); flow presumably influenced residence time. However, Jassby and Powell (1994) cautioned that the strongly nonlinear relationships between phytoplankton and environmental variables complicated the interpretation of linear time-series analyses.

The setup and breakdown of stratification is a major factor in the development of blooms in South Bay, and may be important in other regions. Most of the time the South Bay is vertically well-mixed, except during times of low tidal energy when stratification can develop and persist over several days (Cloern 1984). When this occurs in spring, a phytoplankton bloom develops (Cloern 1984, 1991; Cloern and Jassby 1994; Figure 30C), as has been observed in other estuaries (e.g., Sinclair 1978; Haas 1981). The mechanism behind this bloom has been examined in several field and modeling studies. First, Cloern (1991) developed a simple model of bloom formation that included a cycle of tidally-produced stratification and destratification, benthic and zooplankton grazing, vertical mixing, and sinking. This model was later elaborated by Koseff et al. (1993) using a more realistic, tidal time-scale formulation for mixing. This study demonstrated that hourly variation in strength of turbulence was an important determinant of phytoplankton population growth, that stratification had to last several days for full bloom development, and that strong wind mixing could suppress bloom development. Finally, Lucas et al. (1998) showed that losses from the mixed layer due to sinking and downward turbulent mixing were important in determining whether blooms formed.

Tidal stratification and destratification occurs at too short a time scale to influence blooms, which require days to develop (Lucas et al. 1998; Figure 2). However, tidal variation in water depth in shallow regions of the estuary can influence primary production through its interaction with the (nonlinear) response of phytoplankton to light (Lucas et al. 1999b; Lucas and Cloern 2002).

The effect of benthic grazing on a phytoplankton bloom is complicated by the interaction between grazing and hydrodynamics in the overlying water column. Benthic organisms ingest particles from the near-bottom water, and this removal must be balanced by the resupply of particles from the overlying water or by advection. The resupply rate depends on the degree of turbulent mixing but, because vertical water motions are constrained near the bottom, this rate can often be slow compared to the maximum ingestion rate of the benthic filter-feeders. This imbalance results in the formation of a concentration boundary layer, in which the concentration of phytoplankton (or other particles being consumed) close to the bottom is less than that in the overlying water column (Fréchette et al. 1989; O'Riordan et al. 1993; J. Thompson et al. 1999).

The thickness and extent of the concentration boundary layer depends on the velocity and depth of the water, bottom roughness, the abundance and pumping rate of filter feeders, and the characteristics of their filtration mechanisms. For example, the size and strength of the plume of water discharged by filtering bivalves can determine the thickness of the boundary layer (Monismith et al. 1990; O'Riordan et al. 1995). J. Thompson et al. (1999) conducted field and laboratory studies of the concentration boundary layer, and hypothesized that physical factors determined the strength of the layer (i.e., the degree of chlorophyll depletion), and physiology and behavior of the bivalves controlled temporal variability. A significant consequence of the development of these layers is that extrapolation of measured filtration rates from the laboratory to the estuary may result in overestimates.

Although many of the above results were obtained through studies in the South Bay, the principles should apply elsewhere. Stratification is frequent in Central Bay and the San Pablo Bay channel. Benthic grazing is at least as important in the northern as the southern estuary (Alpine and Cloern 1992). During high freshwater flows of spring 1998, an intense phytoplankton bloom in Central Bay followed, and may have been caused by, a period of strong stratification (Dugdale et al. 1999).

Delta

The freshwater Delta is unique within the estuary in having the largest source of freshwater and also the largest sink, the south Delta export pumps. Several key historical studies of phytoplankton in the Delta have recently been updated through a concerted effort to understand phytoplankton variability, emphasizing patterns on Franks Tract and Mildred Island, two flooded islands in the central Delta (Lucas et al. 2002).

Chlorophyll concentration in the Sacramento River rarely exceeds about 6 µg L^{-1}, while in parts of the Delta values over 100 µg L^{-1} have been recorded (Ball and Arthur 1979; Figure 29). The median chlorophyll throughout the Delta was about 34% higher than that in the rivers (Jassby and Powell 1994). Thus, while the river may provide seed populations, much of the Delta phytoplankton biomass is produced locally. Generally chlorophyll concentrations were higher in the eastern and southern Delta, presumably because long residence time minimizes losses due to transport (Ball and Arthur 1979), but also because sluggish circulation in these regions leads to greater water clarity and therefore higher production. Chlorophyll concentration at the most landward station in the San Joaquin River varied inversely with freshwater flow implying an effect of residence time (Ball and Arthur 1979).

Jassby et al. (2002) calculated primary production in the Delta using an updated version of the model by Cole and Cloern (1984, 1987). Annual primary production varied over a factor of 5, and there were distinct modes of variability. Winter-spring chlorophyll and primary production were inversely related to flow, mainly through the influence of residence time, and had declined over the period of record (Figure 29). Summer chlorophyll concentration in the Delta declined following the invasion of the Amur River clam (Kimmerer and Orsi 1996; Jassby et al. 2002).

As a whole, local net production is balanced by local consumption and transport losses, which include advective losses to the export pumps, and both advective and dispersive losses seaward. Jassby and Powell (1994) concluded from an analysis of chlorophyll distributions that dispersive losses were negligible, and that advective losses to the pumps were a major sink; however, Jassby et al. (2002) identified a much larger internal sink, possibly benthic grazing. A substantial fraction of the chlorophyll produced in the Delta entered Suisun Bay through advection. A steep gradient in chlorophyll between the Delta and Suisun Bay developed after 1987, presumably due to grazing by *Potamocorbula amurensis* (Alpine and Cloern 1992; Werner and Hollibaugh 1993; Kimmerer and Orsi 1996; Kimmerer et al. 1998). This gradient should result in additional dispersive losses from the Delta, which appear to have depressed chlorophyll concentrations in the western Delta (Figure 29B, also Figure 8 in Kimmerer and Orsi 1996). However, this dispersive loss term is still apparently smaller than the advective loss term on the scale of the entire Delta, under an assumption of a dispersion coefficient of about 100 m^2s^{-1} (Jassby and Cloern 2000). Either way, the Delta provides a subsidy to Suisun Bay in the form of phytoplankton biomass.

Phytoplankton in the Delta may also be affected by barriers erected to influence movements of water or fish (Figure 1). Jassby and Cloern (2000) found that installation of the rock barrier at the head of Old River in the southern Delta could have increased the mass loading of phytoplankton to the Delta by 36% to 86% during autumn in 1988-1990, probably less during higher-flow periods.

An additional effect on phytoplankton in the Delta is grazing by the introduced clam *Corbicula fluminea*. Where it is abundant in shallow water it has a strong effect on phytoplankton production in the overlying water column (Lucas et al. 2002). This may be the cause of the large unexplained loss term in the chlorophyll budget calculated by Jassby et al. (2002).

A positive correlation was noted between chlorophyll in the Delta and Secchi depth (Ball and Arthur 1979). This implies light limitation of production through turbidity, with a positive response of production and biomass accumulation when water was clear. Future increases in water clarity in the Delta may lead to higher phytoplankton production, although it is likely that the growth, depth distribution, and extent of *Egeria densa* and other nuisance aquatic weeds would also increase.

Suisun Bay/Low-Salinity Zone

A historical maximum in chlorophyll in the Low-Salinity Zone (salinity ca. 0.5 to 6 psu) has been attributed to the effects of hydrodynamic trapping (Peterson et al. 1975; Arthur and Ball 1979) and exchange between the channel and the extensive, productive shoals of Suisun Bay (Arthur and Ball 1979; Cloern et al. 1983). Model studies showed that both gravitational circulation and exchange between the channel and shoals were necessary for blooms to form (Cloern and Cheng 1981). Diatom cells in this region were aggregated with inorganic particles, presumably increasing their settling rate (Cloern 1979); however, the lack of gravitational circulation in Suisun Bay does not support a mechanism of entrapment (see “Movement of the Salt Field”, p. 27). Since 1987 there has not been a chlorophyll maximum associated with the Low-Salinity Zone (Alpine and Cloern 1992; Kimmerer and Orsi 1996; Lehman 2000b), so effects of hydrodynamic conditions on phytoplankton may be difficult to detect and may in any case be moot. Kimmerer et al. (1998) found no correlation between vertical distribution of chlorophyll (either whole or >10µm) and tidal velocity in the Low-Salinity Zone, i.e., hydrodynamic trapping was not detected.

Effects of river flow on chlorophyll concentration were examined by Cloern et al. (1983), who showed that chlorophyll in Suisun Bay was higher when the Low-Salinity Zone was in Suisun Bay than when it was either upstream or downstream. This was attributed to tight coupling between productive shoals and the deep channels, where gravitational circulation was thought to concentrate the cells. Unimodal peaks in chlorophyll at intermediate river flows have been observed in other estuaries (Bennett et al. 1986). However, analysis of chlorophyll concentrations within the Low-Salinity Zone have yielded conflicting results. Jassby and Powell (1994) concluded that chlorophyll concentrations in the LSZ were higher under intermediate flow conditions than under either high or low-flow conditions, with a negative effect of export flow rate. Kimmerer (2002a) found only a high-flow effect, except for the drought year 1977 when benthic grazing may have had a strong influence (Nichols 1985; Alpine and Cloern 1992). A sharp decline in chlorophyll after 1986 was attributed to benthic grazing (Alpine and Cloern 1992), but it occurred for the most part during a drought when low-flow conditions prevailed, possibly confounding the effects of low flow and benthic grazing. The difference in results between Jassby and Powell (1994) and Kimmerer (2002a) may be due to differences in data used, but should be resolved. Whatever the cause, the reduction in biomass after 1987 was apparently not due to changes in growth rate, since the relationship of productivity to biomass was the same in 1988 as in 1980 (Figure 3 in Alpine and Cloern 1992).

Flow above about 600 $m^3 s^{-1}$ appears to cause a reduction in chlorophyll in Suisun Bay (Cloern et al. 1983, Figure 3 in Alpine and Cloern 1992) as well as in the Low-Salinity Zone (Jassby and Powell 1994, Kimmerer 2002a) and the Delta (Ball and Arthur 1979), presumably because of reduced residence time throughout the northern estuary. It is probably safe to agree with Jassby et al. (1996) that the relative importance of different mechanisms relating river flow to chlorophyll concentration is not yet resolved.

Jassby and Powell (1994) showed a substantial advective transport of chlorophyll from the Delta to Suisun Bay, and argued that this effective subsidy was curtailed by export pumping. Much of the time Suisun Bay is brackish, and freshwater phytoplankton may not survive well there. Common species of the Suisun Bay shoals and the western Delta tended to be different (Ball and Arthur 1979). The advective transport of chlorophyll from the Delta to Suisun Bay may not contribute to bloom development in Suisun Bay except when it is fresh. On the other hand, this transport contributes to total chlorophyll and may represent a substantial organic carbon subsidy for Suisun Bay in the form of freshwater phytoplankton that lyse and release their contents because of salinity stress (Morris et al. 1978), supporting bacterial production in the LSZ (Hollibaugh and Wong 1996).

San Pablo/Central Bay

Relatively little analysis has been done of phytoplankton in this region. San Pablo Bay has rather similar bathymetry to South Bay, but because of its larger salinity gradient it may be stratified more often. San Pablo Bay may also be more turbid than South Bay. The connection of the central bay to the coastal ocean may result in import of phytoplankton blooms during and after upwelling events, as has been noted in Tomales Bay (Smith and Hollibaugh 1997).

South Bay

Many of the features of the phytoplankton of South Bay have already been discussed. One of the key features is the connection with the northern estuary through inflow of low-salinity water from the north, and the potential effect that has on stratification and bloom dynamics. A recent statistical analysis of the dependence of bloom formation on freshwater inputs revealed that only very high-flow events influence the strength of bloom formation (Cloern and Jassby 1994). At lower flows, with higher salinity in Central Bay, the formation of blooms in South Bay depends on local factors such as wind mixing and local freshwater inputs (Koseff et al. 1993; Cloern and Jassby 1994).

Much of the annual productivity in South Bay occurs in spring blooms, unlike Suisun Bay where chlorophyll concentration was previously elevated during spring through fall (Cole and Cloern 1984), although the patterns are now more similar (Figure 30). Bloom formation in the South Bay is spatially as well as temporally variable. Blooms form most often on the eastern shoals, propagating westward into the channel (Huzzey et al. 1990; Lucas et al. 1999a, 1999b). Because of the strongly variable spatial gradients, variation in residual current due to wind, local runoff, or other subtidal effects can be important in promoting or suppressing, distributing, and dispersing the bloom (Huzzey et al. 1990; Powell et al. 1989; May et al. 2003). Consumer organisms including bacteria, zooplankton, and clams respond to these blooms with increased growth rate or biomass (Hollibaugh and Wong 1996; Cloern 1996; Kimmerer unpublished).

Benthic Microalgae

Intertidal mudflat or shallow subtidal habitat occupies a large area of the estuary, and these shallow areas have a high abundance of benthic microalgae (Thompson et al. 1981). Benthic microalgae in Suisun Bay in the 1980-1981 bloom comprised mostly diatom species that had previously bloomed in the overlying water column (Nichols and Pamatmat 1988), and presumably exchange frequently between the bottom and the water column through sinking and turbulent resuspension (Nichols and Thompson 1985a). Thus, in this region the distinction between plankton and benthic microalgal production can be artificial (Nichols and Pamatmat 1988). In San Pablo and South bays benthic microalgae are mainly found in fairly consolidated benthic mats, within which cells may migrate up and down in response to conditions but do not often take to the overlying water (Thompson et al. 1981). Benthic microalgae may be an important food source to both deposit-feeding and suspension-feeding benthos (Nichols and Thompson 1985a).

The only attempt at measuring production of these algae (C. Currin and L. Canuel) obtained too few data for a system-wide estimate. Previous estimates of their the areal extent of mudflats, combined with published productivity data, suggested that benthic microalgae contribute about 30% of primary production in both South Bay and in San Pablo-Suisun bays (Jassby et al.1993). This is a substantial fraction, although the high turbidity of the San Francisco Estuary may cause production of benthic microalgae to be lower than in other estuaries. Net ecosystem metabolism in the South Bay was heterotrophic even during the spring bloom unless Jassby et al.'s (1993) estimate of benthic production was included (Caffrey et al. 1998), and Smith and Hollibaugh (2000) concluded that South Bay was probably autotrophic. Thus, the contribution of benthic microalgae to regional or system-wide productivity may be important but remains to be determined.

Key Findings and Uncertainties

The intensive work by Cloern and colleagues, and by the IEP in the Delta and Suisun Bay, has contributed greatly to our understanding of primary production in the San Francisco Estuary and in estuaries in general.

Key issues include the following:

- *Importance of Higher Plants.* Submerged aquatic vegetation (SAV), particularly seagrass, is a key component of most estuarine ecosystems. Although seagrass does not play a major role, SAV appears to be very important in structuring habitats in the Delta (Brown 2003b). The outcome of competition between phytoplankton and submerged aquatic vegetation could shift with changes in water clarity or increases in the area of shoal and intertidal habitat.
- *Water Clarity.* Throughout the estuary phytoplankton growth rate tends to be limited by light. Therefore increasing water clarity may allow for greater primary production and use of nutrients. This could be exacerbated by sediment capture by *Egeria densa* in the Delta or smooth cordgrass in San Pablo to South Bay. Eutrophication, now largely controlled by low light penetration, could become a major issue in parts of the estuary. An additional consequence of this could be an increase in harmful algal blooms such as red tides.
- *Benthic Grazing.* The importance of benthic grazing in limiting phytoplankton biomass has been demonstrated for South Bay, Suisun Bay, and Franks Tract, and inferred for the Delta as a whole. In particular, the loss of the summer biomass maximum in Suisun Bay has been attributed to grazing by *P. amurensis*. Although there is considerable information on the effects of *P. amurensis*, there is not a general consensus as to its overall impact. *C. fluminea* is nearly as abundant and larger, and could have a substantial impact on phytoplankton in the Delta.
- *Bloom Dynamics.* Work in the South Bay has demonstrated the interaction among tidal currents, stratification, light limitation, benthic grazing, and hydrodynamic effects in controlling the development of phytoplankton blooms. Bloom dynamics in San Pablo and Central bays have received very little attention, and dynamics of Suisun Bay have not been comprehensively examined since *P. amurensis* arrived. The potential role of ammonium in bloom development needs further analysis.
- *Effects of Delta Configuration.* Jassby et al. (1993, 2002) showed that export pumping and Delta barriers could affect phytoplankton biomass. However, it is not clear whether phytoplankton would respond to increases in export pumping rates or to any major changes in plumbing in the Delta.
- *Influence of the Coastal Ocean.* Very little is known about this influence. The coastal ocean supplies a substantial amount of organic carbon, much of it as phytoplankton, to nearby Tomales Bay during the upwelling season.
- *Benthic Microalgae.* Productivity of benthic microal-

gae may be high on shoals and intertidal mudflats, which have significant extent in some areas of the estuary such as San Pablo Bay. However, few measurements have been made of these rates. Changes in extent of intertidal mudflats through erosion, sea level rise, or invasion by the introduced smooth cordgrass, *Spartina alterniflora*, could reduce production of benthic microalgae.

ORGANIC CARBON AND THE ROLES OF MICROBES

Organisms require energy for growth, movement, and reproduction. This energy is obtained as organic compounds either synthesized by the organism or obtained from the environment. Organic carbon is easily distinguished from inorganic forms, so it can be considered synonymous with energy for the ecosystem, although allowance must be made for the degree of lability (availability to the foodweb). An important consideration for the San Francisco Estuary is that most of the organic carbon entering the system comes as refractory plant detritus from the rivers, of which only a small fraction is usable.

Most organic carbon in natural waters is in dissolved form, defined operationally as that which passes through a 0.2 µm filter (DOC); less is in particulate form (POC), and still less is alive. Murrell and Hollibaugh (2000) identified a number of classes of compounds in DOC and POC in the northern estuary, and concluded that most of these materials originated upstream.

Photosynthesis results in the production of organic carbon and oxygen in roughly fixed proportions, while aerobic respiration is essentially the reverse process. Thus, fluxes of organic carbon and oxygen can be used to infer the same processes. Anaerobic respiration occurs in hypoxic to anoxic environments, mostly in sediments, generally consuming oxidized compounds produced in aerobic environments. Exchange of organic carbon and oxygen between sediment and the overlying water column therefore represents a similar process to aerobic respiration, the main difference occurring through net burial of organic matter. Nutrients are taken up and incorporated into organic matter during growth of plants, and released when that organic matter is respired; thus changes in nutrient concentrations also can be used to infer metabolic processes.

The balance between autotrophy (net production of organic matter) and heterotrophy (net consumption of organic matter) has been estimated through several approaches in different parts of the estuary. These approaches generally converge in showing the importance of exogenous carbon supplies from the riverine sources in the northern estuary, and endogenous supplies from phytoplankton blooms in the South Bay.

Organic Carbon Sources and Sinks

Organic carbon produced within the estuary was discussed in the previous section. Considering marshes to be outside the estuary for the purposes of this paper, carbon fixed outside the estuary is transported to the estuary by stream flow, marsh runoff, land runoff, oceanic sources, and wastewater treatment plants. The general trend for the San Francisco Estuary is for organic carbon sources to be dominated by phytoplankton except in the Delta, where the rivers contribute a large amount of organic matter; however, even in the Delta much of the available organic matter is of phytoplankton origin, because much of the land-derived material is refractory. A simplified diagram of carbon flows in the northern estuary, based on the discussion below, shows the relative importance of river-derived material to total carbon supply, and the importance of phytoplankton to the supply of labile organic matter (Figure 31).

Jassby et al. (1993, 1996) and Jassby and Cloern (2000) assembled organic-matter budgets for various regions of the estuary. The basic approach was to use existing data to determine the magnitude of the annual value of major source and sink terms. Each of these studies used somewhat different sets of data. Phytoplankton production was determined using models based on chlorophyll, turbidity, incident light and, in one case, water conductivity (Cole and Cloern 1984, 1987; Jassby and Cloern 2000). Benthic microalgal and macrophyte production and marsh outwelling values were estimated by multiplying areal estimates as medians from the literature by estimates of intertidal mudflat, macrophyte habitat, and marsh areas respectively. River loadings were calculated from concentrations multiplied by gaged river flows, and agricultural discharge and urban runoff from locally-developed estimates of areas and discharge loadings of these regions. Loading from WWTPs was estimated from reports of biochemical oxygen demand (BOD) and mass flow of effluent.

The first carbon budget study (Jassby et al. 1993) constructed a budget for major regions of the estuary west of the Delta for 1980. Production by benthic microalgae was estimated on an areal basis as the median from 28 studies at other locations, and expanded to the entire estuary by calculating the area of the estuary where the water depth was less than the depth of the 1% light level. Other endogenous sources, including production by macrophytes and chemoautotrophy by bacteria, were considered negligible. River loading of organic matter was estimated from Schemel et al.'s (1984) estimates of dissolved and particulate organic carbon and flow volumes. Loading from runoff was estimated from flow measurements or estimates combined with literature data on organic carbon content of urban and agricultural runoff. Other sources, including aerial fallout, oil spills, and groundwater, were considered negligible.

The principal sources for Suisun Bay were river inflow, phytoplankton, benthic microalgae, and marsh export (176, 45, 19, and 16 x 10^3 tonnes year^{-1} respectively; Jassby et al. 1993). However, the riverine source includes refractory forms; and only about 10% of the total organic carbon was labile, based on measurements of biochemical oxygen demand in the Delta (Jassby et al. 1993). Jassby et al. (1996) updated the earlier analysis with more recent estimates of riverine input (Schemel et al. 1996), but the conclusions remained much the same. Much of the particulate carbon is supplied from or through the Yolo Bypass during floods (Schemel et al. 1996), although much of this material may be refractory. Model results showed most of the flow from the Yolo Bypass to enter Suisun Bay rather than the interior Delta (Monsen 2000), and it can inject an elevated concentration of freshwater phytoplankton, especially when the bypass is draining (Sommer et al. 2001a).

In the South Bay the major contributions to the organic carbon budget were endogenous, with phytoplankton and benthic microalgae producing 76 and 36 x 10^3 tonnes year^{-1} respectively (Jassby et al. 1993). Principal sinks were benthic and planktonic respiration,

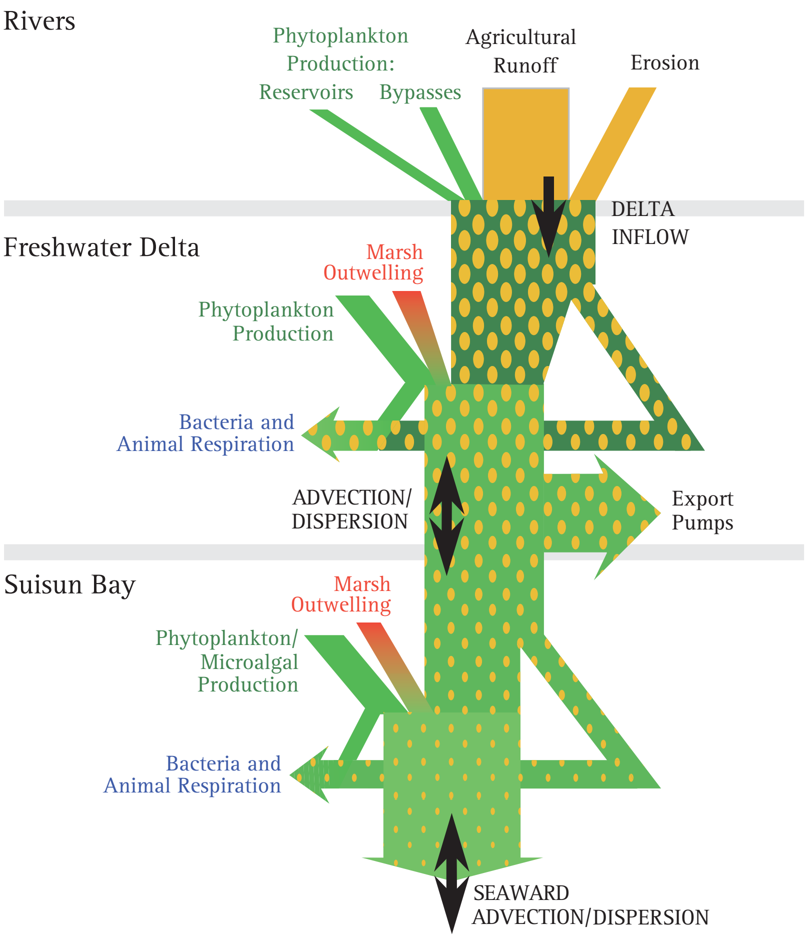


Figure 31. Simplified schematic diagram of carbon flow in the northern estuary. Width of arrows represents relative magnitudes of carbon fluxes between compartments. Colored text and input arrows indicate sources: green for phytoplankton, brown for agricultural runoff and erosion, and red for marsh output. Black text and arrows indicate loss terms including mixing and advection. Respiration (as well as growth) by bacteria and animals is supported mainly by phytoplankton, and to a lesser extent by terrigenous sources. Inputs from runoff are relatively refractory, and the proportion of carbon that is useful is enhanced by inputs of phytoplankton.

which roughly balanced supplies in South Bay (benthic respiration was not measured in the northern estuary).

Jassby et al.'s (1993) general conclusions of an exogenous source of carbon for the foodweb of Suisun Bay are supported by the following evidence, which also helps to contrast Suisun with South Bay where the organic carbon is largely endogenous:

- Isotope ratios of organic carbon in the northern estuary in 1976-1977 (a drought year; Spiker and Schemel 1979) and 1990-1992 (Canuel et al. 1995) indicated a large component of river-derived material, whereas ratios from the South Bay indicated a local phytoplankton source.
- Carbon isotope results showed the particulate organic carbon in the western Delta to be largely of phytoplankton origin rather than from land plants (Spiker and Schemel 1979).
- Delta phytoplankton blooms have been advected into Suisun Bay (Ball 1987, Monsen 2000), presumably providing a source of labile organic carbon either intact or after lysis.
- Biomarkers (refractory organic compounds of known origin) in 1990-1993 included more compounds from phytoplankton in particulate matter samples from South Bay, and more from terrestrial plants in the Sacramento River (Canuel et al. 1995, Canuel and Cloern 1996).
- Water-column respiration rates greatly exceeded primary production in Suisun and San Pablo bays but not in the South Bay (Rudek and Cloern 1996).
- Bacterial production was high in relation to primary production in Suisun and San Pablo bays, whereas in the South Bay bacterial production was of similar magnitude to, and correlated with, phytoplankton production (Hollibaugh and Wong 1996).
- A mass-balance box model supported the importance of exogenous carbon sources in the northern estuary (Smith and Hollibaugh 2000).

Jassby and Cloern (2000) constructed an organic matter budget for the Delta, building on previous work (Jassby et al. 1993, 1996; Jassby and Powell 1994). A particular focus of this study was the impact of proposed rehabilitation actions on the organic matter budget, particularly on the flux of organic matter from the Delta to the Low-Salinity Zone and seaward. This analysis included data from 1968-1995, and used data from the IEP monitoring stations in the northern and southern Delta to estimate river-borne concentrations of organic matter.

The most striking conclusion of this analysis was that, although inputs of river-borne organic matter greatly exceeded local production, phytoplankton production was of roughly equal importance when the degree of availability was considered (i.e., the data are corrected for lability and respiratory losses). Phytoplankton was particularly important in spring and summer and in dry years. Minor sources included agricultural drainage, urban runoff, marsh outwelling, macrophyte and benthic microalgal production, and WWTP discharge (Jassby and Cloern 2000).

Of the organic matter loading derived from rivers, a substantial fraction was of phytoplankton origin (Jassby and Cloern 2000). Although the Sacramento River provided most of the loading because of its higher flow, the San Joaquin River contributed 20% to 42% of the total, much higher than expected based on flow. This higher contribution was ascribed to greater agricultural runoff and to longer residence time and higher temperature, resulting in higher phytoplankton biomass, in the San Joaquin River. Runoff from the San Joaquin River also carries a higher burden of contaminants than that from the Sacramento (Jassby and Cloern 2000).

A major study of organic carbon sources for the Delta foodweb by the USGS and collaborators showed the importance of phytoplankton in the carbon actually used within the Delta (e.g., Jassby et al. 2002). Most of the dissolved and particulate carbon that could be degraded by microbial action was of phytoplankton origin (Sobczak et al. 2002). Furthermore, the growth of cladocerans in bioassay experiments (see "Zooplankton" p.64) was strongly related to chlorophyll, and less strongly related to other measures of food supply such as particulate organic carbon and various lipids (Müller-Solger et al. 2002).

Jassby et al. (1993) identified exchange across the seaward boundary as a possibly important source or sink of organic matter, omitting it from the budget because of a lack of information. Coastal primary production driven by upwelling supplies a significant amount of labile organic matter to nearby Tomales Bay in summer (Smith and Hollibaugh 1997). Gravitational circulation near the mouth of the San Francisco Estuary (Conomos 1979a) may entrain organic-rich particles from the upwelling zone that are then available within the estuary, although exchange with the coastal ocean may be more influenced by physical processes over the shoal seaward of the Golden Gate (Largier 1996). Coastal phytoplankton have been found within the estuary, although coastal zooplankton are rather uncommon (Ambler et al. 1985; Kimmerer et al. 1999). However, research has not been conducted to determine quantitatively the importance of exchange with the coastal ocean to the estuarine carbon budget.

The contribution of marshes to organic budgets of estuaries has been debated in the literature for about four decades without apparent resolution (Nixon 1980). A recent review (Kneib 1997) suggested that active migration by nekton (fish and shrimp) was the primary mechanism for transport of organic carbon produced in marshes into the open waters of estuaries. The contribution of marshes to the organic carbon budget of the open waters of the San Francisco Estuary also remains to be determined. The first-order estimates by Jassby et al. (1993) and Jassby and Cloern (2000) are probably adequate given the relatively small area of extant marshes, but that could change if substantial marsh rehabilitation occurs.

How Organic Carbon Enters the Foodweb

Organic matter occurs in the San Francisco Estuary over a range of particle size from methane molecules to whales. DOC is produced as a byproduct of primary production and through leakage from plant or animal cells, leaching from organic particles, inefficient feeding by animals, and lysis (bursting) of living cells due to changes in salinity. Transformations from the dissolved to the particulate fractions occur through uptake and growth of bacteria as well as larger heterotrophs, adsorption onto mineral particles, and flocculation occurring upon changes of salinity (Jassby and Cloern 2000).

POC entering the estuary through any of the pathways discussed above and in the previous section may be incorporated into the foodweb directly through grazing by plankton or benthos. Estimates of grazing rates and observations of food limitation in the benthos suggest that benthic grazing consumes most of the particulate matter (Foe and Knight 1985; Alpine and Cloern 1992).

The large pool of DOC (Sobczak et al. 2002) guarantees the importance of the bacteria in the San Francisco Estuary. Bacteria readily take up DOC, but are also capable of extracellular digestion of particles. Although some estuarine invertebrates can take up DOC (Manahan 1990), bacteria are the only significant consumers of DOC in the San Francisco Estuary, based on their high abundance, surface area, and metabolic rate (Hollibaugh 1999).

A very heterogeneous group, bacteria have a wide range of roles in aquatic environments: they consume organic matter and convert DOC to particulate form (Azam et al. 1983), fix nitrogen gas into organic nitrogen, convert ammonia to nitrite and then to nitrate (nitrification), convert nitrate to nitrogen gas (denitrification), produce sulfide and methane gas, and a host of other activities (Pomeroy 1974). All of these activities are associated with obtaining either a source of energy or an oxidant to allow the energy to be used. Many of these activities require a reducing (anoxic) environment such as that found in soft sediments.

This report focuses only on the bacterioplankton, i.e., the bacteria in the water column, whose principal role is consuming DOC (and some POC) to fuel either metabolic requirements (i.e., respiration) or growth. Bacteria effectively “repackage” this dissolved material into small particles that are then available for other organisms to consume. Thus bacteria are the key link between processes that create and remove DOC, including processes that result in feeding and growth of larger organisms that generally must feed on particles.

All of the information on water-column bacteria in the San Francisco Estuary has been gathered since 1987 by J.T. Hollibaugh and colleagues (e.g. Hollibaugh and Wong 1996, 2000; Murray et al 1996; Murrell et al. 1999). Thus, there is no information on conditions before the changes in Suisun and San Pablo bays associated with the clam *Potamocorbula amurensis*.

Because bacteria are small (mainly < 1 µm), methods for analyzing their activities tend to be indirect.

Although abundance may be determined by direct microscopic counts (Hobbie et al. 1977), this method gives total abundance or abundance by crude classes of shape and size that may not relate to activity, and may be biased in water samples from turbid environments with a high particulate concentration (Hollibaugh and Wong 1996). Alternative methods have been developed for deducing biomass and activity using radioisotopes and various biochemical methods including nucleic acid analyses. For example, Hollibaugh (1994) used the metabolism of thymidine, a nucleic acid precursor, to deduce that bacteria in the northern San Francisco Estuary were food-limited compared to those from nearby Tomales Bay, a productive estuary. A similar comparison of the variety of organic compounds used for growth revealed that bacteria of the northern San Francisco Estuary could use a much wider variety of compounds than those from Tomales Bay, also suggesting poor nutritional conditions (Hollibaugh 1994). Murray et al. (1996) showed differences in the composition of bacterial communities between Tomales Bay and San Francisco Estuary by analysis of DNA fragments.

Hollibaugh and Wong (1996) provided a comprehensive view of bacterial abundance and production throughout the San Francisco Estuary in 1988-1991. Abundance averaged about 2 x 10^6 cells ml^{-1}, and biomass about 30 mgC m^{-3}, with higher values to the north and south and lower values in Central Bay. This biomass is equivalent to about 200 tonnes of carbon throughout the estuary, somewhat less than the biomass of phytoplankton. The mean doubling time, i.e., the time it would take the bacterial biomass to double if it were not consumed, was estimated to be 1.2 days. Annual production bay-wide was not high compared with other estuaries, but was roughly comparable to phytoplankton production. Bacterioplankton production covaried with phytoplankton production in the South Bay, where the bacteria were probably responding to the increase in availability of fresh, labile DOC produced by algal blooms. No such covariation occurred in the northern estuary, probably because of a lack of blooms. Abundance and temperature-corrected production varied linearly with salinity in winter, suggesting mixing with little net production or consumption. In summer, abundance was unrelated to salinity while production may have responded to short-term pulses of DOC from upstream.

In the brackish northern estuary 10% to 67% of the bacterial production in 1989-1990 was associated with particles larger than 1 µm, much less in South Bay (Hollibaugh and Wong 1996). These particles are aggregates of organic matter and sediment to which bacteria are attached (Murrell et al. 1999). In 1996 the proportion of attached bacteria averaged 31% (range 3% to 86%) with the highest values in Suisun Bay, lowest in Central Bay, and intermediate in the Sacramento River; a greater proportion was attached in spring and summer than autumn (Murrell et al. 1999). The proportion of production that was associated with particles increased sharply on transects from the Delta into and seaward of the Low-Salinity Zone (Hollibaugh and Wong 2000). Differences between the free-living and particle-bound groups have been examined using a variety of techniques. Growth rates did not vary between the two groups (Murrell et al. 1999), and phylogenetic analysis revealed that particle-bound and free-living bacteria from the same sample were more similar than bacteria compared among different environments (Hollibaugh 1999; Hollibaugh et al. 2000). On the other hand, thymidine was incorporated more into DNA in particle-bound bacteria and metabolized more in free-living bacteria, possibly suggesting more favorable nutritional conditions in particles (Hollibaugh and Wong 2000). In addition, ectoenzymes, which are digestive enzymes used by bacteria to digest POC externally, were present in higher concentrations in association with particles, possibly indicating greater availability of usable organic matter (Murrell et al. 1999).

Because phytoplankton biomass was low in Suisun Bay, the moderate bacterial production there exceeded primary production by about five-fold (Hollibaugh and Wong 1996). This high a production requires a carbon subsidy from outside the system, which may have been from freshwater phytoplankton leaving the Delta. The high ratio of bacterial to phytoplankton production also implies a relatively large alternative supply of POC to the food web. In most aquatic systems bacterial production is consumed by protozoans which, because of their small size, require several additional steps in the food web, each with considerable losses, before the carbon becomes available to larger organisms. However, abundance and grazing rates of protozoans on bacteria in the northern San Francisco Estuary were found to be low to negligible, and protozoan abundance was low, although there was some concern that high suspended particulate matter concentrations may have interfered with the methods (Murrell and Hollibaugh 1998).

Taking this result at face value results in a paradox. The bacteria were growing fast enough to double in 1.2 days, but abundance did not increase over the course of the study. Since the doubling time is much shorter than the residence time of the estuary (Figure 2), export to the ocean could not explain the lack of increase. Thus, either the estimated growth is much too high, or something must have been eating the bacteria. Possible candidates include zooplankton and benthos. Although some zooplankton can consume bacteria, particularly those bound to particles, abundance may not be high enough to exert a regulatory effect.

A likely candidate for exerting strong control over bacteria in the shallower parts of the estuary is the clam *Potamocorbula amurensis* and other filter-feeding bivalves. *P. amurensis* is capable of filtering bacteria, although at lower efficiency than phytoplankton, and probably at a higher rate on particle-bound than free-living bacteria (Werner and Hollibaugh 1993). The community filtration rate is of the right order of magnitude to suppress increases in bacterial numbers (Alpine and Cloern 1992; Werner and Hollibaugh 1993). Benthic grazing may have been the cause of a seasonal decline in various measures of bacterial metabolism, including the percent attached to particles, in 1996, although the decline could also have been due to a depletion of labile organic carbon originally supplied by the spring high-outflow event (Murrell et al. 1999).

Net Ecosystem Metabolism

The system-wide balance between autotrophy and heterotrophy, called net ecosystem metabolism (NEM) has been of interest recently because of its importance to the global carbon budget (e.g., Smith et al. 1991; Kemp et al. 1997), although estuaries are small components of that budget. The sign of NEM, when integrated over an appropriate time scale, is an indication of whether the system is running on exogenous or locally produced carbon.

NEM can be expressed in terms of the balance of carbon, oxygen, or nutrients, since primary production, which produces organic C and free O_2, consumes nutrients in roughly predictable proportions (Redfield 1958); aerobic respiration is roughly the opposite process. Estimates of NEM can be based on system-wide mass balance or summation of individual terms in the mass balance. In addition, the sign (but not the magnitude) of NEM can be determined through consideration of the direction of net transport of C, O_2, or nutrients. For example, if Jassby et al.'s (1993) estimates of carbon fluxes for 1980 are accurate, Suisun Bay should be net heterotrophic and the South Bay net autotrophic.

Three estimates of NEM have been attempted in the San Francisco Estuary. Caffrey et al. (1998) constructed a budget of oxygen uptake and release for South Bay, finding that respiration exceeded production in the channels, while production and respiration were approximately in balance over the shoals. Calculated net system metabolism was autotrophic in winter and spring, and heterotrophic in the summer non-bloom period; however, large variability and several key assumptions resulted in great uncertainty in even the sign of these estimates (Caffrey et al. 1998).

Smith and Hollibaugh (2000) constructed a box model of nutrient loadings and concentrations in an effort to deduce NEM system-wide. Central Bay was taken as the oceanic end-member for the analysis, since there were no data from the coastal ocean outside the estuary. The mass balance used nutrient concentrations and salinity to deduce non-conservative fluxes of nutrients. Under the assumption that nutrient uptake and release occurred through production and respiration, organic carbon fluxes were calculated from the nutrient fluxes. The report concluded that in most summers the estuary was net autotrophic, but results were somewhat ambiguous. Inorganic phosphorus was apparently taken up by adsorption onto particles, particularly in the North Bay. Inorganic nitrogen had a slight uptake rate possibly commensurate with denitrification. The principal conclusion of this study was a severe lack of data on nutrient concentrations throughout the estuary at a sufficiently close spatial interval for this kind of analysis, and a lack of data for the coastal ocean.

Jassby and Cloern (2000) calculated ratios of output to input of total organic nitrogen to and from the Delta. If N fixation and denitrification are small these ratios indicate the value of NEM. Jassby and Cloern (2000) found that the system was close to balanced most of the time, with seasonal and interannual variations apparently related to freshwater flow. The ratio was elevated in winters of wet years, possibly indicating agricultural inputs, and depressed in critically dry summers, perhaps because of rapid metabolic activities at high temperatures, and in-Delta diversions (Jassby and Cloern 2000).

Dissolved Oxygen

Oxygen is intimately involved in cycles of organic carbon production and consumption. The concentration of oxygen in the water is the net result of gas exchange between the water and atmosphere, primary production and aerobic and anaerobic respiration in sediments and water column, vertical exchange of oxygen within the water column, and transport by water motion. Oxygen concentration is often expressed as percent saturation, since the concentration at which water is saturated with oxygen decreases as temperature increases. Most of the estuary is close to saturation most of the time, and the slight elevation of near-surface over near-bottom oxygen percent saturation indicates that supersaturation is more common than depletion (Figure 32).

A rough oxygen budget can be calculated for South Bay from existing data. Oxygen uptake by the benthos and water column in South Bay channels was usually a small daily proportion of ambient concentrations (Caffrey et al. 1998). Primary production is on the order of 95 to 150 mgC m^{-2} y^{-1} (Cole and Cloern 1984). Bacterial production is about 50 mgC m^{-2} y^{-1} bay-wide, and therefore bacterial respiration is on the order of 100 mgC m^{-2} y^{-1} (Hollibaugh 1999). Thus, primary production exceeds microbial respiration in South Bay. Water column respiration throughout the estuary in 1993 roughly balanced primary production throughout the estuary except in Suisun Bay and the lower Sacramento River (Rudek and Cloern 1996). The figures above correspond to oxygen turnover times of 2 to 8 months. Gas exchange between the water and the atmosphere depends on wind speed and wave action, resulting in residence times for oxygen due to exchange between the atmosphere and the water column of the South Bay of 2 to 3 days in summer and 4 to 15 days in winter (Hartman and Hammond 1985). This mismatch in time scale implies physical control of oxygen concentration, and depletion of oxygen should be infrequent in most of the estuary. Indeed, oxygen concentrations tended to exceed saturation values in South Bay during the spring bloom (Kuwabara et al. 1996 and Figure 32).

Similar calculations cannot be made for Suisun Bay because of incomplete information, but all of the above results suggest that Suisun Bay should be more heterotrophic than South Bay. Nevertheless oxygen concentrations were equally close to saturated values in the regions presented in Figure 32.

The principal exception to the generally saturated oxygen concentrations occurs in late summer to early

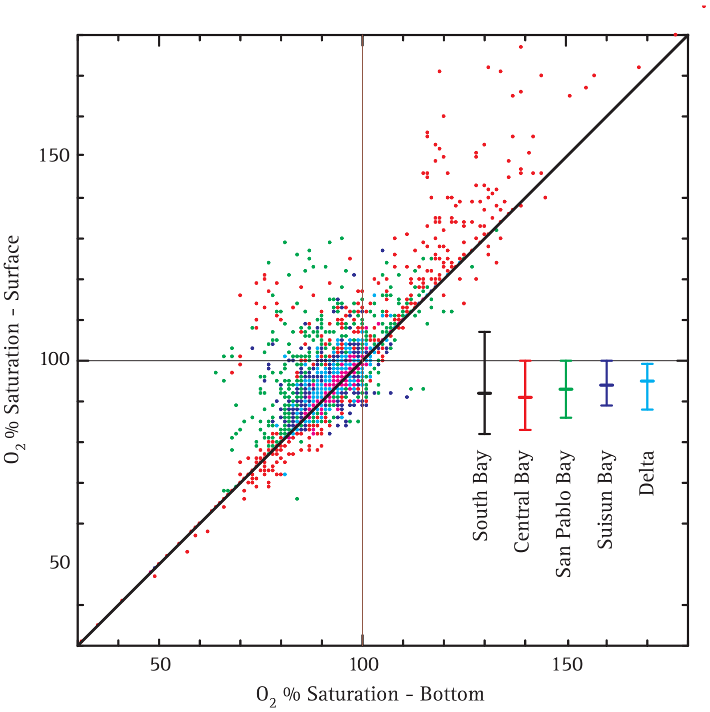


Figure 32. Oxygen concentration as percent saturation in near-surface and near-bottom samples. Color indicates region, and error bars give medians and 10th and 90th percentiles of the data. Data from USGS monitoring program, which focuses on channel stations and the portion of the Delta in the lower Sacramento River.

fall in the San Joaquin River near Stockton (Hayes and Lee 1998, 1999, 2000; Lehman et al. 2004), a region not included in Figure 32. In that region, a combination of high summer temperature and high organic matter loading and phytoplankton production result in high oxygen demand relative to gas exchange with the atmosphere. Furthermore, stratification presumably limits oxygen transport to the bottom, and together with planktonic and benthic oxygen consumption results in low oxygen concentration (less than ~5 mg L^{-1}) near the bottom. This may impede movement of fish through the area (Hayes and Lee 1998, 1999, 2000), although estuarine organisms may tolerate lower values (e.g., Stalder and Marcus 1997). Physiological responses of Sacramento splittail occurred at oxygen concentrations of about 1 mg L^{-1}, but sublethal or behavioral effects may occur at higher concentrations (Young and Cech 1996), as may acute effects on other fish.

Key Findings and Uncertainties

Recent investigations in the Delta have confirmed the importance of phytoplankton in supplying most of the organic matter used by the estuarine ecosystem in all regions of the estuary. The pathway for consumption of phytoplankton appears to differ among the different regions: consumption by grazers in most of the estuary, as well as removal by water diversions in the Delta, and lysis of freshwater phytoplankton and subsequent consumption by bacteria in Suisun Bay.

- *Sources of Organic matter.* Considerable work on organic carbon supplies to the estuary has revealed that phytoplankton are the most important source throughout. The Delta appears to be roughly in balance between autotrophy and heterotrophy, but the rest of the estuary may be net autotrophic. Exogenous carbon supplies to Suisun Bay that fuel high bacterial production there come mainly from freshwater phytoplankton in the Delta. The Yolo Bypass appears to be a major source of particulate matter and especially labile organic matter such as phytoplankton. Alterations to the physical configuration of the Delta or floodplains or seasonal flow schedules could change how carbon is transported to the estuary. Thus, there may be opportunities to increase organic matter supply to the northern estuary. The contribution of benthic microalgae in the estuary west of the Delta may be large and is essentially unknown.
- *Microbial Production.* Bacterial production in the northern estuary is high in comparison to phytoplankton production, and much of the production is by bacteria associated with particles. The fate of that production, and the mechanisms that control bacterial biomass, remain unknown.
- *Pathways of Consumption.* Although benthic grazing is believed to be important in removing phytoplankton in most regions of the estuary, the quantitative importance of different trophic pathways has yet to be determined.
- *Linkage of Sediments to Organic Matter.* Sediment chemistry is closely linked to the cycling of organic matter and the activities of the benthos. Exchange with the overlying water column can be relatively rapid, but the sediments also represent a large, long-term deposit of various biologically active materials. These materials can be sequestered in the sediments, and then remobilized later. Thus the time scales of activities in the sediments are much longer than in the overlying water column, with the potential for significant "memory" effects.

PRIMARY CONSUMERS

This section addresses groups of organisms most of whose members feed on phytoplankton, detritus, or bacteria. This includes the zooplankton, epibenthic macroplankton (mysids and free-living amphipods), and the benthos.

The principal role of these groups from a human perspective is to provide foodweb support to fish and other organisms of interest. A foodweb is an interacting network of feeding relationships that describes where each population or subpopulation gets its food. Comprehensive foodwebs have not been constructed for the San Francisco Estuary, although numerous studies have been conducted of food habits.

The ultimate energy source for the foodweb, as described in the previous section, is a combination of local production by phytoplankton and other plants, and import of organic carbon that is either taken up directly by larger consumer organisms, or taken up by bacteria which then provide food to higher trophic levels. Most of the consumption of bacteria and phytoplankton is through various kinds of filter-feeding (a somewhat inaccurate term used for many modes of feeding on small particles) zooplankton, benthic bivalves, or others. These organisms then become prey for others, which mainly feed raptorially, i.e., by grasping individual prey. At each of these trophic transfer steps in the food web, most of the energy is lost in incomplete feeding or digestion, and through respiration by the predator, so only on the order of 10% to 25% is used for growth. The proportion that is not respired re-enters the detrital pathway of the foodweb, and becomes available for consumption by bacteria and detritivores, particularly in the sediment.

A complication in describing the estuarine foodweb is the degree of variability in the participants. Each of the species in the foodweb has its own response to season, tide, salinity, and temperature, as well as its own schedule of development, which influences movement, feeding patterns, and vulnerability as prey. Predatory relationships change as organisms grow and gain swimming ability, and change habitat. Omnivory blurs trophic relationships among species. Thus a simple flow diagram would not suffice to capture the complexity inherent in the foodweb of the San Francisco Estuary.

Zooplankton

Zooplankton are a key link between primary producers and small fish. Here I discuss the zooplankton species up to a size of about 1 mm, including microzooplankton and meroplankton. Epibenthic macrozooplankton such as mysids and pelagic amphipods are discussed below. Zooplankton may respond to the physical environment at several time scales including generation or doubling time (weeks to months), response time for reproduction (hours to days), and time for behavioral responses (minutes to hours). These imply responses to seasonal and spring-neap tidal cycles, phytoplankton blooms, and, through behavior, tidal velocity.

Distributions of zooplankton in the San Francisco Estuary have been studied in several large-scale programs, and a few studies of processes have been conducted. Notable recent studies of distribution and abundance include the ongoing IEP monitoring in the Delta to San Pablo Bay (Orsi and Mecum 1986; Kimmerer and Orsi 1996), a four-year study of zooplankton throughout the estuary in 1978-1981 (Ambler et al. 1985), and two studies of zooplankton distributions in San Pablo, Central, and South bays in 1997-1999 (Kimmerer et al. 1999).

Key features of the zooplankton of the San Francisco Estuary are: (1) No distinct communities of zooplankton exist in the estuary, as all have distinctly different responses to environmental conditions; (2) Introductions and replacements have been frequent, particularly at intermediate salinity, resulting in apparent changes in trophic structure; (3) A significant decline in abundance of several important groups occurred in the Delta in the mid-1970s; and (4) A significant decline in some species in the LSZ and seaward occurred in 1987-1988, closely followed by an increase in newly introduced species.

Changing Taxonomic Composition

As in other estuaries, the zooplankton of the San Francisco Estuary are dominated numerically by small forms including tintinnids, rotifers and the nauplius larvae of copepods. Larger zooplankton comprise mainly copepods in the brackish and saline regions of the estuary, cladocerans in the freshwater Delta, and meroplankton, the larval forms of benthos and fish. The copepods include calanoids, usually the most common group in marine waters, and cyclopoids, which are numerically dominant now in most parts of the San Francisco Estuary. Harpacticoid copepods can also be abundant, but most of these are early life stages of benthic species.

Substantial changes in abundance and species composition have occurred in the last three decades. I consider here two periods of change in abundance: 1972-1987, and 1987 to the present. The earlier period was characterized by declines in many species in the Delta (Orsi and Mecum 1986; Obrebski et al. 1992). In the Delta, nearly all species of rotifers declined substantially, and are now at about 20% of their original abundance (Orsi 1999). Two genera of cladocerans declined (*Daphnia* and *Diaphanosoma*), but not a third (Bosmina). Freshwater copepods including the calanoid *Diaptomus* spp., cyclopoid copepods, and harpacticoid copepods also declined in the Delta. Finally, the brackish-water copepod *Eurytemora affinis* declined in the late 1970s. The species that declined have not recovered (Orsi 1999).

The reasons for the early declines have not been explained, and may not be amenable to explanation because of changes in the system. Potential candidates include: (1) a reduction in organic input to the Delta when sewage treatment plants were upgraded; (2) effects of increased export pumping either directly or through effects on phytoplankton; (3) a reduction in phytoplankton biomass, possibly due to benthic grazing or increased exports; or (4) effects of pesticides or other toxic compounds. At this point we cannot distinguish among these alternatives. An analysis of effects of export pumping on zooplankton of the LSZ showed that effects were unlikely (Orsi and Mecum 1996), but a similar analysis has not been done for the Delta.

Significant increases occurred in three introduced copepod species during 1972-1987. The small cyclopoid *Oithona davisae* was first described in the San Francisco Estuary, where it arrived from China in about 1963 (Ferrari and Orsi 1984). Its abundance increased throughout the brackish parts of the northern estuary during 1972-1987 (Obrebski et al. 1992). Another small cyclopoid, *Limnoithona sinensis*, became established in freshwater in 1979. The calanoid copepod *Sinocalanus doerrii* was first detected in 1978, occupying a place between the true freshwater fauna and the Low-Salinity Zone where *E. affinis* was abundant (Orsi et al. 1983; Kimmerer and Orsi 1996).

From 1987 to the present the estuarine zooplankton fauna underwent substantial changes, mainly in the brackish regions of the estuary, and mainly associated with species introductions. First, abundance of the copepods *E. affinis* and *Acartia* spp. declined sharply in 1987-1988, due apparently to the effects of the clam *Potamocorbula amurensis* (Kimmerer et al. 1994). At least in the case of *E. affinis* the decline was apparently caused mainly by clams consuming copepod nauplii (Kimmerer et al. 1994). Declines in other species including *Acartia* spp., *Sinocalanus doerrii*, and rotifers in the Low-Salinity Zone could be due to this mechanism or to the decline in food as indexed by chlorophyll concentration (Kimmerer and Orsi 1996).

In 1989 two calanoid copepods of the genus *Pseudodiaptomus* became established: *P. forbesi* became very abundant in summer in the Low-Salinity Zone, with a somewhat broader distribution than the earlier pattern of *E. affinis*, and *P. marinus* established itself at moderate abundance in the lower estuary (Orsi and Walter 1991). In 1993 three copepods of the Low-Salinity Zone or seaward became established: *Limnoithona tetraspina, Tortanus dextrilobatus*, and *Acartiella sinensis* (Orsi and Ohtsuka 1999) The first of these is a very small cyclopoid, which has become the most abundant copepod in the Low-Salinity Zone in summer. The latter two are moderately large calanoid copepods: *Tortanus* spp. are obligate carnivores (Mullin 1979), and *Acartiella* are probably omnivorous.

Limnoithona sinensis disappeared from the monitoring program reports at about the time that *L. tetraspina* became abundant (Orsi and Ohtsuka 1999), although it has been seen in recent samples from the estuary (J. Cordell, U. Washington, pers. comm.). The decline in abundance of *L. sinensis* was almost certainly not due to a direct interaction between the two, because their salinity ranges barely overlap. Both of these small cyclopoids are known only in terms of taxonomy and distribution, although their ecological role is being assessed (Bouley et al. 2003).

These changes in the zooplankton fauna mainly in the northern estuary all involve introductions from China or other eastern Asian countries. The current dominance of this region by introduced species led Orsi and Ohtsuka (1999) to describe the fauna of this region as an “eastern Asian fauna.” East Asian estuaries typically have about five species of copepod in the Low-Salinity Zone (Orsi and Ohtsuka 1999). Before the relatively recent introductions there was at most a single brackish-water copepod, *E. affinis*, in the San Francisco Estuary, and its origin may also be elsewhere (Lee 1999).

Gelatinous zooplankton were uncommon in the zooplankton fauna of the seaward reaches of the estuary in 1997-1999 (Kimmerer et al. 1999). Although large jellyfish (*Aurelia* sp. and other species) are collected frequently during the San Francisco Bay Study sampling (Moreno 2003), smaller medusae, ctenophores, and chaetognaths are common in the estuary only occasionally (Kimmerer unpublished data). These groups often have large impacts on the crustacean zooplankton and larval fish in estuaries (e.g., Deason and Smayda 1982; Purcell 1992; Cowan and Houde 1993). A notable example is the invasion of the Black Sea by a North American ctenophore, resulting in devastating effects on already-depleted fish stocks (Shushkina and Musaeva 1990). Recent reports have described introduced species of jellyfish from harbors and backwaters around the estuary (Mills and Sommer 1995; Mills and Rees 2000; Rees and Gershwin 2000; Rees and Kitting 2002), and have suggested the need for better monitoring of these species.

Distribution in Time and Space

In general, the distribution of zooplankton in the San Francisco Estuary west of the tidal freshwater reaches can be described in terms of salinity (Ambler et al. 1985; Obrebski et al. 1992; Kimmerer and Orsi 1996; Figure 33). This characteristic pattern in estuaries (Miller 1983; Laprise and Dodson 1994) arises not only from patterns of salinity tolerance but also from behavioral or other factors, since the observed distributions do not necessarily coincide with optimal salinity for reproduction (Kimmerer et al. 1998). For convenience we can divide the zooplankton into three categories: freshwater, brackish, and saline. However, that is an artificial division, as the salinity ranges of different species tend to be broad, to overlap, and to have maxima in different ranges (Kimmerer and Orsi 1996; Figure 5).

One advantage of describing the distribution of zooplankton with respect to salinity is that this frame of reference gives a more consistent picture than a geographic frame. Zooplankton, as small animals incapable of swimming against tidal currents, are less likely to be oriented to geography than to salinity (Kimmerer et al. 1998). This feature is characteristic of mobile estuarine fauna, and results in very different patterns of environmental variability than those experienced by the benthos (Laprise and Dodson 1993). For example, the salinity variation experienced by a benthic organism over a few tidal cycles in Suisun Bay can be from freshwater to about half the salinity of ocean water. A planktonic organism moves with the water, and the variation in salinity is probably not more than a few salinity units.

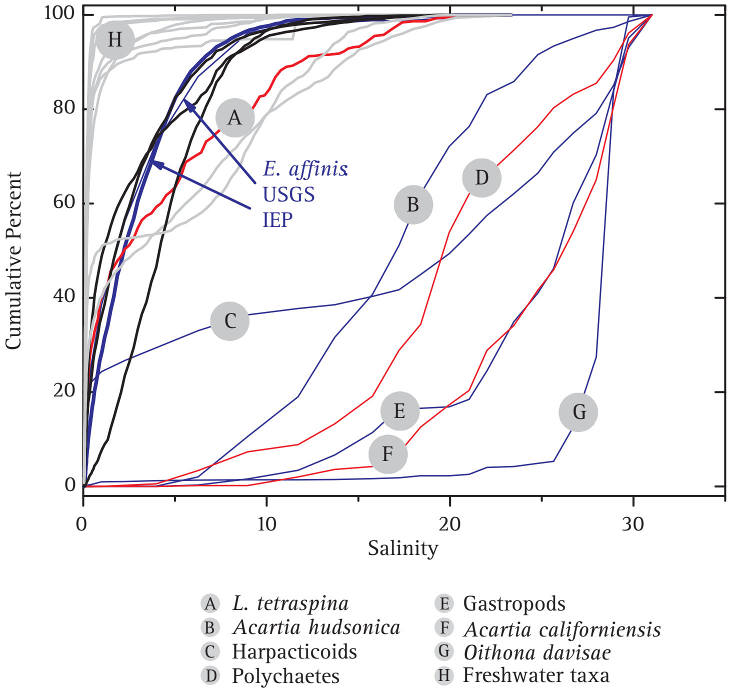


Figure 33. Cumulative salinity distribution of common zooplankton taxa from IEP (thick lines, 1972-98) and USGS (thin lines, 1978-81) sampling programs. Not all taxa have been present for the entire period. Data were binned by salinity, then averaged and converted to cumulative abundance. Bins for IEP data were weighted to produce more bins with fewer samples (minimum 10) at higher salinity, since this sampling program emphasizes the freshwater Delta. Similarly, USGS data emphasize the saline parts of the estuary and were weighted to produce more bins with fewer samples (minimum 10) at lower salinity. Only the copepod *Eurytemora affinis* was abundant in both USGS and IEP samples. The cluster of lines in the upper left corner of the graph is a suite of freshwater taxa including all cladocera, several rotifers, and the copepods *Acanthocyclops vernalis* and *Sinocalanus doerrii*.

Some zooplankton species are present throughout the year, and some reproductive activity occurs in every month, since temperature in the estuary does not go below about 8EC during winter. However, many species have distinct seasonal patterns of abundance (Ambler et al. 1985). It is very likely that seasonal patterns of some species occur through the release of resting eggs, which can survive in bottom sediments through times of unsuitable conditions of salinity or temperature, then hatch when conditions improve (Grice and Marcus 1981; Ambler et al. 1985).

Abundance patterns for meroplankton have not been examined in any detail. Larvae of bivalves, snails, barnacles, and crabs can be abundant at various time of year following major spawning events. However, none of these taxa is routinely identified to species, and in most plankton sampling programs the cost of doing that is considered prohibitive unless there is a specific interest in the life cycle or behavior of selected species. Among the meroplankton, crab zoeae larvae and barnacle nauplii are listed in the database for the IEP monitoring study. Both groups are most abundant in summer, but crab zoeae are uncommon the rest of the year, while barnacle nauplii have high mean abundance throughout the year (Kimmerer unpublished).

Similarly, there is little information on the abundance patterns or dynamics of microzooplankton. The IEP zooplankton monitoring study collects pump samples using a 45 μm mesh net, which is fine enough to collect most copepod nauplii and some tintinnids, which have not been reported. However, other protozoans are not collected quantitatively. There is some evidence, discussed above, that protozoans are not very abundant in Suisun Bay (Murrell and Hollibaugh 1998). However, tintinnids at least are highly abundant in San Pablo, Central, and South bays (Ambler et al. 1985), and other protozoans are abundant in South Bay (Rollwagen Bollens and Penry 2003).

Dynamics

Relatively little work has been done on the dynamics or trophic relationships of zooplankton in the San Francisco Estuary. Orsi (1995) examined gut contents and fecal pellets of several brackish copepod species, and found primarily diatom fragments; however, gut content analysis is biased toward items such as diatoms with hard remains, and against detritus and soft-bodied organisms (Orsi 1995). Most zooplankton feed rather generally within a broad range of prey with suitable characteristics such as motility and size (Paffenhöfer and Knowles 1980; Turner and Tester 1988), so it should be possible to generalize from findings elsewhere. *Eurytemora affinis* can obtain all its nutrition from detritus in the Chesapeake Bay (Heinle et al. 1977), and this and other copepods may do so in the San Francisco Estuary. *Acartia* spp. are generally omnivorous (Landry 1978). *Tortanus* spp. prey on copepods of their own size and smaller including *O. davisae* and *Acartia* spp. (Uye and Kayano 1994, Hooff and Bollens submitted). *T. dextrilobatus* may be an important predator on the small cyclopoids including *O. davisae* (Hooff and Bollens submitted) and *L. tetraspina*. All life stages of Oithona davisae feed only on motile prey, and do poorly on a diet of detritus or diatoms (Uchima and Hirano 1986). This may be true of *Limnoithona* as well (Bouley et al. 2003), presenting a conundrum, since the Low-Salinity Zone is rich in detrital particles (Hollibaugh and Wong 1996) but not in large motile phytoplankton. These copepods could be feeding on protozoa or rotifers.

Consumption of bacteria by copepods could supply a significant proportion of the energy to the food web in Suisun Bay, since bacterial production is high there relative to phytoplankton production (see "Microbial Production" p.63). Adult stages of some estuarine copepods can consume both free-living and particle-bound bacteria, but not very efficiently (Boak and Goulder 1983), although larval stages may be more efficient (Turner and Tester 1992). Rotifers are capable of consuming bacteria (Arndt 1993) and are abundant in Suisun Bay and the Delta (Orsi and Mecum 1986; Kimmerer and Orsi 1996). Larvaceans can eat free-living bacteria (King et al. 1980), but they are common only at higher salinity where the river-borne detrital input is less important (Kimmerer et al. 1999).

The degree of food limitation of zooplankton in the estuary cannot be deduced from studies elsewhere. *E. affinis* apparently is rarely food-limited in the San Francisco Estuary, based on a few egg-production experiments and analyses of egg production in preserved samples (Kimmerer et al. 1994). However, summer abundance of *P. forbesi* is apparently restricted to a narrow range, possibly because of food limitation (Kimmerer unpublished). Egg production of *Acartia* spp. responded to spring blooms in the South Bay in 1990 and in San Pablo and Central bays in 1999-2001 (Kimmerer unpublished), and abundance of nauplii in the South Bay peaked during and after blooms (Cloern 1995). Cladocerans in the Delta appear to be food limited, in that their growth rate is correlated with chlorophyll concentration (Müller-Solger et al. 2002)

Zooplankton of the Low-Salinity Zone migrate vertically in response to tides, with the center of mass of the populations being higher in the water column on the flood than the ebb (Kimmerer et al. 1998, 2002), as did some larval fish (Bennett et al. 2002). This probably aids in position maintenance and retention, although the extent of migration did not appear sufficient for the copepods to overcome advection (Kimmerer et al. 1998). Other mechanisms for position maintenance are being investigated, including the examination of Lagrangian residuals (rather than the Eulerian residuals actually measured), net population growth in a dispersive environment (Speirs and Gurney 2001), and transverse effects (Savenkoff et al. 1997).

The genera of calanoid copepods that inhabit the LSZ (*Eurytemora affinis* and *Pseudodiaptomus forbesi*) are epibenthic in many estuaries, residing on or near the bottom by day and rising into the water column at night, generally as a mechanism to avoid attack by visual predators (Vuorinen 1987; Fancett and Kimmerer 1985; Morgan et al. 1997). The populations of the San Francisco Estuary, however, remain in the water column. Whether this is because of strong tidal mixing, high particulate loads, low visibility, a fluid bottom, or some other cause is unknown.

Zooplankton probably have little effect in the San Francisco Estuary on dynamics of phytoplankton blooms, which are much more influenced by benthic grazing (Cloern 1991). Model studies using reasonable estimates of per capita feeding rates of zooplankton and field data on abundance showed zooplankton consumption to be a minor part of the phytoplankton balance in the South Bay (Cloern 1991; Lucas et al. 1998), although their estimated consumption was a greater fraction of phytoplankton production in San Pablo Bay (Cloern et al. 1985).

Zooplankton are important as food for larval and juvenile fish of most species, as well as adults of some smaller, pelagic species. For example, striped bass larvae and juveniles consume adult and juvenile copepods before switching predominantly to mysids (Heubach et al. 1963). Fish prey on copepods “selectively,” with feeding success varying mainly through the detectability and escape mechanisms of the copepods (Fancett and Kimmerer 1985; Meng and Orsi 1991). Copepods and other zooplankton are also the predominant food of larval and juvenile delta smelt (Nobriga 1998; Lott 1998), anchovy (McGowan 1986), and larval and adult herring (Sandstrom 1980; Munk 1992). The differences in size and feeding mode between the current and previous suite of zooplankton has probably resulted in a foodweb that functions differently and may be less efficient at supporting higher trophic levels. In particular, the shift to small copepods, which tend to be less available to fish than larger copepods, may have resulted in a foodweb with more trophic steps and therefore lower efficiency than before.

Mysids and Epibenthic Amphipods

The macrozooplankton form an important part of the foodweb of many estuaries. Mysids or opossum shrimp are small (<20 mm) shrimp-like crustaceans that are common in estuaries worldwide. Mysids are abundant in the Low-Salinity Zones of many if not most river-dominated temperate estuaries (Jones et al. 1990; Hough and Naylor 1992). Amphipods are also small crustaceans that are usually associated with benthic habitats but can be abundant in the plankton. Both are important food organisms for various kinds of fish. Generation times for these organisms are longer than for smaller zooplankton, in the range of months to years.

Key features of epibenthic macroplankton in the San Francisco Estuary are: (1) The native mysid has been largely replaced by introduced mysids and amphipods; (2) The total abundance of mysids has declined over the period of record; and (3) Mysids and amphipods are important items in the food web of the Low-Salinity Zone.

Of about eight species of mysid in the San Francisco Estuary (Modlin and Orsi 1997) the most common and well-studied has been the native *Neomysis mercedis* (Orsi and Knutson 1979). The smaller, introduced *Acanthomysis bowmani* (Modlin and Orsi 1997) has largely replaced *N. mercedis*, although at a broader salinity range and lower abundance (Orsi 1997, 1999), and several other introduced mysid species have become abundant (Modlin and Orsi 2000). I present here a discussion of the ecology of *N. mercedis* partly for its historical importance, but also because some of the same principles may apply to *A. bowmani*.

N. mercedis was most abundant in the LSZ, between salinities of about 0.5 and 6 (Heubach 1969; Orsi and Knutson 1979; Kimmerer et al. 1998). The annual cycle comprised two generations. Mysids overwintered as adults or late juveniles, then reproduced during spring to produce a summer generation whose offspring remain through the next winter (Heubach 1969; Siegfried et al. 1979). As in most crustaceans the adults produced at higher temperatures were smaller and less fecund than the overwintering generation (Heubach 1969). The population declined annually in summer probably because of increasing temperature, since *N. mercedis* apparently cannot tolerate temperature over about 22EC (Heubach 1969; Orsi and Mecum 1996), although increasing predation pressure from, e.g., striped bass (Heubach et al. 1963) cannot be ruled out.

The distribution of *N. mercedis* with regard to salinity contrasts with its physiological salinity tolerance which is much broader (Siegfried et al. 1979). Possible reasons for this include higher population growth rate in the LSZ and interactions between behavior and hydrodynamic conditions. Heubach (1969) reported a higher proportion of *N. mercedis* females to be gravid (carrying eggs) in the LSZ than out of it.

Heubach (1969) and Orsi (1986) also reported on patterns of vertical migration. Light levels appeared to regulate the vertical position of mysids (Heubach 1969), which were closer to the bottom in clearer water seaward of the LSZ than within it (Orsi 1986). In both cases a tidal component of migration was identified but not tested, nor were data presented on current velocities. Mysids (both *N. mercedis* and *A. bowmani*) in and near the LSZ migrated off the bottom by night in 1994, and to a greater extent on the flood than on the ebb (Kimmerer et al. 1998). This migration may be a mechanism for remaining in the LSZ, since the lack of gravitational circulation in Suisun Bay (Burau 1998; Kimmerer et al. 1998) rules out the two-layer flow mechanism suggested by Orsi (1986). Sampling in 1996, a wetter year than 1994, revealed no migration but a consistently deep position in the water column (Kimmerer et al. 2002). This may reflect an adjustment of the mysids to conditions further seaward in the estuary, where greater water depths allow for gravitational circulation and the possibility of retention (Kimmerer et al. 2002).

Mysids are generalized omnivorous filter-feeders that can take prey through opportunistic raptorial feeding (Kost and Knight 1975; Siegfried et al. 1979; Fulton 1982; Bremer and Vijverberg 1982; Hansson et al. 1990). Most of the identifiable phytoplankton remains in guts of *N. mercedis* were large diatoms, mainly *Coscinodiscus* in brackish water and *Aulacoseira* (*Melosira*) *granulata* in freshwater (Kost and Knight 1975; Siegfried and Kopache 1980). Smaller diatoms, even the abundant bloom diatom *Skeletonema*, were not taken in large quantities (Kost and Knight 1975; Siegfried and Kopache 1980). Kost and Knight (1975) found much of the gut content to be unidentifiable detritus. Although mysids in salt marshes are known to feed on detritus especially in winter (Zagursky and Feller 1985), it is more likely that the detritus identified in *N. mercedis* guts was of animal origin. The plant detritus common in Suisun Bay would have been readily identifiable, yet such remains were rare in a later study (Siegfried and Kopache 1980). Smaller detrital particles would not have been consumed, given the apparent strong selection for large particles by *N. mercedis*. Although young mysids ate mostly plants, mysids larger than 3 mm were mainly carnivorous (over 90% of the energy of 7 mm mysids, Siegfried and Kopache 1980). Mysids ate copepods (*E. affinis*, identified as *E. hirundoides*, also *harpacticoids*) and rotifers (Siegfried and Kopache 1980). *Copepod nauplii* were rare in mysid guts, which was attributed to escape response of *nauplii* (Siegfried and Kopache 1980).

Abundance of *N. mercedis* was high at intermediate freshwater flow (Orsi and Knutson 1979; Knutson and Orsi 1983; Orsi and Mecum 1996; Kimmerer and Orsi 1996). This has been attributed to spatial extent of suitable habitat (Orsi and Knutson 1979; Knutson and Orsi 1983), although this model has not been subjected to rigorous analysis. An alternative explanation may have to do with the interaction among position of the LSZ, hydrodynamic patterns, and vertical migration. The complexity of this interaction requires tests using coupled hydrodynamic and biological models. Export pumping apparently has only a very minor effect on mysids, so that exposure to pumping related to their geographic position is an unlikely explanation of the relationship with freshwater flow (Orsi and Mecum 1996).

Food limitation in *N. mercedis* may be the cause of its severe decline in the late 1980s (Orsi and Mecum 1996). This theory is supported by correlations between chlorophyll concentrations and abundance of *N. mercedis*, stratified by freshwater flow levels (Orsi and Mecum 1996). These correlations apparently did not change during the period reported (1968-1993; Orsi and Mecum 1996). The apparent mechanism for food limitation was reduced growth rate of young mysids. This is supported by their dependence on phytoplankton (Siegfried and Kopache 1980), and the decline in relative abundance of larger mysids in recent years (Orsi and Mecum 1996). Fecundity did not decline, but this can be explained by the diet of mysids: adults are largely carnivorous and total copepod abundance did not decline.

N. mercedis was an important food for numerous fish species including juvenile striped bass, sturgeon, and Chinook salmon, and adult American shad (Heubach et al. 1963; Orsi and Knutson 1979). A decline in carrying capacity of the estuary for striped bass between the ages of one month and three years may have been due to declines in abundance of *N. mercedis*, although relationships were weak (Kimmerer et al. 2000). Fishes of Suisun Marsh channels underwent a reduction in dietary overlap and abundance between 1979-1983 and 1998-1999, apparently due to the decrease in mysid abundance (Feyrer et al. 2003).

The place of mysids in the food web may have been taken partially by the epibenthic amphipod *Gammarus daiberi* (Gartz 1999), which became abundant in 1987. This amphipod is of similar size and has a similar vertical migration pattern in the LSZ to mysids (Kimmerer et al. 1998). The IEP benthic monitoring program routinely collects and analyzes abundance of these amphipods using grab samples. Abundance is highest in the Delta and low in brackish water; thus these are essentially freshwater organisms able to tolerate a moderate increase in salinity. The proportion of *G. daiberi* on the bottom or in the water column at any one time is unknown, but based on a rough comparison of benthic grab sample data near the LSZ and plankton data in the LSZ, they appear to be about equally distributed between both habitats (Kimmerer unpublished). This makes quantitative sampling for these organisms difficult.

Benthos

Most benthic monitoring in the San Francisco Estuary focuses on the macrobenthos, i.e., animals collected by sieving sediments through a 0.5-mm or 1-mm screen. This eliminates the smaller meiobenthos, which are very abundant in other estuaries, and play important roles as prey for larger organisms and as consumers of bacteria (Bell and Coull 1978). Very little is known about meiobenthos from the San Francisco Estuary except for a few studies on benthic foraminifera and two unpublished studies cited by Nichols and Pamatmat (1988). Nematodes and harpacticoid copepods were abundant in one of those studies, and ostracods and nematodes in the other. Macrobenthos have population response times on the order of months to a year (Figure 2).

Two benthic habitats occur in the San Francisco Estuary. Hard substrate includes structures and rocky outcrops mainly in Central Bay, while soft substrate (mainly sand in the channels and mud elsewhere) occurs throughout the estuary. Most of this discussion concerns the soft-bottom benthos. Relatively little has been published on hard-bottom communities except for taxonomic reports, particularly those documenting invasive species (Cohen and Carlton 1995). A research program is underway to document settlement to hard substrates, with particular emphasis on introduced species and contaminant effects (G. Ruiz, Smithsonian Environmental Research Center, pers. comm.). As far as I know no routine sampling program collects organisms from hard substrates.

Studies of the benthos of the San Francisco Estuary described below reveal several key features: (1) Frequent physical, chemical, or biotic disturbance influences abundance of benthos; (2) Most of the species encountered can be described as opportunists, able to recolonize quickly after disturbances; (3) Introduced species form the bulk of the soft-bottom benthos in most of the estuary; and (4) Food limitation appears to be common at least in bivalves.

Distribution Patterns

Benthic species composition and abundance have been examined in several long-term monitoring studies. These include a study of an intertidal mudflat site in the South Bay by the USGS (Nichols and Thompson 1985b), the IEP benthic monitoring program in the northern estuary (Markmann 1986; Hymanson et al. 1994; Peterson 2002), and the Regional Monitoring Program (RMP, B. Thompson et al. 1999). A few shorter-term studies (e.g., Nichols 1985; Hymanson 1991) have also provided useful information on patterns of distribution and abundance. None of the USGS studies or the RMP have sampled in the Delta, and few of the IEP studies have gone seaward of Suisun Bay (none beyond San Pablo Bay). However, recently the RMP and IEP sampling programs have been coordinated to provide a system-wide view of benthic dynamics (B. Thompson et al. 1999).

Temperature is the key variable regulating growth, metabolism, and reproduction of invertebrates. The narrow range of temperature in the San Francisco Estuary (Figure 16) makes it less important than other influences on benthic abundance and activity. For example, most of the common benthic organisms in the San Francisco Estuary have extended reproductive periods lasting from spring through fall, as compared with relatively brief reproductive seasons in estuaries with lower winter temperature (Nichols and Thompson 1985a). The other principal variables controlling benthic abundance and species composition are water depth, sediment composition and grain size, salinity, and current strength (Nichols and Pamatmat 1988).

Characteristics of common benthic species are discussed by Markmann (1986), Nichols and Pamatmat (1988), Hymanson et al. (1994), Fields and Messner (1999), and Peterson (2002). Relatively few species make up the bulk of the numbers: for example, Hymanson et al. (1994) reported four species making up 80% of the numbers in Suisun Bay. Over 90% of the individuals are in three phyla: annelid worms, arthropods (mainly crustaceans), and mollusks. The mollusks, primarily a few species of bivalve, were most common except in the hard-substrate areas of the Central Bay (Thompson and Nichols 1988). In recent years two introduced species of mollusk have dominated the biomass of benthic collections in the northern estuary, *Corbicula fluminea* in freshwater parts of the Delta and *Potamocorbula amurensis* elsewhere (Fields and Messner 1999; Peterson 2002).

The common species can be characterized as opportunistic in that they can recolonize areas rapidly after disturbance, owing partly their long reproductive periods (Thompson and Nichols 1988). In general the number of species is greatest near the mouth of the estuary, where exchange with open coast fauna, availability of a variety of substrates, and relatively low level of physical rigor (i.e., salinity and sediment load, possibly contamination) allow for much greater diversity (Nichols 1979). Biomass was highest in South and Central bays and lower to the north, but biomass and abundance patterns were highly irregular (Nichols 1979).

Species composition and relative abundance were remarkably persistent during a ten-year study of an intertidal mudflat in South Bay (Nichols and Thompson 1985a). However, abundance of all species varied substantially between and within years in response to observed and unobserved factors. The key to persistence of the pattern was inferred to be a combination of recurrent disturbances on the same time scale as the life cycle of the organisms, and opportunistic life history strategies that enabled these species to recolonize the habitat rapidly after a disturbance. These strategies include brooding of young (as opposed to release of young into the plankton): at high abundance almost all of the individuals were of brooding species. Disturbances included low-salinity events, scouring due to tidal flows, and inundation with detritus after a die-off of macroalgae (Nichols 1979).

Data collected from other regions of the estuary were consistent with the above findings: the species composition of the benthos changed little over three decades of study, although large interannual and seasonal variability was evident (Nichols and Thompson 1985b). This has all changed with the introduction of *P. amurensis*, which is now predictably the most abundant species in many parts of the estuary (Peterson 1996). Both RMP and IEP monitoring show similarly that benthic species composition is generally consistent among years if salinity variation is taken into account (B. Thompson et al. 1999; Thompson and Peterson 1998). Small-scale spatial variability in benthos, however, can be quite high (Vayssières and Peterson 2003).

The short-term variation in benthic abundance due to disturbance events suggests that sampling intervals of one month or more may be too long to capture the dynamics of the benthos. These intervals are suitably scaled to the mean life-span of the organisms, but not to the sporadic nature of the disturbance events.

Most of the common benthic species present up to 1983 west of the Delta were introduced (Nichols and Thompson 1985b), and since that time introductions have continued (e.g., Nichols et al. 1990, Hymanson et al. 1994). Only the soft-bottom marine species of the Central Bay have a significant native fraction (Nichols and Pamatmat 1988). Carlton (1979, 1985) and Cohen and Carlton (1995, 1998) have detailed the spread of exotic organisms, mostly benthic, in the San Francisco Estuary. Mechanisms for introductions include fouling organisms attached to ships, larvae in ballast water, and deliberate introductions bringing additional cryptic species. The latter have included fouling organisms of oysters brought in for aquaculture (Carlton 1979), as well as hitchhikers with introduced fish, live bait, and aquarium weeds (Cohen and Carlton 1998).

The introduction of the Amur River clam, *Potamocorbula amurensis*, in 1986 is particularly noteworthy because of its impact on the overlying water column and on other benthic species (Nichols et al. 1990; Carlton et al. 1990; Alpine and Cloern 1992; Kimmerer et al. 1994; Peterson 2002). Its success may be due to its broad salinity tolerance, long larval period, and apparently rapid growth and reproductive rates (Nicolini and Penry 2000). *P. amurensis* has spread throughout the brackish to saline regions of the estuary, and has been abundant in some regions of the estuary since its introduction (Figure 34). Analysis revealed little differentiation and therefore possibly high gene flow among clams collected from different parts of the Bay (Duda 1994), which could indicate extensive dispersal of planktonic larvae or post-settlement movement by currents or human activities. Spatially-intensive surveys in the northern estuary have revealed that *P. amurensis* was more abundant at sites with mud bottom rather than sand, and that recruitment events occurred downstream of freshwater (Hymanson 1991; Peterson 1996).

A recent analysis of the long-term record of benthic species composition in Grizzly Bay (Peterson 2002) has shown the importance of *P. amurensis* in its influence on benthic communities. The greatest impact appeared to be on filter-feeding species that release young as planktonic larvae; presumably *P. amurensis* was both a predator and competitor of these species. The picture was somewhat confounded by other introductions, but none had the impact of *P. amurensis*, particularly when years of similar freshwater flow were compared (Peterson 2002).

Salinity Effects

The principal modes of variability throughout the estuary include regional and seasonal effects largely due to salinity. Since generation time of benthos is long compared to the response time of salinity (Figure 2), the abundance of benthos responds to changes in salinity, and high variation in salinity results in low benthic abundance and diversity. The number of species has been consistently lowest in low-salinity water (Markmann 1986; Nichols and Pamatmat 1988; Hymanson et al. 1994). This is consistent with the general pattern of estuarine diversity, in which relatively few species can withstand the fluctuations between freshwater and brackish water (Remane 1971).

The influence of salinity is most easily seen in Suisun Bay during high- or low-flow events. During extended droughts species normally found at higher salinity begin to work their way up the estuary (Nichols 1985,

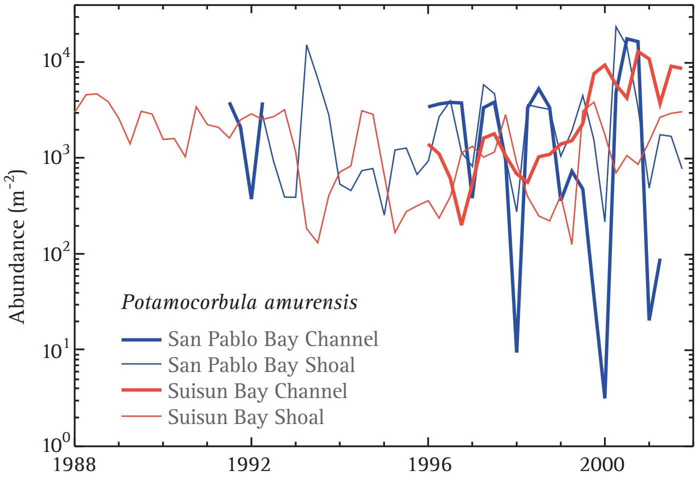


Figure 34. Quarterly mean abundance of *Potamocorbula amurensis* from several stations based on DWR monthly monitoring (Peterson 2002).

Markmann 1986). During high-flow periods freshwater species characteristic of the Delta, such as *Corbicula fluminea* and *Corophium* spp., move seaward into Suisun Bay (Markmann 1986; Hymanson et al. 1994). However, since these movements involve either settlement of young or movement of adults along the bottom, they can take several months depending on the time of year. Therefore the benthos of Suisun Bay has sometimes been depauperate, particularly during a dry period after a flood or high flows following a drought (Nichols 1985; Markmann 1986; Nichols et al. 1990).

P. amurensis may have invaded rapidly because it arrived during a drought following a high-flow event, when the benthic fauna of Suisun Bay was depressed (Nichols et al. 1990). Although it is more euryhaline than most of the estuarine species, *P. amurensis* is still apparently excluded from regions of freshwater, and is more abundant in Suisun Bay during periods of elevated salinity (Hymanson et al. 1994; Peterson 2002). Abundance in Suisun Bay was reduced when salinity was depressed in 1995-1999 (Figure 34).

Most of the apparent movements of benthic species are presumably due to settlement of larvae or juveniles into newly suitable habitat, but there are exceptions. Many of the mudflat species brood their young, yet disperse throughout the estuary (Thompson 1982). Some species (e.g., the amphipod *Ampelisca abdita*) can move into channels when salinity gets too low (Nichols and Thompson 1985b). Others move when sediment is mobilized by strong currents, e.g., *P. amurensis* which lives relatively high in the sediment (J. Thompson, USGS, pers. comm.).

Effects of Water Movement

The sand waves that are a common feature of the deeper channels of the estuary indicate conditions not conducive to settlement for most species. Similarly, instability of shallow sediments may contribute to non-equilibrium in the benthos (Nichols 1979; Nichols and Thompson 1985b). For example, a change in sediment elevation due to shifting sediments caused a loss of many benthic organisms at a mudflat site in South Bay (Thompson 1982). Changes in texture and elevation of sediments arise through sediment-transport processes occurring at tidal to interannual time scales (Nichols and Thompson 1985b).

The benthic organisms themselves can alter hydrodynamic conditions near the bottom. This has been shown in flume studies, in which the incurrent and excurrent siphon currents of artificial clams altered the hydrodynamics and particle distributions in the benthic boundary layer (Monismith et al. 1990, O'Riordan et al. 1993, 1995). Mats of tubes or clusters of shells built by organisms (worms, amphipods, bivalves) can alter hydrodynamic conditions near the bottom (Crimaldi et al. 2002), leading to undercutting, erosion, and eventual washout of sediments, or alternatively can armor the bottom against disturbance by currents (Nichols 1979).

Although the movement of *Corbicula fluminea* from the Delta into Suisun Bay has been attributed to the scouring effects of high freshwater flows (Markmann 1986), net flow velocities due to freshwater flow are typically smaller than tidal flows (Figures 14 and 21). Thus only the most extreme floods would seem capable of moving benthic organisms, and it is more likely that the reported movement was tidally driven.

Effects of Food Supply

Nearly all benthic organisms fall into three categories according to feeding modes: filter-feeders, which feed in the overlying water column; deposit feeders, which feed on the sediments; and predators. The bivalves are mostly filter-feeders, with a few deposit feeders such as the formerly abundant *Macoma balthica* (Nichols and Pamatmat 1988). Several studies have shown food limitation of these organisms.

Thompson (1982) studied growth of the intertidal clam *Gemma gemma* on a South Bay intertidal mud flat in 1974-1975. This clam can reproduce twice yearly, and the brooding season extended over about ten months. Growth was fastest in spring and early summer and low or nonexistent the rest of the year. The high growth season coincided with the spring bloom, suggesting a response to elevated food supplies. Compared to two other studies of *G. gemma* at higher latitudes, growth was slower or equal, maximum size smallest, and life span the longest in the San Francisco Estuary. Competition for food by *M. balthica* limited the growth of *G. gemma* (Thompson 1982).

Growth of *Macoma balthica* was examined on the same mud flat by Nichols and Thompson (1982). The growth pattern was surprisingly similar to that in higher latitudes in spite of much milder temperature conditions and a longer period when temperature should be conducive to growth. The clams grew faster than reported from other estuaries, but only during a brief period in spring, presumably because of higher food supply from the spring bloom. Their life span was also much shorter, although final size tended to be larger than elsewhere. Two cohorts were observed, some recruited in spring and some in the fall. The primary source of food for *M. balthica* was the benthic algal mat and the phytoplankton cells near or on the sediment surface.

The Nichols and Thompson (1982) study was extended to three additional locations during a two-year study by Thompson and Nichols (1988). Growth of *M. balthica* was apparently limited by high temperature in summer (both years), and was positively correlated with phytoplankton biomass at each of two South Bay sites (one of two years each site). Growth at the Suisun Bay site (sampled during one year only) was positively correlated with benthic algal biomass, while at the San Pablo Bay site growth was correlated with phytoplankton biomass (both years) and benthic algal biomass (one of two years). Thus, food limitation was frequent but apparently sporadic. Some clams transplanted from a low-chlorophyll site to a high-chlorophyll site grew much more rapidly after they were transplanted, also suggesting a positive response to elevated food concentration.

Field and laboratory experiments on feeding and growth were combined to demonstrate food limitation in *Corbicula fluminea* in the western Delta (Foe and Knight 1985). Growth rates were higher in laboratory containers at high food concentrations than at low, and higher in the laboratory than at a field site. They also inferred food limitation throughout the Delta based on chlorophyll concentrations, finding that food in spring and fall was insufficient to support growth. They estimated that feeding would saturate at chlorophyll concentrations of 20 µg Chl L^{-1} in spring and 47 µg Chl L^{-1} in summer. The concentration of inorganic particles had no significant effect on feeding, implying possible food selection. Experiments with other filter-feeding bivalves have also shown the capability of food selection (e.g. Kiørboe et al. 1980), and Canuel et al. (1995) inferred possible selection from high concentrations of organic biomarkers of algal origin in *P. amurensis* from Suisun Bay.

Growth of *Potamocorbula amurensis* is also sometimes food limited (J. Thompson, USGS, pers. comm.). Several other species of benthic invertebrate grew fastest during spring, presumably because of food supply, including the amphipod *Ampelisca abdita*, an isopod, and a salt marsh mussel (summarized by Nichols and Thompson 1985b).

Biotic Interactions

Predation on benthos is a likely control on abundance, although difficult to observe. The clam *P. amurensis* was an important food resource for greater and lesser scaup in San Pablo Bay, and clam abundance declined during winters possibly because of predation by scaup (Poulton et al. 2002). In contrast to subtidal habitats, no apparent effects of bird predation on abundance of intertidal benthic organisms have been noted (Thompson 1982).

Some biota may physically disturb the bottom (bioturbation). For example, bat rays (*Myliobatus californicus*) create depressions during feeding, consuming and disrupting the benthos in those areas (Nichols 1979). Apparent predatory or competitive effects have been observed in benthic communities. The tube-dwelling amphipod *Ampelisca abdita* appears to control the abundance of *M. balthica* (Nichols and Thompson 1985a). The evidence for this control was an inverse correlation between the two, plus the observation that on the few occasions when both were abundant the clams had settled before the amphipods became abundant. This suggests either interference with or predation on the juvenile clams by the amphipods.

Similarly, *P. amurensis* apparently suppressed other species as shown by inverse abundance patterns (Nichols et al 1990, Peterson 2002). This suppression was probably due at least partly to consumption of planktonic larvae by the clams, which are able to capture small zooplankton (Kimmerer et al. 1994). The result has been a rather dramatic shift in taxonomic composition in Grizzly Bay, particularly for filter-feeding species and those that have planktonic larvae (Peterson 2002).

Human Disturbance

Some of the effects of flow and salinity discussed above could be attributed to human intervention in the ecosystem, but the big flow events and droughts, which have the greatest effect on the benthos, are not under direct human control. Other human disturbance includes dredging, sewage discharge, and current or historic discharge of various contaminants. Dredging probably has a small impact on the benthos because a relatively small proportion of the San Francisco Estuary is dredged annually, and benthic communities are able to recolonize rapidly (Nichols and Pamatmat 1988). However, sand dredging may have aided the dispersal of *P. amurensis* to the South Bay. Sewage discharge no longer contains high concentrations of organic matter, and the nutrients added generally would have little effect on benthos.

Contaminants are discussed elsewhere (Spies in prep.); here I discuss briefly the expected effects on benthic populations. Attempts to detect contaminant effects have used a variety of approaches with only limited success. Comparisons of disturbed and undisturbed sites have been used to assess the effects of pollutants, but these effects can be obscured by large natural fluctuations in abundance (Nichols 1985). In addition, some indicator organisms used for detecting pollution effects are ambiguous: for example, some worms of the genus *Capitella* are used as indicators of polluted conditions, but they are also abundant in organic-rich, but unpolluted, areas (Nichols and Pamatmat 1988). The use of indicator organisms for toxicity is fairly common, but has not worked very well to date in the San Francisco Estuary (B. Thompson et al. 1999), perhaps because of the overriding influence of natural disturbances (Nichols and Pamatmat 1988).

However, there are frequent indications of toxicity of water and sediments to benthic test organisms, although not necessarily those found in the estuary (e.g., B. Thompson et al. 1999). Benthic organisms can be useful as “biosentinels” of contamination in that they accumulate some contaminants (e.g., heavy metals) over time, provided estuarine conditions (e.g., salinity) are taken into account (e.g., Luoma and Cain 1979; Brown and Luoma 1995, 1998). Sites contaminated with DDT had reduced abundance of species known to be sensitive to DDT and increased abundance of insensitive species (Swartz et al. 1994; Ferraro and Cole 1997), and reproduction of bivalves was reduced by metal contamination near a sewage treatment plant (Hornberger et al. 2000). To date there is no clear evidence that populations and communities have been adversely affected in the long run or over a wide area; however, such evidence is extraordinarily difficult to obtain, and the available evidence certainly suggests numerous potential problems at the population level.

Role of Benthos

The benthos have several important roles in the ecosystem of the San Francisco Estuary. First, they are probably the most important consumers of phytoplankton, benthic microalgae, and detritus in the estuary. Since at least the bivalves are large relative to their food, they provide an efficient trophic pathway between primary producers and large fish and birds; by contrast, zooplankton are generally consumed by smaller fish, adding at least one additional trophic step.

Second, benthic organisms are important to the cycling of materials between the sediment and the water column, both by their metabolism and by bioturbation. Bioturbation exposes deep sediment to irrigation by oxygenated water and increases sediment mixing (e.g., Officer and Lynch 1989). The net result is greater aerobic respiration in the sediments and more effective remineralization of nutrients and other substances that would otherwise be buried. In addition, efficient transfer between the overlying water column and benthos, and the incorporation of sediment contamination into tissues, may also result in rapid incorporation of toxicants into the benthic food web (Brown and Luoma 1998; Hinton 1998).

Third, the benthos provides a large food resource for predators. Numerous predators on benthos have been identified through behavioral studies and gut content analyses. Several species of fish, including sturgeon, starry flounder, and bat rays, feed almost exclusively on benthos, and young striped bass consume prey both in the water column and on the bottom (Heubach et al. 1963; Stevens 1966). During times of high abundance of *P. amurensis*, sturgeon guts have been full of clams (Peterson 1997). The bay shrimp *Crangon franciscorum* feeds at least partly on benthic organisms. Intertidal mudflats are important feeding habitat for shorebirds, which feed on a variety of organisms (Nichols and Pamatmat 1988), and scaup feed on clams in shallow areas (Poulton et al. 2002). These feeding relationships are of great concern given the concentration by bivalves of contaminants, particularly selenium (Linville et al. 2002). Apparently the benthic foodweb is more efficient at transferring selenium to higher consumers than is the planktonic foodweb (Baines et al. 2002). Body condition of several species of diving ducks was inversely related to body concentrations of several contaminants (Takekawa et al. 2002).

Key Findings and Uncertainties

Considerable research has gone into the interactions between the soft-bottom benthos and the overlying water column. Current investigations are examining the changing relationships in the foodweb of the estuary, particularly in the plankton. Investigations into the dynamics of planktonic organisms are more limited, particularly for the macrozooplankton. Some of the key issues are:

- *Introduced Species*. The zooplankton and benthos have been altered by introduced species, and in both cases the consequences for higher trophic levels appear to be substantial. However, determining the relative roles of these zooplankton, particularly the small copepod species, has proved difficult.
- *Effect of Potamocorbula amurensis*. The invasion of this one species of clam has had a greater effect on the foodweb than any other invasion during the course of the long-term monitoring programs. The principal apparent effects have been the loss of the summer phytoplankton biomass maximum in Suisun Bay, declines in phytoplankton in San Pablo Bay and the Delta, changes in abundance and species composition of the zooplankton, possible changes in abundance of some fish species, and a restructuring of benthic communities in Grizzly Bay. However, we do not yet understand the consequences of the increase in benthic animal production to higher trophic levels, nor is it clear yet how the remaining zooplankton species are able to maintain abundance in Suisun Bay with the reduction in phytoplankton. A possible alternative food source for the remaining zooplankton is consumption of particle-bound bacteria or their protozoan predators.
- *Retention Mechanisms*. Intensive studies of the migratory behavior of zooplankton and larval fish greatly showed the importance of tidal migration in position maintenance. However, the observed migration appeared insufficient to maintain the copepods in position, in contrast to mysids. Model studies are planned to investigate this question further.
- *Importance of Protozoans*. Although protozoans seem to be uncommon in Suisun Bay in and near the LSZ, they are extremely abundant in the lower estuary and an important food source for mesozooplankton. If protozoans are indeed uncommon in the LSZ, then the moderate bacterial production there poses a conundrum, in that the consumer of all that production remains unidentified.
- *Contaminants*. The frequency of localized effects of contaminants, and of toxic contamination events in bioassays using animals similar to those in the estuary, suggest the possibility of population-level effects. These effects are subtle and may require considerable effort to detect. Since agricultural chemicals are designed to kill either plants or arthropods, it would be somewhat surprising not to find similar effects on aquatic organisms in the estuary.
- *Macrozooplankton*. The early work on feeding and dynamics of mysids led to an appreciation of the key role of these organisms in diets of some fishes. To some extent the introduced amphipod *Gammarus daiberi* may now occupy the role of mysids. However, there is little information on its biology and no sampling program currently obtains reliable abundance estimates.
- *Roles of Benthos*. Information has been obtained from the estuary on the role of benthic organisms in consuming phytoplankton and bacteria, altering substrates, mediating chemical fluxes, and providing food for fishes. However, it is difficult to extrapolate some of these localized analyses because of the patchy distribution of the benthos and the limited spatial extent of the monitoring programs.

FISH AND EPIBENTHIC MACROINVERTEBRATES

Fish and large epibenthic macroinvertebrates, including bay shrimp and various crabs, are discussed here together because they are collected in the same sampling programs. This discussion focuses on several issues common to these groups, and on several species that have receive particular attention in estuarine research; the intent is not to describe status and trends of these groups. Skinner (1962) provides an excellent early review of fish and wildlife resources of the estuary. Information on the basic biology of other species can be obtained from several key publications (e.g., Moyle 2002; Herbold et al. 1992; Baxter et al. 1999). Four important species not covered here are addressed in separate review papers: Chinook salmon and steelhead (Williams and Yoshiyama in prep.), Sacramento splittail (Moyle et al. in prep.), and delta smelt (Bennett in prep.).

The taxa discussed here have generation times of one to several years, but populations reproduce annually. The interaction between reproductive time scale and that for recurrence of droughts or ENSO cycles (Figure 2) may be the most important mode for environmental influence on these taxa.

General Features

Individual species were selected mainly because research and data analysis have revealed important features of their life histories and abundance patterns relevant to the objectives of this paper. For discussions of life histories of fish see Emmett et al. (1991). Abundance patterns in the San Francisco Estuary are summarized from the IEP San Francisco Bay study and other sources by Baxter et al. (1999). Appendix A lists the frequency of occurrence of all fish species collected in the San Francisco Bay study (Baxter et al. 1999), IEP fall midwater trawl survey (Moyle et al. 1992), and IEP summer townet survey (Turner and Chadwick 1972; Stevens et al. 1985).

Key features with regard to fish, shrimp, and crabs are: (1) Most of the data available are on abundance and distribution patterns, and little synthesis or process-oriented work has been done; (2) Complex life cycles of these populations practically ensure that multiple factors regulate their abundance; and (3) Many species connect the estuary with the coastal ocean or the watershed, and changes in those regions have a noticeable effect on abundance of these species in the estuary; (4) Introduced species play a major role in the estuary, particularly in the Delta, and native species have declined in recent decades; and (5) Effective sampling is extraordinarily difficult, although the high intensity of the sampling programs has resulted in robust data sets.

Sampling Issues

Sampling for fish and epibenthic macroinvertebrates is complicated by their typically heterogeneous spatial and temporal distributions, including schooling behavior, and their strong ability to swim and to avoid sampling nets. To some extent these problems can be overcome through brute force by taking large numbers of samples. This is effective for the most common species, although confidence limits on individual annual abundance indices can still be large. For rarer species these problems are so severe that some scientists are reluctant even to estimate abundance, preferring to use indices (Herbold 1996).

Long-term studies, mostly conducted by the IEP (Table 2), include the summer townet survey (1959-present), the fall midwater trawl survey (1967-present), the San Francisco Bay Study (1980-present), the Chipps Island trawl survey, the striped bass egg and larval survey (16 years during 1968-1993), the Suisun Marsh Study (UC Davis, 1979-present; Moyle et al. 1986; Meng et al. 1994; Meng and Matern 2001; Matern et al. 2002; Feyrer et al. 2003), and a study of the South Bay (NMFS 1974-1982 study, as reported in Pearson 1989). Each of these studies has its target species, and each has advantages and disadvantages for any particular analysis; furthermore, inconsistencies among different surveys can make interpretation difficult. Nevertheless, results of these surveys together with research into particular life history aspects of key species is leading to important new insights into the variables that control population abundance.

Community Composition and Distribution

The long-term monitoring programs, particularly that of the bay study because of its broad geographic scope, have revealed some key patterns regarding the fishes and epibenthic macroinvertebrates of the San Francisco Estuary (Baxter et al. 1999). The most obvious pattern is in the differences in habitat use among the different species, particularly with regard to salinity (Figure 35). For example, of the 54 most commonly collected species in the bay study, 38 had salinity distributions with means above 20 psu, i.e., these were marine species. Most of the remaining species were anadromous.

A large community resident in the freshwater Delta was missed by the bay study, which has had only a few stations in the Delta, although more have been added in recent years. Subtidal areas of Suisun Marsh and the freshwater Delta are overwhelmingly dominated by introduced species (Moyle et al. 1986; Meng et al. 1994; Grimaldo et al. 1998; Christophel et al. 1999; Matern 2000; Brown 2003b). Most of these species were deliberately introduced in attempts to establish fisheries; such efforts are known for many species including American shad, striped bass, common carp, several catfishes, centrarchids such as largemouth and smallmouth bass, black crappie, and various sunfish (Skinner 1962; Dill and Cordone 1997). Many resident fishes in the Delta are more common in shallow inshore waters than offshore (Brown 2003b), and are not sampled effectively by the trawls. For example, in the fall midwater trawl survey (1967-2001), which samples throughout the Delta and Suisun Bay, anchovy made up 53% of the catch, followed by longfin smelt, threadfin shad, striped bass, and American shad, whereas centrarchids were uncommon. Several species of goby (Meng et al. 1994; Matern and Fleming 1995; Matern 2000; Greiner 2002) and the wakasagi, a congener of delta smelt (Aasen et al. 1998) have been introduced in various parts of the estuary.

Several key differences appear to exist in the responses of native and non-native fish species to environmental conditions in the freshwater reaches of the estuary. Native species such as splittail and Chinook salmon are able to capitalize on shallow, ephemeral habitats such as floodplains more than non-natives (Sommer et al. 1997, 2001a, 2001b, 2002). Marchetti and Moyle (2001) noted that native fishes in a regulated stream were associated with higher flow and velocity, lower temperature, and greater shading than non-natives. Likewise, native species were associated with high flow and low temperature, when most (not all) introduced species were less abundant, both in Suisun Marsh (Meng and Matern 2001) and in the south Delta (Feyrer and Healey 2003). These results suggest the value of flow regimes approximating natural conditions for restoring native fishes (Marchetti and Moyle 2001). Conversely, the introduced wakasagi had broader tolerances than its close relative, the native delta smelt, suggesting caution in assuming that flow regimes alone could benefit natives over introduced species (Swanson et al. 2000).

In the brackish to saline parts of the estuary (Suisun Bay and seaward), the catch of fishes in the bay study has been overwhelmingly dominated by northern anchovy, which made up 74% of the catch during 1980-2001 (Appendix A). Other common species making up at least 2% of the total catch were Pacific her-

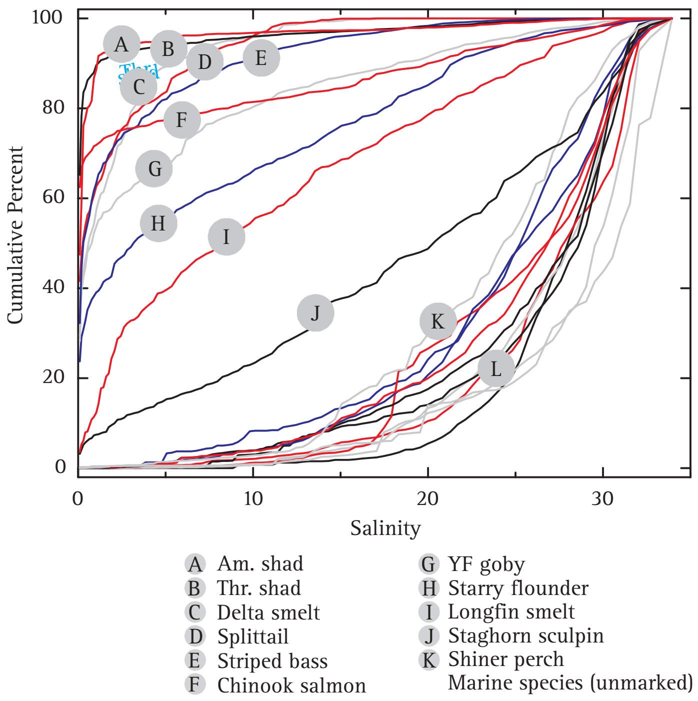


Figure 35. Cumulative salinity distributions of common fish species collected in the IEP San Francisco Bay Study monitoring program. Calculations were as in Figure 33 but the salinity bins were all of equal size. The group of unlabeled lines in the lower right is a suite of marine species including northern anchovy, Pacific herring, white croaker, and jacksmelt.

ring, longfin smelt, bay goby, and striped bass. In contrast to the freshwater regions of the estuary, and to the benthos and plankton throughout the estuary, most of the fish species collected in the bay study were natives (Appendix A): of the 38 common species with mean salinity above 20, only one was introduced (Baxter et al. 1999). This reflects the large fraction of samples in this study taken in high-salinity waters, and the relatively low degree of invasions of the marine fish community. There are several reasons why marine invasions appear to have been uncommon. First, recreational fishing in marine regions of the estuary can target a variety of native species, with little consequent need for deliberate introductions. Second, marine species are more broadly distributed geographically than freshwater and brackish species, providing little opportunity for invasion by new species. Third, the marine environment is much less variable than the estuarine environment, so conditions conducive to establishing new introductions are less common in saline regions than further up-estuary. Finally, fishes may not be efficiently transported by ballast water, which would explain the difference in marine invasions by fishes with, for example, the extensively invaded marine fouling communities (Cohen and Carlton 1995).

Baxter et al. (1999) classified the most commonly collected species in the bay study according to their use of the estuary. These included estuarine residents that spend their entire lives in the estuary (e.g., delta smelt); obligate nursery species that rear only in estuaries (not necessarily only the San Francisco Estuary; e.g., the Bay shrimp *Crangon franciscorum*); non-obligate nursery species that can rear in the estuary or elsewhere (e.g., Dungeness crabs); opportunist species that either live in the coastal ocean and saline reaches of the estuary (e.g., northern anchovy) or in the freshwater Delta (e.g., white catfish); and anadromous species that reproduce upstream and either rear in the estuary or in the ocean (e.g., salmon). The life histories of the resident and obligate nursery species seem to emphasize retention in the estuary, including adhesive eggs, live young, and tidal migration patterns in larvae (Bennett 1998; Bennett et al. 2002). The abundance of several of these species is related positively to freshwater flow (discussed below) Opportunistic and non-obligate nursery species generally do not respond to estuarine conditions other than by avoiding low salinity; their populations are presumably subject to broader-scale conditions along the coast.

A major concern with fish in the estuary is the decline in several native species. This has been noted in the Suisun Marsh (Moyle et al. 1986; Meng et al. 1994; Matern et al. 2002), as well as in the estuary as a whole (Herbold et al. 1992). Declines in tule perch in the Delta were coincident with an increase in centrarchids such as black bass (Nobriga and Chotkowski 2000). Declines in the many species of surf perch in Central Bay have gone unexplained, but could be due to fishing or changing ocean conditions (Baxter et al. 1999). Thus, not all declines can be attributed to upstream activities.

Ecological Interactions

One of the goals of ecological research is to identify causes of observed variation in abundance. Life histories of fish and invertebrates are complex, influences on abundance subtle (Houde 1989), and the estuarine environment intensely variable. Linking causes to observed changes in abundance would be difficult enough if there were only one cause; however, different factors can influence a population at different times, each one obscuring the causative linkages of the others (Bennett and Moyle 1996). Data on abundance of fish and macroinvertebrate populations are generally available on an annual scale because of their reproductive patterns, so for each species we are fortunate to have ~20 to 30 data points. Although this data record is unusually long, statistical analyses of the relationships between abundance and potential causative variables should be limited to about one parameter for each ten data points, or two to three linear explanatory variables (Jassby 1999). This mismatch between the time needed to gather data and the number of points needed for adequate statistical power is a major hindrance in fishery research, and the genesis of a lot of argument about cause and effect.

The degree of difficulty in assigning causes of observed changes does not imply that these causes cannot be found. In fact, evidence has been presented or is developing on causes of population variation in a number of key species in the estuary. For example, progress has been made in determining mechanisms for variability in certain life stages of splittail (Sommer et al. 1997, 2002), striped bass (Stevens et al. 1985; Bennett and Howard 1997,1999; Kimmerer et al. 2000, 2001), and delta smelt (Moyle et al. 1992; Stanley et al. 1995; Bennett in prep.). Several potential mechanisms for population regulation have been identified for various species (EET 1997), and these are being investigated using a variety of approaches. Larvae of several important fish species migrated vertically in synchrony with tides on some occasions, in a likely adaptive mechanism for retention (Bennett et al. 2002).

Diets of fishes of the San Francisco Estuary generally reflect their feeding mode, food environment, and responses of potential prey. Diets of several individual fish species are discussed below. Feyrer et al. (2003) found a shift in diets of fishes of the Suisun Marsh toward low dietary overlap after mysid abundance declined in the late 1980s.

Many of the species discussed here, as well as other fish and epibenthic macroinvertebrates, spend at least some of their time outside the estuary. This means that ocean conditions have consequences for survival, growth, and abundance of some species including Chinook salmon, striped bass, and Pacific herring. It also imposes difficulties with assessing the effect of estuarine conditions on variability in abundance, and limits the explanatory power of variables within the estuary. Ocean conditions vary over time scales of years to decades and longer, providing ample opportunity for interaction with life cycles of fish (Figure 2). As discussed below, such an interaction may be responsible for the decline in striped bass.

Bay Shrimp

Shrimp have been collected routinely in the San Francisco Bay Study otter trawls since 1980, and larvae were collected in bay study plankton samples from 1980 to 1989 (Hatfield 1985; K. Hieb CDFG unpubl.). Six species of caridean shrimp inhabit the San Francisco Estuary. In decreasing order of long-term mean abundance, these are *Crangon franciscorum*, C. *nigricauda, C. nigromaculata, Heptacarpus stimpsoni,* the introduced *Palaemon macrodactylus*, and *Lissocrangon stylirostris* (Hieb unpublished). *C. franciscorum* has been the most abundant bay shrimp in all years except during the extended drought in the 1990s. Over all years it comprised 70% of all shrimp caught, but in 1992 it was only 18%, and *C. nigricauda* and *C. nigromaculata* were more abundant. These species and *H. stimpsoni* are marine-oriented, with lower salinity limits of 18, 25, and 24 psu respectively (10th percentile of population). *C. franciscorum* ranges from 3 to 26 (10th to 90th percentile), while the range for *Palaemon macrodactylus* is 2-27 (Hieb unpublished).

Only *C. franciscorum* and *P. macrodactylus* can be considered estuarine dependent (Hieb unpublished), and because of this and its numerical abundance most of the research attention has focused on *C. franciscorum*. The life cycle was described by Hatfield (1985). This species reproduces early in the spring, mainly in the coastal ocean but to some extent in Central Bay. Planktonic larvae, assumed to be mostly *C. franciscorum* since the larvae cannot be distinguished by eye, are abundant outside the Bay, but can be abundant in Central and South bays. High salinity may be beneficial for egg and larval development (Wahle 1985). Juveniles recruit to the Bay later in spring and settle in shallow areas, gradually moving landward in the north bay with the salt field. There is a peak in abundance of maturing shrimp in late summer-early fall, as in other estuaries.

Abundance of *C. franciscorum* varies significantly with outflow and X2 (see ”The Fish-X2 Relationships” p.86). However, there also appears to be an effect of size of the spawning stock, because the population took some time to recover from depressed levels late in the drought of the 1990s (Hieb, unpublished). Abundance in 1998 was the highest recorded, and 1997 was second highest, so *C. franciscorum* appears to have recovered fully from effects of the drought.

Sitts and Knight (1979) examined guts of *C. franciscorum* and *P. macrodactylus* in Suisun Bay and the Delta in 1976. Both shrimp species were carnivorous, and the most abundant identifiable prey was *Neomysis mercedis*. The proportion of shrimp with *N. mercedis* in their guts increased as the shrimp grew, and the size of the prey mysids increased with predator size. The two shrimp species differed very little in their feeding characteristics. Estimated predatory impact on *N. mercedis* was moderate in the fall and low at other times. Differences between gut fullness by day and night were noted on some occasions, with nighttime guts being somewhat fuller than those of shrimp caught by day. Siegfried (1982) also found predation by both of these shrimp species on mysids.

Wahle (1985) examined guts of *C. franciscorum* and *C. nigricauda* at a shallow and deep station in San Pablo Bay in 1980-1981. Nearly all of the identifiable gut contents were animal, and the most abundant items were amphipods, juvenile bivalves, polychaete worms, and in the smallest shrimp, *foraminifera*. Prey size was related to predator size. Three amphipods were important: *Corophium* spp., *Ampelisca abdita*, and *Grandidierella japonica*. Thus, the shrimp were essentially benthic predators in this study. Although the diets were generally similar, *C. nigricauda*'s diet was more heavily weighted toward amphipods. *C. franciscorum* frequently consumed shrimp including its own species, and fish were occasionally eaten. This study, together with previous studies in this and other estuaries, suggest that crangonid shrimp are generalist predators, consuming any animal prey in their environment that is of a suitable size.

Introduced Crabs

Two introduced species of crab have become abundant in the estuary (Halat and Hieb 1996). The European green crab (*Carcinus maenas*) has invaded numerous temperate estuaries around the world (Cohen et al. 1995), and was first seen in 1989-1990 in the South Bay. It is a voracious predator on other benthic organisms (Grosholz et al. 2000) and was expected to have significant ecosystem impacts (Cohen et al. 1995). Although significant impacts have been observed in other California coastal sites, impacts on the San Francisco Estuary to date have not been significant. The crab appears to be restricted to salinity greater than about 16 psu (Halat and Hieb 1996).

The mitten crab, *Eriocheir sinensis*, is a native of coastal waters of China that may have been introduced deliberately as a food resource. It was first found in the San Francisco Estuary in 1992 and since that time has increased rapidly in abundance and range, as it did previously in the Thames Estuary (Attrill and Thomas 1996). In contrast to most crabs, the mitten crab is catadromous, rearing in rivers and sloughs upstream and reproducing in brackish water (Halat and Hieb 1996; Rudnick et al. 2003).

Abundance of mitten crabs is sufficient to constitute a nuisance, and the crabs could have significant economic consequences (Hymanson et al. 1999). Efforts have been required to remove and exclude crabs from the Delta fish facilities, where they clog screens and damage fish that would otherwise be salvaged (Siegfried 1999). In addition, they interfere with shrimp trawling as well as hook-and-line fishing. Potential impacts identified earlier during the invasion, including burrowing into levees (Veldhuizen 2000), have not materialized. There is controversy over whether the mitten crab can act as an intermediate host for lung flukes (Wang and Hess 2002; Cohen 2003). The fluke has not been found in crabs of the San Francisco Estuary (Wang and Hess 2002).

The IEP began annual surveys of mitten crab abundance in summer 1997, and crabs are also collected and counted in the salvage surveys and the bay study. Abundance at the salvage facilities in 2002 was much less than in previous years (Foss 2003).

Striped Bass

Striped bass (*Morone saxatilis*) were introduced to the San Francisco Estuary in 1879 and have since supported a major recreational fishery (Radovich 1963). Because of the prominence of this fishery and the high abundance of young striped bass in low-salinity waters of the estuary, striped bass for many years were used as the sole indicator of ecosystem condition, and regulatory measures were primarily designed to protect striped bass. The increase in concern over native non-fishery species, and the unique characteristics of the striped bass life history compared with native species (Bennett and Moyle 1996), have led to a shift in management emphasis away from striped bass. To some extent this sift has been exacerbated by its status as an introduced predator on native species, and concerns over predation impacts on threatened species of fish (Lindley and Mohr 2003) have led to restrictions of the stocking program.

In spite of the above, striped bass offer a useful case history because of the extensive data collection and the large amount of published information on this species from the San Francisco Estuary, Chesapeake, Hudson, and other locations (e.g., Goodyear 1985; Stevens et al. 1985; Cowan and Rose 1991; Secor and Piccoli 1996; Kimmerer et al. 2000, 2001). At least 11 long-term data records exist on some aspects of striped bass in the San Francisco Estuary, covering all life stages except the period between age one year and age three years.

The life history of striped bass is well known. Negatively buoyant, free-floating eggs spawned in freshwater during spring drift downstream as they develop, and late larval and juvenile stages occur mainly in brackish regions of the estuary (Calhoun 1952; Turner and Chadwick 1972). Larvae feed on small zooplankton; feeding experiments revealed a greater consumption rate of native copepods over recently introduced species, due to escape response of the copepods (Meng and Orsi 1991). After metamorphosis, juveniles feed on copepods, switch to mysids and amphipods after several months, and become piscivorous late in the first year of life (Heubach et al. 1963; Stevens 1966). Striped bass mature at four to five years of age and can live to over 30 years. Mature individuals migrate to brackish or salt water during summer and return to freshwater during the fall and winter (Calhoun 1952). Year-class strength is indexed by the young-of-the-year (YOY) index determined during summer when the striped bass are about one to three months old (Turner and Chadwick 1972).

Abundance of young striped bass in the San Francisco Estuary has declined substantially over the last three decades (Stevens et al. 1985), although there has been a recent resurgence in abundance of adults. In considering the influence of environmental conditions, including human actions, on striped bass it is useful to separate conditions that may have led to the decline from those that influence year-to-year variability. Environmental effects identified as potentially important to young striped bass include effects of food on growth, contaminants on survival, river flow on transport or survival, and diversions of freshwater on survival (Turner and Chadwick 1972; Stevens 1977; Stevens et al. 1985; Bennett et al. 1995). Potential influences on older fish include fishing mortality, variable migration patterns (Radovich 1963; White 1986; CDFG 1987; Bennett and Howard 1997), and toxic contaminants (Whipple et al. 1981; Brown et al. 1987; Young et al. 1994). In addition, the effects of a stocking program should be included in any analysis of this species.

The history of conceptual models about the decline in striped bass is instructive. The influence of freshwater flow on abundance of young-of-the-year was known as early as 1972 (Turner and Chadwick 1972). This influence was shown to extend to recruitment into the fishery at age three (Stevens 1977). The flow effect was so strong that CDFG developed a simple statistical model relating the YOY index to flow alone. However, this relationship began to fall apart in 1976-1977, when the measured YOY index became consistently lower than the predicted value. Although the influence of the large decline in egg production at that time was recognized (Stevens et al. 1985), a revised model was developed in which YOY was related to Delta outflow and export flow, but not egg production. The significant contribution of export flow to the model, and the huge number of young striped bass taken at the export pumps, were taken as evidence that export pumping was the major cause of the decline in YOY striped bass, and therefore in recruitment.

The flow-export theory was the only explanation of the decline in striped bass until the late 1990s, when two alternative, though not necessarily competing, theories were developed. The first held that the migratory patterns of adult striped bass had changed with the increase in El Niño events since the late 1970s (Bennett and Howard 1997). This has resulted in greater migration to sea by the older, larger striped bass that account for the bulk of the egg production. The striped bass in the ocean, paradoxically, are more vulnerable to fishing, and the ratio of catch in the ocean to that in the Bay has been higher since 1976 than before (Bennett and Howard 1999). Thus, the decline could have been due to a loss of the larger females resulting in a substantial step decline in egg production, which was observed, and a consequent step decline in YOY, which was also observed.

The second theory holds that density dependent survival between the time of the YOY index and recruitment at age three suppresses most of the variability caused by flow conditions. Five different sets of data on striped bass gave evidence of density dependence, and one showed a declining carrying capacity of the estuary for striped bass between YOY and age three (Kimmerer et al. 2000). This decline in carrying capacity was interpreted as possibly due to increasing food limitation, although data on size at age do not indicate a strong interaction between population abundance and growth rate (Gartz 1999).

These theories are summarized in Figure 36, which depicts the life cycle of striped bass and indicates several of the key relationships implicated in population control. The principal difficulty in determining cause and effect in biological populations is the expected dependence of abundance at any stage on a previous stage. Thus, a “null model” would state that the supply of eggs depends on adult abundance and body size; that the abundance of juveniles is related to egg supply; that juvenile abundance can limit recruitment to the adult population; and that poor adult survival can reduce the abundance of the larger, more fecund females. To address this fundamental problem requires analysis of survival rates or indices, by which interannual differences in abundance are eliminated from the analysis. Such analyses have revealed a decline in adult survival, and the strong density-dependence discussed above.

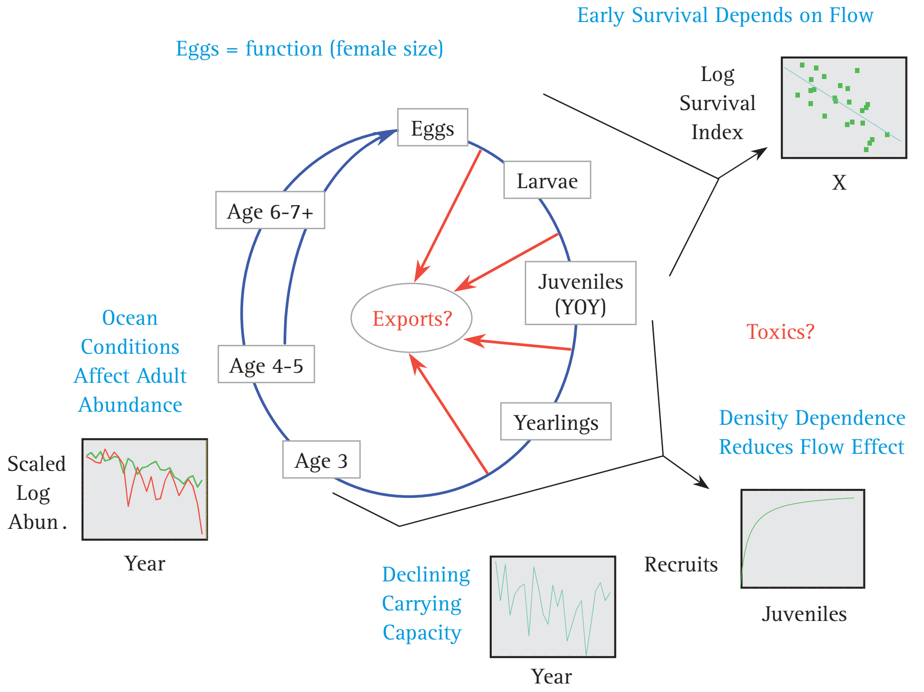


Figure 36. Conceptual model of important controls in the life history of striped bass. Important or potentially important influences on the population are shown in blue, some with graphical depictions. Egg production is strongly influenced by size of the female, so that loss of older adults in 1976-1977 caused a 60% decline in egg production. Survival from egg to larvae and from egg to YOY increases with flow (decreases with X2), and there may be a small effect of export flow on survival between larvae and YOY. Density dependence between YOY and recruits at age three reduces the variability due to flow; furthermore, a significant decline in carrying capacity has caused a reduction in recruitment over time. In addition, low survival of adults, particularly in El Niño years, has reduced the proportion of older adults (red line in left-hand graph) in the population compared with adults three to five years of age (green line). Effects of export flow and toxic substances, identified in several publications, are uncertain or unlikely. Data and conclusions from Kimmerer et al. (2000 and 2001) and Bennett and Howard (1999).

Resolution of these potentially competing models is being sought through the use of an individual-based simulation model (Rose and Cowan 1993). The results of the simulation model point to food limitation, exports, density dependence, and adult survival as key variables limiting the striped bass population. Analysis and modeling of time trends in various survival measures and environmental variables has shown that export pumping is unlikely to have contributed significantly to the decline in striped bass (Kimmerer et al. 2001). Neither X2 (used to represent flow conditions), export flow, nor the survival of striped bass from egg to 6 mm larva or YOY (the period most vulnerable to flow conditions) had a time trend over the period of record. This does not support any of these variables as a cause of the decline, although it does not rule them out. However, long-term decreases in carrying capacity and adult survival, as discussed above, were consistent with a role in the decline, and in fact the overall level of adult mortality alone may have been sufficient to explain the decline (Kimmerer et al. 2001).

Recent increases in adult abundance of striped bass have not been preceded by increases in the YOY index (Kohlhorst 2002). This suggests an increase in survival, since the contribution of hatchery releases to this increase appear to be small. Adult survival may have increased when ocean conditions apparently shifted back to a cool phase. Thus, these results do not necessarily repudiate the two newer models described above, although the earlier models based on flow effects are inconsistent with this increase.

These results remain controversial. Nevertheless, the following general conclusions can be drawn from these analyses: (1) Alternative models should be considered when attempting to determine the causes of abundance patterns; (2) More than one factor is usually at work; (3) Expert opinion should be backed up by rigorous analysis; and (4) There is almost always something to be gained by a thorough analysis of the available data.

At present there is little emphasis on protecting and enhancing striped bass, despite its continuing value in a recreational fishery. Instead there is concern over the role of striped bass as a predator on Chinook salmon, delta smelt, and other fishes of concern. A recent model study suggested that striped bass could have a substantial negative influence on extinction probability for endangered winter-run Chinook salmon (Lindley and Mohr 2003).

Despite the lack of restoration emphasis on striped bass, it remains an important species not only because of the economic value of the recreational fishery, but also by virtue of its numbers: even after the decline it was the second most abundant fish in the bay study catch (after northern anchovy) in San Pablo Bay and east during 1980-2001. Furthermore, its position as a top predator in the food web ensures that this species has an important ecological role. Knowing how and why its abundance varies will be essential for understanding how the ecosystem functions.

Longfin Smelt

The longfin smelt (*Spirinchus thaleichthys*) is a native anadromous fish that was second in overall abundance in the bay study data from 1980-1996. Juvenile longfin smelt are found throughout the estuary and into the Gulf of the Farallones. Abundance is closely tied to spring flow conditions (Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002a) , and the population was severely depressed during the 1987-1992 drought. Longfin smelt have the strongest of the fish-X2 relationships, although that relationship has had a lower mean abundance since 1987. A petition to list this species under the Endangered Species Act was rejected by the U.S. Fish and Wildlife Service because of apparently strong gene flow among populations on the west coast (Stanley et al. 1995).

Longfin smelt spawn at age two in freshwater, probably laying eggs on rocks or vegetation (Moyle 2002). Spawning occurs from December through April (Moyle 2002), with peak hatching in January or sometimes February (Baxter unpublished). Pelagic larvae move downstream to and beyond the Low-Salinity Zone, and young longfin smelt rear in Suisun and San Pablo bays. Because of the early hatching and migration of the larvae, this species may be less vulnerable to effects of export pumping than some other species.

Relatively little has been published on the ecology of longfin smelt in the San Francisco Estuary. Larval sampling showed early larvae (<12 mm length) were near the surface, while larger individuals were deeper in the water column (Baxter et al. 1999). This agrees with findings by Bennett et al. (2002), who noted surface orientation in early larvae and tidally-oriented vertical migration in later larvae during day and night sampling. Presumably the surface orientation of early larvae moves them downstream as rapidly as possible, whereas the deeper orientation and vertical migration is a mechanism for reducing seaward transport. As with other larval and juvenile fish, the distribution of longfin smelt larvae was related to the salinity distribution in the estuary.

The cause of the post-1987 decline is probably the change in productivity of the estuarine water column following the spread of *P. amurensis*, although this hypothesis remains to be tested. Effects of changing food availability are difficult to determine, since little has been published on the diet of longfin smelt, although in general smelt are planktivores. In addition, the analysis of the change in the pattern of dependence of longfin smelt on X2 needs to account for the size of the spawning stock, since there is some evidence in the data of a stock-recruit relationship.

Starry Flounder

One of the most common flatfish in the San Francisco Estuary, starry flounder (*Platichthys stellatus*) is the most estuarine-dependent and therefore most responsive to estuarine conditions. Starry flounder use the estuary as a nursery area. Flounder spawn in winter in Central Bay and the coastal ocean (Wang 1986), and the buoyant eggs are found in the coastal ocean. Larvae migrate into the estuary in spring, presumably using some combination of tidal stream transport and landward bottom currents to get there, as flatfish do elsewhere (e.g., Harden Jones 1978). In the San Francisco Estuary, starry flounder settle in low-salinity water: monthly mean salinity where flounder were abundant in April to June was <2 psu (Baxter et al.1999). Abundance of starry flounder at age one year is significantly related to X2 in spring of the previous year, and an apparent decline in abundance relative to that relationship was not significant (see "The Fish-X2 Relationships" p.86).

Larvae are planktivorous, while juveniles and adults are predators on soft-bottom benthos and epibenthic invertebrates, including amphipods, bay shrimp, and bivalves (Orcutt 1950). Starry flounder appear to be particularly vulnerable to contaminants, presumably because their demersal habits expose them to high concentrations in the sediments and their prey. For example, reproductive condition of starry flounder was impaired by organic contaminants (Spies et al. 1988; Spies and Rice 1988).

Starry flounder are near the southern limit of their range, and if the decrease in abundance is real it may be due to increasing mean sea surface temperature. Catches of California halibut, another flatfish which is at the northern end of its range, have increased over the same time period, possibly also indicating an effect of changing ocean conditions (Baxter et al. 1999).

Pacific Herring

An important commercial fish stock in the San Francisco Estuary, Pacific herring (*Clupea pallasiare*) valued for their roe (Smith and Kato 1979). Pacific herring range across the northern Pacific, but along the west coast of North America the San Francisco Estuary is near the southern limit of their range (Alderdice and Velsen 1971). Populations associated with different estuaries appear to be discrete, so that most of the adult herring in the San Francisco Estuary hatched there.

Schools of adult herring enter the estuary in early winter, and spawn by attaching adhesive eggs to hard surfaces and seagrasses in the intertidal and high subtidal zones. Some depression of salinity is apparently required for spawning. The optimum salinity for hatching success is around 16 psu (Alderdice and Hourston 1985; Cherr and Pillai 1994).

Larvae rear in the estuary, mainly in San Pablo Bay. There is some evidence of food limitation in the larvae (Gartside 1995). Juvenile herring rear in the estuary at a mean salinity of about 20 psu during the first few months, increasing during summer. Most herring leave the estuary in their second year (Baxter et al. 1999) and mature at either age two or age three. Adult herring remain in the coastal ocean except to spawn.

Pacific herring have a weak X2 relationship using survival from egg to young-of-the-year. This is consistent with their biology, in that they appear to require intermediate salinity for spawning, hatching, and rearing. In 1983 salinity in Central Bay decreased sharply in March (bay study data), which may have either exposed eggs to harmful salinity or reduced the area available for larvae to rear. There may also be an increase in habitat with seaward movement of X2. Pacific herring may now be less abundant at intermediate flows than in the 1980s, possibly because of increasing temperature in the Pacific Ocean that affected the adults; adult abundance has declined (Spratt 1992). The abundance of young herring in the estuary may be important to subsequent recruitment to the adult stock (Smith 1985).

Northern Anchovy

The numerical dominant in catches of the bay study (Baxter et al. 1999), northern anchovy (*Engraulis mordax*) is commercially fished from British Columbia to Baja California and is present in all estuaries on the west coast of the U.S. (Emmett et al. 1991). Eggs and larvae are pelagic, and in contrast to herring their abundance in oceanic waters suggests that low salinity is not required for good survival.

Anchovy are present in the estuary year-round in at least one life stage. Eggs are present all year except in winter, and larvae all year (McGowan 1986). Age-0 juveniles and age-1 adults, distinguished by length at earliest sexual maturity, were abundant in Bay Study samples in all months except December-February.

Several advantages to estuarine residence have been suggested. McGowan (1986) suggested that larval residence in the San Francisco Estuary may expose the larvae to a higher concentration of food than offshore in the California Current, and may also reduce seaward advective losses which are likely to be heavy for larvae along the open coast. Fleming (p. 137 in Baxter et al. 1999) suggested that higher temperature in the estuary would provide a growth advantage.

Juvenile and adult anchovies are planktivores, feeding either by filtering or by picking individual particles, depending on food concentration (O'Connell 1972). They form a substantial prey base for a variety of fishes, including striped bass and California halibut (Emmett et al. 1991).

Abundance patterns of anchovy show no time trend, nor do they appear to respond to flow conditions in the estuary. This may be because the estuarine population consists essentially of vagrants from the larger coastal population, in contrast to herring. Larvae are most abundant away from the Central Bay (McGowan 1986), whereas juveniles and adults are most abundant in Central Bay (Fleming 1999, cited above).

Key Findings and Uncertainties

The principal uncertainties regarding fish arise from the difficulty of sampling and the heavy emphasis on monitoring compared to process-oriented research.

- *Abundance Patterns*. Most of the information on fishes and epibenthic macroinvertebrates is on their patterns of abundance. These data come from some of the longest-running, most complete surveys of estuarine organisms anywhere. Most of the information remains in the form of raw data or abundance indices, although efforts are underway to analyze these data sets and develop new knowledge based on the observed patterns. For modeling populations and the ecosystem, actual abundance estimates rather than indices are needed.
- *Lack of Fisheries*. Other major estuaries in North America support important, vibrant commercial fisheries. The largest commercial fishery in the San Francisco Estuary is the herring roe fishery which, though dependent on the estuary to attract the fish, is still harvesting biomass produced almost entirely in the coastal ocean. Modeling and analyzing actual and potential production would be a major undertaking, but necessary to assess the long-term possibilities both for restoration of the estuary and for increasing economic activity.
- *Habitat Use*. Much of the information on use of estuarine habitats is from tidal marshes and floodplains. To the extent that open-water species use these habitats, restoring marshes and floodplains may result in increases in abundance of some species.
- *Life Histories*. Knowledge of the life histories of some estuarine species is extensive, particularly for striped bass but also increasingly for splittail (Moyle in prep.) and delta smelt (Bennett in prep.). These investigations have provided some surprises, such as the importance of climate for dynamics of striped bass. Similar investigations are needed for some of our other common species, as well as listed and candidate species.
- *Predation*. Major piscivores in the estuary include striped bass and centrarchids such as largemouth bass. Information on their predatory activities is qualitative. For example, striped bass are believed to be important predators on young salmon and other small fish. Competition and predation by inland silversides may have a role in limiting delta smelt (Bennett in prep.).
- *Biomass*. Efforts are underway to estimate fish biomass from the extensive bay study monitoring data set. Energetic considerations suggest that the total production and biomass of fishes in the estuary should have decreased over the last three decades. These effects need to be quantified and modeled to place them in a broader context, and to evaluate the effects of these interactions on the likely success of various restoration actions.

THE FISH-X2 RELATIONSHIPS

The physical basis and interpretation of X2 are discussed above. X2 is being used, in somewhat altered form, to manage the estuarine ecosystem. The water costs of this management may be high in dry years, so there is considerable management interest in ways to reduce the water costs of the X2 standard while providing adequate protection of the estuarine ecosystem and key species.

The history, definition, and measurement of X2 presented here are excerpted from two recent papers (Kimmerer 2002a, 2002b). Although the idea of using the 2 psu isohaline for ecosystem management arose in the late 1980s (Williams and Hollibaugh 1987), it received its major impetus in a series of workshops in 1991-1992 organized by the San Francisco Estuary Project and moderated by Jerry Schubel (Kimmerer and Schubel 1994). In those workshops the concept of X2 was defined and the relationships between X2 and abundance of several estuarine species were developed (Jassby et al. 1995). The report of the workshops recommended that X2 be used as an index of estuarine condition. This recommendation was later incorporated in the X2 standard that is now used to control freshwater outflow during spring.

Concern about the basis of the X2 standard and about deterioration apparent in some of the relationships between estuarine populations and X2 (called the “fish-X2 relationships) led to a workshop in March 1998 to discuss these issues. Results of that workshop were described by Monismith (1998), and Miller et al. (1999) gave an alternative view. However, the most complete analysis of these relationships was that in Kimmerer (2002a).

The Basis for X2

X2 has been misinterpreted as a variable describing the status of low-salinity habitat. It is better described as an indicator of the physical response of the estuary to variation in freshwater flow. Flow has a large number of covariates (Figure 37). As discussed below, many of these covariates are involved in hypothesized mechanisms for X2 relationships. Thus, the presence of an X2 relationship does not necessarily imply anything about conditions at the location where the salinity is near two.

To some extent X2 can be regarded as a surrogate for flow. The estuary responds to freshwater flow on a time scale of two weeks, as characterized by the statistical relationship between X2 and flow (Jassby et al. 1995). Most of the fish- X2 relationships have averaging times of months, so there is little difference in results of analyses using X2 or flow. Part of the original impetus for developing this index was that freshwater outflow from the Delta was not being measured. That is no longer true because of measurement systems now being used in the Delta (Oltmann 1999). Furthermore, although X2 was estimated from salinity during development of the historic data base and the index, its value has been determined since 1992 by its relationship to flow.

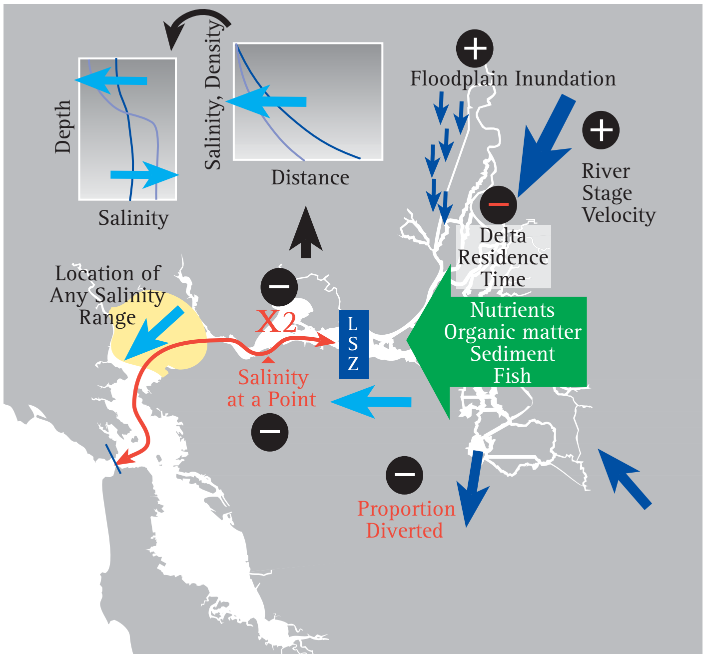


Figure 37. Schematic diagram illustrating how fluxes into the estuary and physical attributes of the estuary change with increasing freshwater flow. Dark blue arrows indicate direction of water flow, and cyan arrows and plus and minus signs indicate direction of change with increasing flow. Inset graphs show schematically how compression of the salinity and density gradients by increased freshwater flow can result in increased stratification and asymmetric residual currents.

From a purely statistical perspective, and certainly in terms of ultimate causes, flow would be just as good as, if not better than, X2. Nevertheless, I believe that X2 has certain advantages. First, it ties the flow regime to geography: to sample for a certain species, it is helpful to know where X2 is (and by implication, any other salinity value). Second, organisms generally respond to events and forces that they can detect in their immediate environment, and have no capability to respond to distant conditions. Since under most conditions freshwater flow affects the estuary mainly through the increase in mean level, the addition of buoyancy, and the addition of a small seaward residual current, direct effects of flow are probably limited to the extreme landward margin of the estuary, or extreme flow events. Thus, X2 is a much better index of proximate conditions for the biota of the estuary than flow.

Ultimately, X2 is an ecosystem-level indicator that generally represents conditions that favor (or not) several species of fish and macroinvertebrates. It might seem more useful to develop an index of these responses to flow, since they are the reason for the X2 standard in the first place. However, fish and invertebrates respond to other factors as well, most of which are not under human control. Therefore, while a comprehensive index of biological response might be desirable, it would not serve the purpose that X2 does as a quantity that can be measured, controlled, and understood.

The Nature of the Relationships

Relationships between freshwater flow and abundance or survival of estuarine populations are not unusual. However, the set of relationships for the San Francisco Estuary is probably the broadest in terms of number of species included and the amount of data available (Jassby et al. 1995; Kimmerer 2002a, 2002b). Monotonic relationships between X2 and abundance have been developed, and found significant at least some of the time, for estuarine-dependent copepods, mysids, bay shrimp (*Crangon franciscorum*), and several fish including longfin smelt, Pacific herring, starry flounder, splittail, American shad, and striped bass (Kimmerer 2002a). Chinook salmon have been omitted from this list even though survival of marked salmon smolts from the Sacramento River through the Delta is weakly but positively related to freshwater flow (Newman and Rice 2002). Abundance of young white sturgeon is high following extreme floods (Kohlhorst et al. 1980). Abundance of several other species was positively related to freshwater flow in the South Bay in 1973-1982 (Pearson 1989), but this could have been due to movement patterns rather than changes in overall abundance since other parts of the estuary were not sampled.

Three issues have been raised regarding these relationships: (1) the existence and statistical reliability of the relationships; (2) the appropriate mathematical description of the relationships; and (3) the underlying mechanisms. The statistical issues can best be addressed through analysis of covariance, including all of the data but allowing for a change in either the slope, the intercept, or both. This analysis shows that for most of the fish and macroinvertebrate populations, there is no difference in slope between the two periods, although several changed in intercept (Kimmerer 2002a; Table 4). The principal exception is the summer townet index for delta smelt, which changed slope in 1980-1981 rather than later (Table 4). In contrast, the fall midwater trawl index for delta smelt is unrelated to X2 (Bennett in prep.).

Flow does not produce fish; therefore we should expect to see that egg production influences the subsequent abundance of young fish. Many fishery studies use "stock-recruit" relationships to take this influence into account. The relationships for striped bass and Pacific herring account for the stock effect by using an egg-young survival index rather than abundance. For most of the other species the stock size does not seem to matter very much, because the influence of flow conditions is so strong. However, the long drought of 1987-1992 depleted at least some stocks, which took several years of high flow to rebound. This is particularly evident for *Crangon franciscorum*, which had its lowest abundance value after 1988, but later achieved its highest value during the high-flow period following the drought. This increased variance during and after the drought, due primarily to internal dynamics of the populations, has contributed to the poor fit of the linear models using only the post-*Potamocorbula* data. This is another example in which single factors alone are insufficient to explain population trajectories (Bennett and Moyle 1996).

Regardless of the details of the individual relationships, there is a general trend for abundances of fish and macroinvertebrates to be higher under high-flow conditions than low-flow conditions (Kimmerer 2002a). Whether these are strong enough to continue to govern management of flows is a matter for policy discussion. Certainly, there are opportunities to make

Table 4. Summary of parameters of models from Kimmerer (2002a Table 4) with estimated 95% confidence limits. Values in bold are significantly different from 0 at $p < 0.05$ (two-tailed). The basic model was an analysis of covariance with X2 as a covariate and YearCat (0 before 1987, 1 after) as a categorical variable. Where interaction terms were significant, data were split into two groups for regression. S under Response Variable refers to salinity ranges for planktonic variables.

Taxonomic Group	*Response Variable*	*Averaging Period*	*N*	*X2 Effect Flow Effect*	*YearCat Step after 1987*	*Years*	*Remarks*
Phytoplankton	Chlorophyll (S = 0.5-6)	Survey March-May	24	0.009 ± 0.011 -0.008 ± 0.013	**-0.4 ± 0.21**	1975-87 1988-99	No data for 1995; significant interaction ($\gamma \neq 0$)
Phytoplankton	Chlorophyll (S = 0.5-6)	Survey June-Oct	25	-0.002 ± 0.010	**-0.63 ± 0.17**	1975-99	
Phytoplankton	Chlorophyll (S = 6-20)	Survey March-May	24	-0.004 ± 0.010	**-0.48 ± 0.22**	1975-99	No data for 1995
Phytoplankton	Chlorophyll (S = 6-20)	Survey June-Oct	25	-0.004 ± 0.009	**-0.59 ± 0.15**	1975-99	
Eurytemora affinis	Abundance +10 (S = 0.5-6)	Survey March-May	16 12	-0.004 ± 0.0.019 **-0.029 ± 0.018**	**-0.86 ± 0.32**	1972-87 1988-99	Significant interaction ($\gamma \neq 0$)
Eurytemora affinis	Abundance +10 (S = 0.5-6)	Survey June-Oct	28	0.001 ± 0.01	**-1.88 ± 0.20**	1972-99	
Acartia spp.	Abundance +10 (S = 6-20)	Survey March-May	25	-0.015 ± 0.02	**-0.83 ± 0.44**	1972-99	1974, 75, 95 missing
Acartia spp.	Abundance +10 (S = 6-20)	Survey June-Oct	28	-0.005 ± 0.02	**-1.64 ± 0.38**	1972-99	
Synchaeta bicornis	Abundance (S = 0.5-6)	Survey June-Oct	28	0.006 ± 0.019	**-1.03 ± 0.33**	1972-99	
Neomysis mercedis	Abundance (S = 0.5-6)	Survey May-Oct	15 12	**-0.036 ± 0.021** **0.034 ± 0.032**	**-1.67 ± 0.39**	1973-87 1988-99	Significant interaction ($\gamma \neq 0$)
Bay shrimp	Abundance index	Mar-May	21	**-0.024 ± 0.011**	-0.04 ± 0.26	1980-2000	
Starry flounder	Abundance index + 1	Mar-Jun	21	**-0.023 ± 0.015**	**-0.58 ± 0.36**	1980-2000	
Pacific herring	Survival index	Jan-Apr	20	-0.021 ± 0.022	-0.01 ± 0.5	1980-2000	No data for 1994
American shad	Abundance index	Feb-May	32	**-0.014 ± 0.009**	**+0.25 ± 0.22**	1967-2000	No data for 1974, 1979
Delta smelt	Summer Abundance index	Feb-Jun	39	0.017 ± 0.022 -0.011 ± 0.012	**-0.44 ± 0.33**	1959-87 1988-2000	Significant interaction; but the shift occurred in 1980-81. No data for 1966-68
Longfin smelt	Abundance index	Jan-Jun	32	**-0.053 ± 0.012**	**-0.60 ± 0.27**	1967-2000	No data for 1974, 1979
Sacramento splittail	Abundance index	Feb-May	31	**-0.031 ± 0.013**	-0.07 ± 0.3	1967-2000	No data for 1974, 1979
Striped bass	Survival index	Apr-Jun	25	**-0.027 ± 0.012**	-0.08 ± 0.3	1969-94	No data for 1983

this management tighter or more responsive to our growing understanding of the ecosystem. However, the X2 standard is one of the few extant examples of ecosystem-level management, which is a general approach supported by several resource agencies and the ERP Strategic Plan (CALFED 2000).

Lower trophic level organisms (and functional groups) did not respond strongly or consistently to flow (Table 4). The reason for the difference between higher and lower trophic levels is unclear, but it suggests that the relationships for the higher trophic levels may be due to direct physical factors rather than foodweb relationships (Kimmerer 2002a).

Conceptual Model

The IEP's Estuarine Ecology Team prepared a report on the likely causes of these relationships based on data analysis and expert opinion (EET 1997). That report forms the basis for this conceptual model, which was further elaborated by Kimmerer (2002b). The physical aspect of the conceptual model was discussed previously.

Biological responses to flow patterns (Table 5; Kimmerer 2002b, Table 2) are generally speculative. These responses fall into categories that can be described on an axis between trophic responses (i.e., through stimulation at the base of the foodweb) and direct physical responses of habitat (Figure 38). Because of the comparative lack of response at the base of the foodweb, physical mechanisms appear more likely to affect populations of fish and epibenthic macroinvertebrates in the estuary (Kimmerer 2002a).

Effects of freshwater flow on physical habitat are largely based on speculation except for splittail, which appear to respond to increases in feeding, spawning, and rearing habitat due to inundation of the Yolo Bypass and other floodplains (Sommer et al. 1997, 2002). Freshwater habitat certainly increases when flow increases and X2 decreases (moves seaward). In addition, certain kinds of brackish habitat may also increase, especially in the vicinity of hard substrates near the mouth of the estuary, which are used by herring for spawning. However, it has been suggested that physical habitat for a variety of species dependent on brackish habitat is positively related to freshwater flow, despite the fact that X2 decreases with increasing flow, suggesting less habitat between 2 psu and the ocean. Evidence against this argument was presented by Kimmerer (2002b) for striped bass and longfin smelt.

An alternative mechanism for effects of flow/X2 is that gravitational circulation may increase as the longitudinal density gradient is compressed. This mechanism may apply to several species in the LSZ, and may depend on variable bathymetry (Kimmerer et al. 2002; Monismith et al. 2002). Further down estuary species that recruit from the ocean such as bay shrimp and starry flounder could have better recruitment when gravitational circulation is strong in the lower estuary. However, this class of mechanisms is equally speculative. Thus, there is little evidence to support one mechanism over another for most species.

Key Findings and Uncertainties

The suite of species that respond to freshwater flow is as extensive as in any estuary. Furthermore, the relationships of the fishes and bay shrimp to flow/X2 did not change in slope after the introduction of the Amur River clam, in spite of substantial declines in abundance of some species. The fish-X2 relationships are retrospective, not predictive. If the physical configuration of the estuary changes, these relationships may change in ways that cannot now be predicted. The nature of the relationships and the underlying mechanisms are the major uncertainties regarding these relationships. If these mechanisms can be determined, the timing of the X2 standards could possibly be refined, and the same level of environmental protection might be achieved with less water (CALFED 2000).

EFFECTS OF IN-DELTA DIVERSIONS ON THE ESTUARINE ECOSYSTEM

Export flows can be considered either in relation to inflow or, as argued previously, in relation to Delta volume during low-flow periods. The proportion of Delta volume exported daily typically is less than 2% in summer (Figure 6D). This can be compared to typical turnover times for chlorophyll, which can be up to

Table 5. Conceptual model of fish- X2 relationships. This table summarizes potential mechanisms underlying the relationships, based on analysis by the Estuarine Ecology Team (1997) and other reports. The table does not include mechanisms occurring entirely upstream of the Delta. The order does not relate to relative importance or likelihood of the mechanisms.

Mechanism	***Species***	***Evidence or Source***
Habitat increases or becomes more available as X2 moves seaward		
Spawning habitat area or access	Pacific herring	Herring require rocky or seagrass substrate with somewhat reduced salinity to spawn
	Striped bass	Habitat on the lower San Joaquin is expanded when flow is high
	Splittail	Yolo bypass floods at high flows, providing feeding and spawning habitat for splittail (Sommer et al. 1997)
Rearing habitat area	Bay shrimp	Require intermediate-salinity habitat for rearing; area may increase as flow increases
	Pacific herring	Herring require low salinity for rearing; area may increase as flow increases
	Starry flounder	As for Bay shrimp
	American shad	Uncertain status
	Striped bass	Area of low-salinity habitat may increase as flow increases
	Longfin smelt	As for striped bass
Adult habitat	Splittail	As for spawning habitat; Sommer et al. 1997
Circulation patterns become more conducive to survival as flow increases		
Strength of gravitational circulation	Bay shrimp	Shrimp recruit from the ocean and therefore recruitment may vary with GC strength, potentially a function of X2
	Starry flounder	As for Bay shrimp
Residence time in Low-Salinity Zone	Mysids	Tidal vertical migration may be more effective when gravitational circulation is strong (Kimmerer et al. 1998)
	Longfin smelt	As for mysids (Bennett 1998)
	Striped bass	As for mysids (Bennett 1998)
Transport to rearing area	American shad	High flows may disperse eggs and larvae
	Striped bass	Egg-6mm larval survival positively related to flow, as is transport rate
	Longfin smelt	Similar to striped bass
Reduced entrainment	American shad	Peak emigration is in the low-flow time of year
	Striped bass	Entrainment losses of striped bass related to position of population, which is centered on salinity of about 2.
	Longfin smelt	As for striped bass (mainly larvae)
Feeding becomes more successful with seaward X2		
Higher food production	American shad	Abundance of mysids is higher in wet years
	Striped bass	Food supply may increase (Turner and Chadwick 1972)
	Longfin smelt	Food supply may increase with flow
Co-occurrence with food (match-mismatch)	Pacific herring	Timing of spring blooms may be important
	Striped bass	Timing of arrival in LSZ vs. food supply
	Longfin smelt	Timing of spring blooms may be important

Table 5. Conceptual model of fish- X2 relationships, continued

Mechanism	***Species***	***Evidence or Source***
Other mechanisms		
Predator avoidance through turbidity	Mysids	Turbidity in the LSZ increases with increasing flow, possibly reducing effectiveness of visual predators
Toxic dilution	Splittail	Splittail are vulnerable to agricultural and industrial discharges for most of life cycle
Migratory cues	American shad	Proportion of repeat spawners is related to flow in tributaries
Inputs of nutrients or organic matter	Various	Unlikely mechanism, since lower trophic levels have little response to flow.

$1\ d^{-1}$. For example, using Equation 1 and parameters in Jassby and Cloern (2000), assuming an extinction coefficient of $2\ m^{-1}$, incident radiation of $30\ E\ m^{-2}\ d^{-1}$, mean depth of 6 m, and a carbon:chlorophyll ratio of 30, gives a specific growth rate around 30% d^{-1}. Bacterial turnover rates are of a similar order of magnitude (see "Organic Carbon" p.56). Compared to growth rates of phytoplankton and bacteria, the export and in-Delta diversion rates are small but may influence biomass accumulation, as shown statistically by Jassby and Powell (1994). Zooplankton can sustain population growth rates on the order of 20% d^{-1} but the actual rate of growth is often considerably less because of food limitation and predation (e.g., Kimmerer and McKinnon 1987). However, statistical analyses have not yet shown an effect of export pumping on zooplankton abundance.

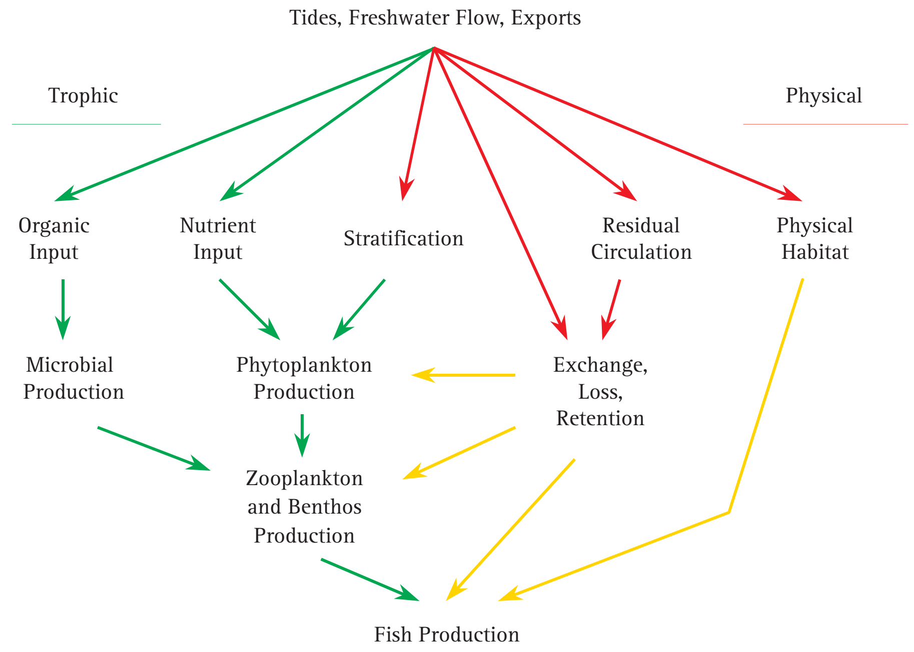


Figure 38. Conceptual model of alternative pathways by which physical forcing (as depicted in Figure 37) affects fish production. Pathways on the left (green arrows) can be considered "trophic" pathways, by which stimulation through the food supply affects fish production, while those toward the right depict physical relationships (red) or direct physical influences on biological populations (gold).

Larval fish resident in the Delta are entrained and removed from the system by the export pumps and diversions, and losses of larvae are probably roughly proportional to the fraction of the Delta volume exported as described above for other plankton. However, fish differ from the other plankton in being produced on an annual cycle rather than through continuous reproduction. Therefore export flows that entrain young fish resident in the Delta may have a large cumulative impact on the year-class strength. The importance of this mortality has not yet been determined for any Delta-resident fish species. Calculations similar to those above are particularly inappropriate for juvenile and adult fish because of their motility and because some fish are salvaged and returned to the estuary.

Mortality directly attributable to the pumps arises the louvers, mortality during capture and return to the estuary, and mortality due to predation or stress that occurs after release (Raquel 1989, Brown et al. 1996). Pre-screen predation mortality for chinook salmon and young striped bass in the Clifton Court Forebay (Figure 1) is estimated to be on the order of 75% (Brown et al. 1996, Gingras 1997), but this is inconsistent with the generally similar salvage abundance data at the State and Federal pumping facilities at least for common, widespread species such as striped bass (Kimmerer, unpublished). Furthermore, the data on which this estimate is based came from a relatively small number of mark-recapture experiments with a number of potential biases (Gingras 1997). Efforts to remove striped bass from the Forebay have met with limited success because of movement of the fish to and from the forebay (Gingras and McGee 1996).

Screening efficiency is low for fish smaller than about 25-50mm and on the order of 70-80% for larger fish (Skinner 1973). Mortality during handling and transport is low for Chinook salmon, but higher (on the order of 50%) for other species such as striped bass and shad, and negatively related to fish length (Raquel 1989). Values for more delicate fish such as delta smelt are unknown but likely to be high. Post-release mortality is unknown for any fish, but anecdotal evidence suggests that predators aggregate in large numbers at release sites.

The above results give an inconsistent picture, but the underlying theme is that for many of the kinds of fish we are concerned about, being entrained in the water leading to the export pumps results in high mortality. However, only limited analysis has attempted to link export effects to population dynamics, and these results are rather inconclusive. For striped bass, the proportion of the year class entrained during the first year of life can be very high, judging from abundance patterns and export flow rates (Kimmerer et al. 2001). Nevertheless, the effects of these losses are largely eliminated by density-dependent mortality occurring between ages one month and three years (Kimmerer et al. 2001).

Entrainment of Chinook salmon is a major concern of salmon biologists, but here too the evidence is equivocal. Analyses of environmental effects on survival of marked Chinook smolts released in the Delta showed influences of temperature and flow but not export flow (Newman and Rice 2002). Relatively few tagged smolts are recovered at the salvage facilities, but this could be due to high pre-screen mortality as discussed above.

Statistical analyses show that delta smelt may be negatively affected by export pumping (Bennett in prep.). delta smelt are vulnerable to export pumping for a large part of their life cycle, and large numbers of delta smelt have been collected at the salvage facilities in late spring in some recent years, exceeding allowable limits (DWR data).

The Delta agricultural diversions are a different potential source of mortality of unknown magnitude. Limited studies of fish entrainment in agricultural diversions did not recover many fish species of concern from the diverted water (Cook and Buffaloe 1998; Nobriga et al. 2003). The CALFED Ecosystem Restoration Program Science Board in 2001 recommended against further support for fish screens pending further evidence on their effectiveness as a tool for ecosystem restoration.

Key Findings and Uncertainties

The entire issue of entrainment in export or diversion flows represents a major uncertainty for the entire CALFED process. Particular issues that need resolution include the following:

- *Pre-Screen Mortality.* The experiments that form the basis for estimates and assumptions about pre-screen mortality due to predation need to be replicated with greater attention to experimental design and conditions.
- *Magnitude of Export Losses.* Large numbers of fish are entrained, but at least for striped bass the population-level consequences appear to be minimal. Other species may respond differently to this mortality term.
- *Effect of Screening Diversions.* At present there are no data supporting the idea that unscreened diversions present an important source of mortality. Furthermore, potential negative effects, including opportunity costs of not taking other actions and possible effects of structures on predator-prey relationships, have not been examined.

SYNTHESES

Most of the material above has been presented by subdiscipline, which parallels trophic levels or functional groups within the estuary. It is generally easier to assemble material, and may be easier to follow, when the material is organized this way. However, the ecosystem is an integrated whole and efforts are needed to understand it that way.

There have been surprisingly few attempts at synthesis of available knowledge about the estuary. Cloern (1996) used the San Francisco Estuary as an example in a review of estuarine phytoplankton dynamics, incorporating knowledge about physical forcing and circulation, benthic grazing, and other factors on phytoplankton. The IEP Estuarine Ecology Team prepared several syntheses (EET 1995, 1997), but these were summaries of the opinions of members of the group, not review papers. Thus, syntheses are needed that cross spatial and temporal scales as well as disciplines. In particular, the large amount of information on distribution and abundance of selected fish and epibenthic macroinvertebrates needs to be synthesized into a body of knowledge.One approach to synthesis is the development of models that cut across trophic levels. Considerable work has been done on statistical modeling in the estuary (e.g., Jassby et al. 1995; Rice and Newman 1997; Kimmerer 2002a), and on estimating mass balances (Hagar and Schemel 1992; Smith and Hollibaugh 2000; Jassby et al. 2002). However, few ecosystem or population simulation models have been developed for the estuarine ecosystem. Good examples of the use of coupled biological-physical models in the San Francisco Estuary have been developed for phytoplankton dynamics in the South Bay (Koseff et al. 1993; Lucas et al. 1998, 1999a, 1999b) and the Delta (Lucas et al. 2002).

I do not believe that knowledge about the ecosystem is adequate to support full-scale simulations of the entire system. However, simulation modeling efforts aimed at specific topics would be very valuable in investigating ecosystem dynamics, and should help to crystallize knowledge about key issues for restoration using an adaptive approach. Specific issues for which modeling may be useful, including some modeling projects now underway, are:

1. Examining carbon or energy flows in various subbasins of the estuary for determining the important pathways of energy flow.
2. Examining the movement of materials and organisms through the mouth of the estuary.
3. Assessing different mechanisms for retention in the Low-Salinity Zone and other parts of the estuary.
4. Assessing the effects of export pumping and predation by striped bass and other fish in the Delta.
5. Determining the potential effect of increases in the area of tidal marshes in different regions of the estuary.
6. Examining the likelihood that key inter-specific interactions may cause conflicts among restoration goals and actions; for example, predation by striped bass could reduce the effectiveness of actions designed to enhance salmon smolt production.
7. Assessing the effects of hatchery production on natural stocks of fish including salmon and striped bass.
8. Investigating the mechanisms behind the Fish-X2 relationships.
9. Examining environmental influences on population dynamics of particular species such as delta smelt and Chinook salmon.

CONSEQUENCES FOR RESTORATION

The previous sections describe the current state of scientific knowledge about the open waters of the estuary. Although the initial impetus was to provide a basis for deliberations about restoration, most of the likely restoration actions have already been identified. This section interprets these likely actions in the context of the understanding laid out in previous sections, and then addresses uncertainties, opportunities, and constraints that are relevant to restoration.

Goals for restoration in general reflect broader societal functions, some with high economic value (Costanza et al. 1997). For the purposes of this paper, however, I focus on the narrower goals of the CALFED Ecosystem Restoration Program. The ERP goals were outlined in the Strategic Plan (CALFED 2000) which also strongly supported ecosystem-level restoration and adaptive management. These approaches are suitable where understanding of the system is incomplete, but require conceptual models that incorporate the current state of scientific knowledge, including areas of uncertainty or disagreement.

RECENT AND CURRENT RESTORATION ACTIONS

Several classes of restoration action that may influence the open-water habitat have been proposed in CALFED documents and some are being implemented by CALFED and other organizations. Only a few of these classes are actually being implemented; many of the proposed actions have not been fully explored as to their likely effectiveness.

Current Restoration Actions in the Estuary

Only a handful of restoration actions to date directly target the open waters of the estuary. The most notable of these is the establishment of the X2 standard. That standard prescribes salinity or freshwater outflow according to a sliding scale based on available stored water and recent unimpaired flow in the watershed. This target consists not of a value for X2, but a number of days in a month for which salinity must be no greater than 2 psu at one of three monitoring sites: Collinsville (river kilometer 81), Chipps Island (river kilometer 75), and Roe Island (river kilometer 64). This not only sets the mean value for X2, it also ensures that variability in X2 is similar to historical values. The standard may be met for a given day in one of three ways: the salinity at the control point for that day is less than 2 psu; the 14-day running mean salinity at the control point is less than 2 psu; or the net Delta outflow for that day is at or above the value that would make the salinity less than 2 psu according to a flow-salinity statistical model.

The X2 standard and the underlying analyses have engendered a lot of controversy. Although it is based on relationships between several estuarine-dependent species and X2 or flow, the mechanisms underlying most of these relationships are not known. Thus, it is possible that the standard could be refined with improved understanding of the mechanisms. However, the X2 standard operates at the ecosystem level, in contrast to many of the actions taken on behalf of listed species. Thus, it provides a way of obtaining benefit for a variety of species while having no apparent negative effects on species of concern (net effects on humans are part of the controversy).

In addition to the X2 standard, regulatory limits on export:inflow ratios have been established. There is probably little physical basis for using such a ratio except during periods of very high freshwater inflow, since at other times dispersive transport probably dominates flow patterns in most of the Delta. In addition, evidence that diversions have large effects at the population level has not been strong for any species (see "Effects of In-Delta Diversions" p.90).

The Vernalis Adaptive Management Program (VAMP) was established as an experimental program to refine estimates of the effects of freshwater and export flows on survival of salmon smolts migrating through the Delta from the San Joaquin River. Each spring, San Joaquin River and export flows are set at one of several specified levels (depending on available water) to set up conditions believed to be beneficial to salmon smolts, and also suitable for detecting effects on survival of hatchery smolts in a mark-recapture study.

Finally, three water accounts have been established for environmental protection. The first, under the Central Valley Project Improvement Act (CVPIA), is an allocation of up to 800,000 acre-feet of CVP yield to provide environmental benefits to anadromous fish. The second, the Environmental Water Account (EWA), is a system by which water is purchased and used to support protection of fishes of concern, primarily by curtailing exports in the Delta. Both the CVPIA water and the EWA are being controlled by CALFED's Water Operations Management Team, primarily to allow for short-term operations to protect fish. The Environmental Water Program falls within the Ecosystem Restoration Program, and is a similar effort to the EWA except that it is administered separately and for somewhat different purposes. The challenge for all three of these operations is to establish a scientific basis for the actions, and a system of evaluation and feedback to refine them.

A number of species-specific actions have been taken, mostly for species not included in this review. Protective measures previously established for striped bass have been superseded by the X2 standard and export limits for endangered species. The export limits have proved nettlesome recently: in late spring of both 1999 and 2000 the ”red-light” limit of delta smelt capture at the pumps was exceeded, causing a great deal of concern and some reduction in exports. These actions have been superseded since 2001 by the use of EWA water to support curtailment of export pumping.

Actions Proposed in the CALFED Ecosystem Restoration Program Plan

The Ecosystem Restoration Program Plan (ERPP, CALFED 1997) proposes about 600 actions. These have been summarized in a database which has allowed for easy access to categories of actions, e.g., by ecological zone. The open-water region includes parts of two ecological zones as defined by the ERPP: the Sacramento-San Joaquin Delta and Suisun Marsh/North San Francisco Bay. Many of the actions proposed for these zones involve habitats not discussed here, particularly marshes and managed floodplains (e.g., Yolo Bypass).

I identified roughly 70 actions in the ERPP that were designed to affect, or could reasonably be expected to affect, the estuary. I omitted those designated for research only. The remaining 63 actions (Table 6) were then aggregated for discussion, since many of them share features in common and differ only in the exact location of effect or method of taking the actions.

Little detailed rationale has yet been presented for these actions, nor is it clear from the ERPP why various locations and quantities were selected. However, the actions presented in the ERPP provide at least a starting point for evaluation. Some of the actions more directly aimed at open-water habitat are listed below. This discussion is based on the detailed summaries above.

Physical Habitat (Items 1-5)

Many of the actions involve the construction or rehabilitation of shallow habitat of some sort. Although shallow habitats are addressed at length elsewhere (Brown 2003a, 2003b, 2003c; Orr et al. 2003; Davis et al. 2003), they occupy such a key position in the ERPP that some discussion of their potential impact on the open waters is warranted.

Restoration of different kinds of shallow habitat may have very different effects on the ecosystem. Most of the habitat under discussion here (i.e., excluding terrestrial habitat or disconnected marshes) falls into three categories: floodplain (e.g., Yolo Bypass), tidal marshes, and subtidal areas. There is clear evidence of benefits of flooding in the Yolo Bypass to splittail (Sommer et al. 1997, 2001) as well as evidence that rearing salmon grow better there than in the adjacent river (Sommer et al. 2001). This implies that increasing the quantity of floodplain or frequency of flooding, or possibly making structural improvements, could result in higher production of these species.

Subtidal habitat in the Delta, on the other hand, appears to support mainly introduced species of plants and fish (e.g., Grimaldo et al. 1998; Grimaldo and Hymanson 1999; Christophel et al. 1999; Brown 2003b). Building more of it may not result in improved conditions for species of concern, although there are other reasons to restore marshes (Brown 2003a). Intertidal marsh habitat may provide some support to species of concern but it is not clear that restored freshwater marshes would do so, given their tendency to be occupied by introduced species of plants and fish. Marshes in the brackish to saline reaches of the estuary might be better targets for restoration, but preliminary indications are that the fishes of these habitats are not juveniles of open-water species (K. Hieb, CDFG, pers. comm. 2001; Brown 2003b) as is commonly the case on the east coast of North America (Kneib 1997).

Quantitative targets defined by the ERPP for marsh restoration are not supported by any analysis of the relative benefits. Such an analysis would probably hinge on knowing more than we do about the outcome of restoration for species of concern. This suggests an adaptive approach in which different methods and sites were tried.

One outcome of restoration of shallow habitat is likely to be increased primary production in the shallow channels, sloughs, and lakes. It is unknown whether this benefit is sufficient to overcome the potential harm due to increased mobilization of contaminants,

Table 6. Summary of actions described in the Ecosystem Restoration Program Plan (ERPP, CALFED 1997) For the Bay and Delta ecological zones that are likely to affect the open waters of the San Francisco Estuary. The Ecosystem Elements are identified in the ERPP, and Action Numbers are taken directly from the sections of the ERPP dealing with each element in each ecological zone. Programmatic actions have been rephrased for simplicity and comprehensiveness.

No.	*Ecological Zone*	*Ecosystem Element*	*Action Number*	*Programmatic Action*
1	Delta	Natural Floodplain and Flood Processes	1a, b, c, e	Restore tidal wetlands using setback levees and connect dead-end sloughs
2	Bay, Delta	Tidal Emergent Wetlands, Tidal Sloughs	Bay 1a, 2a, 3a; Delta 1a-e	Develop and rehabilitate tidal freshwater to saline marshes including adjacent sloughs and uplands
3	Bay, Delta	Tidal Perennial Aquatic	Bay: 1a; Delta: 1a-1e	Restore areas of shallow subtidal habitat
4	Delta	Mid-channel Islands and Shoals	2a	Manage sediments for deposition and accretion, and otherwise maintain shallow habitat
5	Delta	Central Valley Stream Temperatures	1a, b, c, e	Improve riparian habitats along Delta channels where salmon migrate.
6	Bay, Delta	Central Valley Streamflow	Bay: 1a; Delta: 1a-4a	Make flow into the Delta and Bay in winter-spring more closely resemble the natural hydrograph, including winter "first flush" and spring peaks
7	Delta	Central Valley Streamflow	4a	Maintain a Delta inflow of 13,000 cfs in May of all but critical years.
8	Delta	Bay-Delta Hydrodynamics	1a - c, 3a, 4a, 4b	Alter the physical configuration of the Delta, including the use and modifica tion of barriers, to reduce flow velocities or net transport in selected channels.
9	Delta	Bay-Delta Hydrodynamics	1d	Close the Delta Cross Channel gates in winter when possible
10	Bay, Delta	Water Diversion	1a (Both)	Consolidate and screen or eliminate agricultural diversions
11	Delta	Water Diversion	1b	Upgrade screens and fish salvage facilities at the SWP, CVP, and Pacific Gas and Electric intakes
12	Bay, Delta	Contaminants	1a	Reduce inputs of toxic materials, either directly or by supporting other programs
13	Bay, Delta Organisms/Plants	Invasive Aquatic (Bay only), 2a;	Animals: 1a, 1b Plants: 2a	Provide funds for enforcement and other activities to exclude or manage invasive plants and animals.
14	Bay, Delta	Invasive Aquatic Plants	Bay: 1a; Delta: 1a,b	Conduct weed-eradication programs in sloughs and channels and explore commercial harvest
15	Bay, Delta Organisms	Invasive Aquatic	1b (Both)	Help fund research on ballast water treatment to eliminate invasive species before release
16	Bay, Delta and Wildlife	Harvest of Fish	1a - d (Both)	Provide funding for law enforcement and education to reduce poaching

Table 6. - continued

No.	*Ecological Zone*	*Ecosystem Element*	*Action Number*	*Programmatic Action*
17	Bay, Delta	Bay-Delta Aquatic Foodweb	1a (Both)	Increase primary and secondary productivity through actions taken for other purposes.
18	Bay	Predation and Competition	1a	Plant hatchery striped bass at age 2 years instead of 1

and the generation of trihalomethane precursors that would reduce drinking-water quality (Brown 2003c).

Flow Conditions (6, 7)

The ERPP calls for various increases in freshwater flow, particularly to maintain flows more similar to natural flows at various times of the year. According to the fish- X2 relationships, more flow generally produces more of certain species. However, the relative impact of the proposed flow changes could be quite small and should be analyzed; one analysis showed that further movement of X2 using purchased water would be very expensive (Kimmerer 2002b). For example, the entire allocation of the Environmental Water Program (300,000 acre-feet or 0.4 km^3), if applied over the 5-month period of the X2 standards (~30 m^3s^{-1}), would result in a movement of X2 about 1 kilometer in a dry year. Although high flow clearly benefits some fish populations (Table 4), the advantage of small incremental increases in flow are unclear and any such increases should be analyzed carefully.The action calling for a minimum of 13,000 cfs (cubic feet per second, or 368 m^3s^{-1}) in the Sacramento River in May was originally intended to support movement and survival of striped bass eggs down the river. This has a weak basis and could be replaced by an experimental flow manipulation if sufficient interest remains in using flow to support striped bass.

Delta Hydrodynamic Conditions (8, 9)

I have combined two somewhat different concepts in item 8: flow velocities in Delta channels, and net flows of freshwater toward the export pumps. Presumably, the closer to the export pumps, the greater the residual component of the flow relative to the tidal component, but the tidal velocities are still large in the south Delta channels (Oltmann 1999). The evidence that reducing these flow velocities will benefit species of concern has not been developed.

There is evidence that barriers in the Delta have an effect on phytoplankton. Survival of fall-run Sacramento Basin hatchery salmon smolts migrating through the Delta is higher when the Delta Cross-Channel gates are closed than when they are open (Newman and Rice 2003). A temporary rock barrier is placed each spring in the head of Old River to protect migrating San Joaquin basin smolts.

Diversions (10-11)

Improving the effectiveness of the screening operations at the CVP and SWP, and either improving or eliminating the need for screens at the Pacific Gas and Electric power plants, seems laudable. However, this will probably be an expensive solution and some consideration needs to be made of the characteristics of the target species. For example, delta smelt are very sensitive to handling and may not survive well under any scenario of improved screening. Salmon smolts probably are not entrained in sufficient numbers to be worth a major effort. No fish larvae would be salvaged. There is good reason to investigate the large salvage data set as thoroughly as possible before embarking on a major overhaul of the salvage facilities.

Scientific support for screening the Delta agricultural diversions is weak. The limited evidence suggests that these diversions may not have much impact on fishes in the Delta, and there has been no analysis of their likely effect on populations.

Contaminants (12)

Although we lack direct evidence linking contaminants to population dynamics of aquatic species, the indirect evidence suggests that effects should be occurring. The Strategic Plan (CALFED 2000) lists reduction of contaminant effects as a goal, irrespective of any direct links to populations. This was a deliberate choice guided by the knowledge that such links are extraordinarily difficult to detect.

Invasive Species (13-15)

Similarly, one of the goals of the Strategic Plan (CALFED 2000) is to reduce the rate and effects of invasions. In most cases actions are limited to preventive measures, so it makes sense to foster measures to limit the spread of invasive species by the better-understood pathways such as ballast water and boating. The issue of weed control in the Delta is complex, since the use of herbicides may cause additional harm to the aquatic environment. Other means of control have not been commonly considered, and this might be a fruitful avenue for research.

Fish Harvest (16)

This action applies only to poaching, about which there is little information. This may be an area where some research is needed to at least establish bounds on the magnitude of the problem.

Aquatic Productivity (17)

The ERPP seems overly optimistic that the combination of actions listed would result in higher productivity. Research is now underway to further elaborate the causes of the reduced productivity.

Predation (18)

It is not clear what the later planting of striped bass would do.

UNCERTAINTIES AND INFORMATION NEEDS

Key uncertainties have already been enumerated and discussed under each of the sections above. This section addresses some of the key issues that cut across the above sections in an attempt to summarize and synthesize these issues.

Monitoring

Current monitoring programs were examined and additional monitoring programs suggested by the Comprehensive Monitoring, Analysis, and Research Program (CMARP) work teams. The products of these analyses were presented as a series of technical appendices, and some recommendations for monitoring water quality and lower trophic levels are being adopted by IEP. The CMARP appendices represent the efforts of groups of experts in each subdiscipline, including hydrodynamics, water quality, and productivity of lower and higher trophic levels. Given the level of effort and range of expertise that went into these efforts, there is no reason to repeat the effort. Rather, I present here some thoughts about monitoring that either cut across disciplines or are important enough to reiterate.

The most obvious feature of the existing monitoring programs is that emphasis is still on collecting data rather than on analyzing and publishing results using the data. Many of the publications using monitoring data on fish are the work of academic scientists, although numerous papers have been published by agency scientists on phytoplankton and zooplankton.

Gaps in spatial coverage of the monitoring programs are most severe for the water quality, phytoplankton, zooplankton, and benthic monitoring programs, although a bay-wide zooplankton program has been planned. At present, IEP monitors water quality, phytoplankton, and benthos from the Delta to San Pablo Bay. The USGS currently monitors phytoplankton biomass, temperature, salinity, and sometimes nutrients on monthly transects from the South Bay to Rio Vista in the northwestern Delta. The Regional Monitoring Program (RMP) monitors water quality and benthos, and is coordinating efforts with IEP. However, the RMP samples only quarterly, which is too long an interval for effective observation of seasonal patterns.

These programs should be brought together in a coordinated framework to allow for ease of data analysis and interpretation. The entire estuary should be sampled using similar methods, and sampling for phytoplankton and water quality should be coordinated with monitoring for zooplankton, benthos, and fish and epibenthic macroinvertebrates.

Monitoring for some ecosystem components may be inadequate even where spatial coverage is adequate. The amphipod *Gammarus daiberi*, an important foodweb species, may not be monitored effectively by the benthic program, since it is epibenthic at least part of the time.

Zooplankton from San Pablo Bay east have been monitored consistently since 1972, but some concerns were raised during a recent Environmental Monitoring Program review about the methods being used. Phytoplankton biomass is measured adequately, but chlorophyll in various size fractions needs to be measured, particularly those available to most zooplankton. In addition, a consistent program of phytoplankton identification and biomass estimation should be established. Nutrients are measured monthly in the IEP monitoring program but only in Suisun Bay and the Delta.

The San Francisco Bay study has excellent spatial and temporal coverage, but could provide better coverage in the Delta during seasons when other programs are not sampling there. Large jellyfish are often caught in this program, and were counted for some time but are no longer counted. Their abundance and biomass should be estimated, since they could have important ramifications for higher foodweb productivity. In fish and zooplankton monitoring programs, effort needs to be made to provide biomass estimates as well as abundance, since sizes of the collected organisms vary widely; in addition, biomass estimates are needed for most kinds of modeling.

Several important ecosystem components are not being monitored at all. These include microzooplankton smaller than 45 µm, bacteria, benthic microalgae, and submerged aquatic vegetation. Although I do not suggest adding these to the monitoring program, pilot studies could be conducted to assess their importance. In addition, the monitoring programs need to be more adaptable to changing conditions, particularly the introduction and spread of new species with different life histories from the extant community.

New techniques for sampling and analysis are continually becoming available. These should be incorporated as they prove their utility. A current example is remote sensing: satellites are now flying that can provide information at useful resolution in terms of pixel size and wavelength. Remote sensing for chlorophyll and turbidity seems feasible, and would provide vastly improved resolution of the spatial field of these key variables. The network of continuous monitoring stations that have proved so valuable in Suisun Bay and the Delta should be expanded into the lower estuary.

Key Issues for Research

Areas for research by discipline were identified in the individual sections of the previous chapter, and additional areas are identified in the CMARP appendices. Several areas of research are interdisciplinary, and some will need to be addressed in Stage I of the CALFED program to establish the knowledge base needed for the decisions expected to be made at the end of Stage I. The importance of various issues will change as new information becomes available and new problems arise; thus, lists of key issues such as this become obsolete rapidly and need to be updated. As with any research program, the interests and motivations of individual researchers will have a strong influence on proposals they write and the research that is accomplished.

- *Hydrodynamics.* Hydrodynamic conditions in the estuary provide the framework for everything else that goes on there. Top-quality research has revealed a great deal but more remains to be done. Particularly important areas for research include the following.

- *Flux Measurements.* Fluxes across several key boundaries and within basins in the estuarine system need to be determined to help in constructing mass balances and to aid in the assessment of population dynamics. Fluxes could be measured and estimated using three-dimensional models. Important boundaries include the south Delta pumps, the rivers near or above the reach of tides, the mouth of the estuary, and the Low-Salinity Zone.

- *Modeling.* Efforts are needed not only to develop and expand the use of more sophisticated models, but to assess capabilities and limitations of both existing and new models. In addition, new data on bathymetry may be needed, particularly in the Delta, so that models can be correctly calibrated. Models of hydrodynamics need to be coupled with sediment models of increasing sophistication, and with various ecological models.

- *Net Flows and Transport in the Delta.* Progress is needed in integrating the growing understanding of flows in the Delta with information needed to predict movements of sediments and organisms, even fish. This will require a coordinated effort with model, field, and possibly laboratory components.

- *The Fish-X2 Relationships.* These have already been discussed above. Preliminary studies of mechanisms underlying these relationships are underway.
- *Limiting Processes and Life Stages.* The limitations on growth of biological populations is a core issue in ecology. For relatively few biological populations do we have a good idea of the key life stages or the processes controlling abundance. The major exception may be striped bass, although there is still disagreement on what those are. For many other species we have some ideas (see "Fish-X2 Relationships" p.86), and some of these ideas have sufficient contrast and resolution that they can probably be tested. Knowledge of some of these processes may be essential for placing better-known processes (e.g., export losses, fishing) in a population context.
- *Transport of Young into the Estuary.* Several species of fish and invertebrates are transported into the estuary from the coastal ocean (e.g., bay shrimp, starry flounder). This transport depends not only on the supply of larvae or juveniles, but also on the physical interaction between the Bay and the coastal ocean. This in turn depends on freshwater flow and tide in the estuary, and wind and upwelling in the coastal ocean. Since these conditions vary substantially between years, this process is likely to be important in population regulation.
- *Density-Dependent Effects.* Convincing evidence of density dependence has been developed for striped bass, and delta smelt may also have a density-dependent life stage (Bennett in prep.). This process is the most important in any life cycle, since it regulates population abundance. Potential declines in carrying capacity identified for striped bass may be due to declines in production at the base of the foodweb, and therefore suggest a decline in system capacity. The mechanisms behind these density-dependent feedbacks need to be discovered before opportunities for easing the limits can be investigated.
- *Foodweb Productivity.* Phytoplankton dynamics in the South Bay are probably understood better than for any other estuary in the world. However, the level of understanding is less for other regions of the estuary, and information on other aspects of the foodweb is lacking. Productivity at the base of the foodweb may limit some populations, and certainly limits system-wide production at higher trophic levels. The limits to productivity, and the effects that recent introductions may have had, are important areas for research.

It is conceivable that productivity of the foodweb could be increased, although considering the overriding effects of turbidity and benthic grazing this seems unlikely in much of the estuary. There may be opportunities to manipulate residence time in the Delta so as to achieve high production, although this may also produce noxious blooms.

OPPORTUNITIES AND CONSTRAINTS

From a restoration perspective, the issues fall into five broad categories, not in order of priority:

1. What are the most important problems that need to be solved?
2. How much control can humans exert on the estuarine ecosystem?
3. What are the likely impacts of proposed or contemplated rehabilitation actions in adjacent wetlands or in the watershed?
4. What is the likely long-term trajectory of the ecology of the estuary, and to what extent can that trajectory be altered?
5. What opportunities are there for system-wide adaptive management experiments?

Problems That Need to Be Solved

Endangered and threatened species: Listings of delta smelt and winter run Chinook salmon provided much of the impetus for the CALFED program. Despite efforts to avoid further listings through proactive measures, two additional fish species (spring run salmon and steelhead) have been added to the list. One effect of these listings is to limit options for flexible management of the hydrologic system, which has consequences both for California's economy and the ecosystem. There is evidence that at least some of these declines have been reversed.Contaminants. Population-level impact of contaminants in the San Francisco Estuary have been difficult to detect. This is not to say there are none, merely that these impacts are extremely difficult to distinguish from natural (or other human-produced) variability. Results of toxicity testing using bioassays consistently turn up toxic contamination at locations throughout the estuary and in the rivers. Although the organisms used in these bioassays are not necessarily found in the estuary, they are probably closely related enough to suggest population-level problems are occurring. In addition, advisories have been published on health risks associated with eating fish or shellfish collected in the estuary. Many of today's contaminant problems are not of today's making: mercury, DDT, and PCBs are all residue of past activity and opportunities no longer exist for source control. Nevertheless, numerous contaminants are now being discharged into the estuary and its tributaries, and at least in principle these could be controlled or reduced.

Invasive Species

Although it is too late to do anything about most of the species that are already here, there may be some opportunity for control measures. These could include the formation of quick-response teams that could identify, locate, and eradicate small populations of invasive species quickly before they have had a chance to spread.

Equally important is stopping further invasions, which could have unknown and unforeseen impacts on the estuarine ecosystem. In addition, changes in the ecosystem due to the species introduced within the last 15 years should be assessed and understood, both as a way of understanding the ecosystem as it currently exists, and possibly to help scale back expectations for the results of rehabilitation.

Habitat Availability

Most of the marsh habitat around the estuary was lost long ago, and recent declines in abundance of various species must have other causes. Considerable interest has developed in the regional scientific and environmental communities in rehabilitating marshes. Although this interest is based partially on providing habitat for fishes, research results to date indicate that species using shallow habitats are marsh specialists rather than the young of open-water species. This pattern needs to be confirmed, but it suggests that restoration through construction of shallow habitat may not benefit fish species of concern.

Human Influence on the Estuarine Ecosystem

Humans have an overwhelming influence on the estuarine ecosystem, but relatively little control. The reason is that many human activities that affect the ecosystem are either irreversible (e.g., global change, habitat loss in urban areas) or have a long recovery period (e.g., sediment-bound contaminants). Actual controls on the ecosystem include the following.

Freshwater Flow and Export Flow

This is one of the few areas where humans can influence the ecosystem over relatively short time scales. At present, protective measures for the ecosystem are established through limits on X2 or outflow, and on export flow or the ratio of export flow to Delta inflow. These controls need to be put on a firmer scientific footing by investigating mechanisms behind population responses to them, and in the case of export:inflow ratios by determining whether they really capture the important impacts of export flow.

Conventional wisdom is that keeping X2 seaward of the confluence of the Sacramento and San Joaquin rivers in spring benefits native fishes. However, the native species presumably evolved in a system where salinity penetrated far up-estuary in most summers and some dry springs; thus, allowing salinity in the Delta to increase could have beneficial effects. The implications to water supply may preclude full-scale actions along these lines, but there may be opportunities to test these ideas in small, localized parts of Suisun Marsh or the Delta.

Forestalling Irreversible Impacts

Failing to take an action is an action in itself. In 20 years, certain options that are open today will no longer be open. For example, in retrospect a greater effort to prevent species introductions would have benefited the estuary. The same may be true for land-use patterns and encroaching urbanization. Although it may not be possible to anticipate where the most suitable locations would be, if action is not taken soon the opportunities will be gone.

Dredging

Although dredging affects a relatively small area of the estuary, it may have broader impacts including release of biological and chemical contaminants into the water, alteration of bathymetry and circulation, and local increases in suspended sediment concentrations. All of these impacts may be amenable to reduction or alteration. Dredging of deep channels may have substantial effects in certain areas on circulation patterns and salt flux.

Harvest

Many species in the estuary are harvested and some may be over-harvested. The level and kinds of harvest should be included in the mix of actions considered for rehabilitation.

Hatcheries

Hatcheries for salmon in the watershed are an essential part of management and mitigation, although awareness has been increasing of the negative effects of salmon hatcheries, e.g., on genetics and harvest rate of wild populations. Hatcheries for striped bass have been used in the past to supplement this population, although that use has been discontinued because of high population abundance in recent years. To the extent that supplementing the striped bass population does not have a negative effect on other species of concern, this supplementation would be a viable way to enhance sport-fishing opportunities in the estuary.

Nutrient Inputs

Since most of the nutrients entering the estuary come from treatment plants, there are opportunities to control the loading rate. This may not be an effective management action now, given the infrequency of nutrient limitation, but it could become so in the future if estuarine waters become clearer. The potential effect of ammonium in suppressing bloom formation is being investigated.

Fish Screens

The benefits of screening small agricultural diversions in the Delta have not been determined. These fish screens could actually do considerable harm through the addition of hard structures which may provide habitat for predators on native species of concern. In addition, money spent on fish screens is unavailable for other uses. A significant research effort is warranted to quantify the net benefits of fish screens to populations of concern.

Impacts of Rehabilitation Actions in Other Parts of the System

Actions focused in upstream regions are unlikely to have major effects in the estuary unless they significantly alter organic carbon or sediment supply or flow regimes, or greatly alter the numbers of anadromous species passing through or using the estuary. At this point there is insufficient information to determine the numbers of salmon rearing in the estuary, for example, let alone assess their effect on the rest of the ecosystem or the potential effect of adding to their numbers.

Planned or proposed larger-scale restoration actions such as enlarging Delta channels, converting large areas to subtidal habitat, or moving or splitting the point of diversion from the south Delta, will probably have unpredictable, major consequences for the estuarine ecosystem. It seems prudent to embark on an intense program of research to try to predict how these actions may influence the estuary.

Long-term Trajectory

Several issues will affect the estuarine ecosystem in the long run and influence the effectiveness of rehabilitation actions. Some of these are predictable, others not. Among the more predictable:

Global Warming and Climate Change

Most scientists now accept that global warming is happening as a result of release of anthropogenic greenhouse gases, although details of the cause, future trajectory, and responsiveness of the global climate system to large-scale intervention are in dispute. At the local scale climate change must be accepted as part of the background. It may result in more extreme weather patterns in the future, and the trend in the timing of precipitation will probably continue. Sea-level rise is accompanying warming and, although slow, it will eventually inundate low-lying areas. Some marshes are apparently able to accumulate sediments to stay ahead of the rate of rise, but not all shoreline areas will do so.

Decrease in Sediment Supply and Concentrations

Between the cutoff of major sources in the watershed, increasing erosion of estuarine basins, and the possible increase in trapping by marshes, the net supply rate of sediment to the estuary has probably become negative. This may have already affected water clarity in the Delta; should this trend continue, eutrophication is a possible consequence. In combination with sea level rise, the decrease in sediment supply will cause erosion of fringing areas of marshes, particularly those (e.g., in western San Pablo Bay) produced following the sediment pulse caused by hydraulic mining. Retreat of fringing marshes in these areas has already been noted (M. Josselyn, SFSU, pers. comm.).

Increase in human population: Demand for water, land, and food will continue to grow, placing increasing pressure on these natural resources. Conflicts over water and land will continue to grow, placing a premium on taking actions now to prevent irreversible impacts later.

System-wide Adaptive Management Experiments

In contrast to upstream and marsh habitats, the open waters are less amenable to active (i.e., experimental) adaptive management. The main reasons are the lack of duplicate subsystems to use as experimental and control systems, and the high natural variability in the system. For these reasons, active adaptive management may not be helpful in learning more about the X2 relationships than can be learned through natural variability. Potential opportunities for experiments in open waters include the following.

Productivity in the Delta

Flow and exports in the Delta could be manipulated experimentally to determine their effect on production at the base of the foodweb, particularly for phytoplankton and rotifers, and possibly also bacteria. Although such flow manipulations for this purpose are unlikely, this could be done in conjunction with ongoing experimental manipulations of flow and diversions for determining salmon survival (Vernalis Adaptive Management Program). Since residence time appears to have an important influence on phytoplankton production in the Delta, it might be expected to respond to such changes on a time scale of weeks. This experiment would have to be run using replication in time, since spatial replication is not possible.

Salinity Intrusion

Many of the invasive species in the Delta are freshwater species with little tolerance for salinity. Allowing salt to intrude into certain regions of the Delta or Suisun Marsh on a regular seasonal basis could provide important information about the use of these areas by natives vs. invasive species.

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ABBREVIATIONS

CALFED	Now California Bay-Delta Authority, CBDA
CMARP	Comprehensive Monitoring, Analysis, and Research Program
CVPIA	Central Valley Project Improvement Act
DCC	Delta Cross Channel
DFG, CDFG	California Department of Fish and Game
DIC	Dissolved inorganic carbon
DIN	Dissolved inorganic nitrogen
DOC	Dissolved organic carbon
DWR	California Department of Water Resources
E:I ratio	Export:Inflow ratio
EET	Estuarine Ecology Team of the IEP
ENSO	El Niño-Southern Oscillation
ERP(P)	Ecosystem Restoration Program (Plan)
ETM	Estuarine turbidity maximum
EWA	Environmental Water Account
CVP	Central Valley Project
IEP	Interagency Ecological Program for the San Francisco Estuary
LSZ	Low-Salinity Zone
NEM	Net ecosystem metabolism
POC	Particulate organic carbon
QWEST	Calculated net flow in the lower San Joaquin River at Jersey Point
RMP	Regional Monitoring Program
SAV	Submerged aquatic vegetation
SPM	Suspended particulate matter
SRP	Soluble reactive phosphorus
SWP	State Water Project
TRIM2D, 3D	Tidal, Residual, Intertidal Mudflat hydrodynamic model
USGS	U.S. Geological Survey
WWTP	Wastewater treatment plant
YOY	Young-of-the-year index

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Appendix A. Table of percent occurrence of fishes in samples from three monitoring programs. Data included are from the San Francisco Bay study for 1980-1996 including midwater and otter trawl and beach seine data; fall midwater trawl data for 1967-1993 except for 1974 and 1979; and summer townet data for 1959-1995 (1966-1968 missing). Species that are discussed in text or figures are highlighted in bold.

			Frequencies				
			Bay Study Data			**Fall**	**Summer**
Family	***Species Name***	***Common Name***	***Mid-water***	***Otter***	***Seine***	***Midwater***	***Townet***
Acipenseridae	*Acipenser transmontanus*	**White sturgeon**	2.90	3.62		3.59	0.10
	Acipenser medirostris	Green sturgeon	0.14	0.48		0.20	0.02
Agonidae	*Odontopyxis trispinosa*	Pygmy poacher		0.16			
Alopiidae	*Alopias vulpinus*	Thresher shark	0.02				
Ammodytidae	*Ammodytes hexapterus*	Pacific Sandlance		0.06	0.11		
Anarhichadidae	*Anarrhichthys ocellatus*	Wolf eel				0.01	
Atherinidae		Silversides					0.39
	Atherinops affinis	Topsmelt	5.70	0.48	63.45	4.23	1.75
	Atherinopsis californiensis	Jacksmelt	28.28	0.68	41.21	4.14	0.43
	Menidia beryllina	Inland silverside	0.05	0.06	11.61		
	Menidia audens	Mississippi silverside				0.54	2.78
Batrachoididae	*Porichthys notatus*	Plainfin midshipman	10.76	24.39	0.29	3.19	1.04
Blenniidae	*Hypsoblennius gilberti*	Rockpool blenny			0.06		
Bothidae	*Paralichthy californicus*	California halibut	0.41	7.62	0.92	0.01	
	Citharichthys sordidus	Pacific sanddab	0.02	0.26		0.05	
	Citharichthys stigmaeus	Speckled sanddab	1.13	30.68	0.40	0.14	
Carangidae	*Trachurus symmetricus*	Jack mackerel	0.05				
Carcharhinidae	*Mustelus henlei*	Brown smoothhound	1.94	11.04		0.32	
	Mustelus californicus	Grey smoouthhound				0.01	
	Triakis semifasciata	Leopard shark	0.91	3.82	0.06	0.03	
Catostomidae	*Catostomus occidentalis*	Sacramento sucker	0.02	0.03		0.01	0.02

Appendix A - continued

			Frequencies				
			Bay Study Data			**Fall**	**Summer**
Family	***Species Name***	***Common Name***	***Mid-water***	***Otter***	***Seine***	***Midwater***	***Townet***
Centrarchidae		Sunfish	0.02		0.06		0.04
	Lepomis microlophus	Redear sunfish		0.10			
	Lepomis cyanellus	Green sunfish				0.05	0.03
	Lepomis macrochirus	Bluegill sunfish	0.03	0.04		0.11	0.07
	Micropterus salmoides	Largemouth bass	0.02	0.01	0.06	0.01	0.10
	Pomoxis annularis	White crappie			0.06	0.06	0.08
	Pomoxis nigromaculatus	Black crappie	0.03	0.01		0.25	0.43
	Archoplites intuptus	Sacramento perch				0.01	0.01
	Micropterus dolomieu	Smallmouth bass					0.02
Clinidae	*Gibbonsia metzi*	Striped kelpfish			0.11		
	Neoclinus uninotatus	Onespot fringehead		0.01			
Clupeidae		Shad					3.05
	Alosa sapidissima	**American shad**	16.81	2.41	1.90	36.92	14.51
	Dorosoma petenense	Threadfin shad	4.83	1.53	3.79	26.69	7.03
	Clupea harengus pallasi	**Pacific herring**	33.40	8.60	14.37	11.21	1.32
	Sardinops sagax	**Pacific sardine**	1.34	0.10	0.06		
Cottidae		Sculpins					0.14
	Oligocottus snyderi	Fluffy sculpin			0.06		
	Artedius notospilotus	Bonehead sculpin	0.02	1.01	0.06		
	Leptocottus armatus	Staghorn sculpin	4.67	37.73	32.99	2.09	0.26
	Cottus asper	Prickly sculpin	0.02	1.12	0.17	0.02	0.02
	Artedius harringtoni	Scalyhead sculpin		0.01			
	Scorpaenichthys marmoratus	Cabezon			0.11		
	Hemilepidotus spinosus	Brown Irish lord		0.04			
	Hemilepidotus hemilepidotus	Red Irish lord		0.01			
Cyclopteridae	*Cyclopteridae*	Unidentified snailfishes (snailfishes)		0.01			
	Liparis pulchllus	Showy snailfish	0.02	1.14			

Appendix A - continued

			Frequencies				
			Bay Study Data			Fall	Summer
Family	***Species Name***	***Common Name***	***Mid-water***	***Otter***	***Seine***	***Midwater***	***Townet***
Cyprinidae		Carps and Minnows		0.01	0.06		0.10
	Notemigonus crysoleucas	Golden shiner			0.06	0.03	0.08
	Cyprinus carpio	Carp	0.45	0.35	0.11	2.57	0.52
	Carassius auratus	Goldfish	0.02	0.01		0.03	0.12
	Pogonichthys macrolepidotus	**Sacramento splittail**	3.54	2.80	4.54	3.16	3.23
	Mylopharodon conocephalus	Hardhead					0.07
	Ptychoceilus grandis	Sacramento pikeminnow	0.08	0.10	2.07	0.20	0.01
	Lavinia exilicauda	Hitch			0.11	0.03	0.01
	Orthodon microlepidotus	Sacramento blackfish			0.06	0.13	
Cyprinodontidae	*Lucania parva*	Rainwater killifish	0.03	0.03	3.51		0.01
Embiotocidae	*Embiotoca jacksoni*	Black perch	0.02	0.91	0.75	0.01	
	Rhacochilus vacca	Pile perch	0.38	1.67	1.21	0.06	
	Micrometrus minimus	Dwarf surfperch	0.02	0.88	19.94		0.02
	Amphistichus argenteus	Barred surfperch	0.06	1.57	2.13		
	Amphistichus koelzi	Calico surfperch	0.02		0.11		
	Rhacochilus vacca	Pile surfperch				0.06	
	Hysterocarpus traski	Tule perch	0.08	1.56	0.86	0.12	0.12
	Amphistichus rhodoterus	Redtail surfperch	0.02				
	Rhacochilus toxotes	Rubberlip surfperch	0.03	0.17	0.40	0.01	
	Hyperprosopon anale	Spotfin surfperch		0.01		0.01	
	Hyperprosopon argenteum	Walleye surfperch	3.49	2.30	5.06	0.34	
	Cymatogaster aggregata	Shiner perch	16.03	30.49	22.53	5.09	0.05
	Hyperprosopon ellipticum	Silver surfperch	0.03	0.04	0.11		
	Hypsurus caryi	Rainbow seaperch		0.03			
	Phanerodon furcatus	White seaperch	0.59	1.05	0.29		
Engraulididae	*Engraulis mordax*	**Northern anchovy**	63.02	23.03	36.78	35.04	16.20
Gadidae	*Microgadus proximus*	Pacific tomcod	0.56	5.76		0.89	

Appendix A - continued

			Frequencies				
			Bay Study Data			Fall	Summer
Family	***Species Name***	***Common Name***	***Mid-water***	***Otter***	***Seine***	***Midwater***	***Townet***
Gasterosteidae	*Gasterosteus aculeatus*	Three-spine stickleback	1.05	1.32	22.36	0.66	3.84
	Aulorhynchus flavidus	Tube-snout		0.01			
Gobiidae		Gobies					0.74
	Acanthogobius flavimanus	Yellowfin goby	7.11	25.77	23.45	5.40	8.66
	Eucyclogobius newbyi	Tidewater goby					0.02
	Clevelandia ios	Arrow goby	0.02	0.99	25.17	0.03	0.05
	Ilypnus gilberti	Cheekspot goby	0.08	6.64	2.64		
	Tridentiger trigonocephalus	Chameleon goby	0.75	7.02	0.63	0.19	0.52
	Tridentiger bifasciatus	Shimofuri goby	0.21	1.29			0.06
	Lepidogobius lepidus	Bay (fine scaled) goby	5.94	34.34	1.95	0.08	0.01
	Gillichthys mirabilis	Longjaw mudsucker		0.01	0.17		0.01
Hexagrammidae							
	Ophiodon elongatus	Lingcod	0.35	0.89		0.02	
	Hexagrammos decagrammus	Kelp greenling	0.02	0.06	0.11		
Hexanchidae	*Notorynchus maculatus*	Sevengill shark		0.03		0.01	
Ictaluridae		Catfish					3.77
	Ictalurus catus	White catfish	0.69	3.32	0.06	4.95	7.26
	Ictalurus punctatus	Channel catfish	0.38	3.67	0.06	0.67	0.77
	Ictalurus melas	Black bullhead	0.02				
	Ictalurus nebulosus	Brown bullhead	0.02	0.03		0.04	0.04
Mugilidae	*Mugil cephalus*	Striped mullet			0.06		
Myliobatididae	*Myliobatis californica*	Bat ray	4.02	3.79	0.29		0.56
Ophidiidae	*Chilara taylori*	Spotted cusk-eel		1.16			
Osmeridae		Smelt					1.68
	Spirinchus thaleichthys	Longfin smelt	31.55	31.94	2.82	38.66	11.51
	Hypomesus transpacificus	**Delta smelt**	7.27	3.28	2.24	19.56	34.74
	Spirinchus starksi	Night smelt	0.38	0.30	0.23	0.16	
	Hypomesus pretiosus	Surf smelt	0.96	0.10	7.93	0.25	

Appendix A - continued

			Frequencies				
			Bay Study Data			Fall	Summer
Family	***Species Name***	***Common Name***	***Mid-water***	***Otter***	***Seine***	***Midwater***	***Townet***
Osmeridae	*Allosmerus elongatus*	Whitebait smelt	0.73	0.54	0.06	0.83	
	Hypomesus nipponensis	Wakasagi	0.03				
Percichthyidae	*Morone saxatilis*	**Striped bass**	29.84	29.20	29.83	75.78	76.72
Percidae	*Percina copelandi*	Logperch				0.01	0.03
	Percina macrolepida	Bigscale logperch		0.60	0.06		
Petromyzontidae							
	Lamptera spp.	Lamprey		0.03			0.10
	Lampetra tridentata	Pacific lamprey	0.18	0.88		0.15	0.01
	Lampetra ayresi	River lamprey	0.14	1.57		0.05	0.02
Pholidae	*Apodichthys flavidus*	Penpoint gunnel			0.11		
	Pholis ornata	Saddleback gunnel		0.07	0.11		
Pleuronectidae		Right-eyed Flounders		0.01			
	Platichthys stellatus	**Starry flounder**	4.32	18.97	4.94	0.48	1.90
	Pleuronichthys coenosus	C-O sole		0.01			
	Pleuronichthys decurrens	Curlfin sole		0.96			
	Pleuronectes vetulus	English Sole	2.71	27.50	5.46	0.13	
	Inopsetta ischyra	Hybrid sole		0.01			
	Pleuronectes bilineatus	Rock sole				0.02	
	Psettichthys melanostictus	Sand sole	0.10	0.92	0.34		
	Hypsopsetta guttulata	Diamond turbot	0.16	3.36	2.18		
	Pleuronichthys verticalis	Hornyhead turbot		0.06			
Poeciliidae	*Gambusia affinis*	Mosquitofish		0.03	1.90	0.01	0.04
Rajidae	*Raja binoculata*	Big skate	0.32	3.82		0.09	
Salmonidae	*Oncorhynchus tshawytscha*	**Chinook salmon**	13.08	0.71	10.63	5.37	1.08
	Oncorhynchus gairdneri	Steelhead				0.45	
	Oncorhynchus kisutch	Coho salmon	0.02				
	Salmo gairdneri	Rainbow trout	0.40		0.34		

Appendix A - continued

			Frequencies				
			Bay Study Data			Fall	Summer
Family	***Species Name***	***Common Name***	***Mid-water***	***Otter***	***Seine***	***Midwater***	***Townet***
Sciaenidae	*Genyonemus lineatus*	White croaker	16.19	31.33	1.09	0.90	0.04
	Seriphus politus	Queenfish	0.10	0.01			
Scombridae	*Scomber japonicus*	Chub mackerel	0.02				
Scorpaenidae	*Sebastes* spp.	Rockfish	0.03	0.13	0.06		
	Sebastes melanops	Black rockfish	0.06	0.04			
	Sebastes mystinus	Blue rockfish		0.01			
	Sebastes auriculatus	Brown rockfish	0.02	5.43	0.40		
	Sebastes flavidus	Yellowtail rockfish		0.01			
Soleidae	*Symphurus atricauda*	California tonguefish	0.05	7.52			
Sphyraenidae	*Sphyraena argentea*	Pacific barracuda	0.02				
Squalidae	*Squalus acanthias*	Spiny dogfish	0.57	0.72		0.12	
Stromateridae	*Peprilus simillimus*	Pacific butterfish				0.33	
	Peprilus simillimus	Pacific pompano	3.94	0.17			
Syngnathidae	*Syngnathus leptorhynchus*	Bay pipefish	0.21	4.43	13.05	0.03	0.07
Synodontidae	*Synodus lucioceps*	California lizardfish	0.14	0.35			
Torpedinidae	*Torpedo californica*	Pacific electric ray	0.06	0.04		0.02	

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Volume 2, Issue 2, Article 1
Erratum

San Francisco Estuary and Watershed Science
Volume 2, Issue 1, Article 1, February 2004
Kimmerer (2004), “Open water processes of the San Francisco Estuary:
From physical forcing to biological responses”

Page 17, paragraph 1: The last sentence originally read:

Analyses of effects of outflow (or X_2) together with export flow (not export:inflow ratio) have revealed nonexistent (salinity; Kimmerer unpublished) or very weak (striped bass survival, Kimmerer et al. 2001) effects of export flow.

The last sentence should be replaced with the following to clarify that salinity in the Delta can be affected by export flow:

Analyses of effects of outflow (or X_2) together with export flow (not export:inflow ratio) have revealed nonexistent (salinity in Suisun Bay; Kimmerer unpublished) or very weak (striped bass survival, Kimmerer et al. 2001) effects of export flow.

Page 48, paragraph 1: The last sentence originally read:

Blooms of *Microcystis* have occurred in the southern Delta (Lehman and Waller 2003).

The last sentence should be revised as follows to state that *Microcystis* blooms throughout the Delta.

Blooms of *Microcystis* have occurred throughout the Delta (Lehman and Waller 2003).

Page 63, paragraph 1: The first three sentences of the paragraph originally read:

The principal exception to the generally saturated oxygen concentrations occurs in late summer to early fall in the San Joaquin River near Stockton (Hayes and Lee 1998, 1999, 2000; Lehman et al. 2004), a region not included in Figure 32. In that region, a combination of high summer temperature and high organic matter loading and phytoplankton production result in high oxygen demand relative to gas exchange with the atmosphere. Furthermore, stratification presumably limits oxygen transport to the bottom, and together with planktonic and benthic oxygen consumption results in low oxygen concentration (less than ~5 mg L-1) near the bottom. This may impede movement of fish through the area (Hayes and Lee

1998, 1999, 2000), although estuarine organisms may tolerate lower values (e.g., Stalder and Marcus 1997).

The first three sentences should be restated as follows to correct an erroneous citation:

The principal exception to the generally saturated oxygen concentrations occurs in late summer to early fall in the San Joaquin River near Stockton (Hayes and Lee 1998, 1999, 2000, Lehman et al. 2004), a region not included in Figure 32. High oxygen demand relative to gas exchange with the atmosphere in that region was previously attributed to high summer temperature and high organic matter loading and phytoplankton production, but Lehman et al. (2004) presented results showing that loading of nitrogenous nutrients from sewage treatment plants could account for most of the biological oxygen demand. Low dissolved oxygen may impede movement of fish through the area (Hayes and Lee 1998, 1999, 2000), although estuarine organisms may tolerate lower values (e.g., Stalder and Marcus 1997).