

Physical, Biological, and Management Responses to Variable Freshwater Flow into the San Francisco Estuary

W. J. KIMMERER*

Romberg Tiburon Center, San Francisco State University, 3152 Paradise Drive, Tiburon, California 94920

ABSTRACT: Freshwater flow is the principal cause of physical variability in estuaries and a focus of conflict in estuaries where a substantial fraction of the freshwater is diverted. Variation in freshwater flow can have many effects: inundation of flood plains, increase loading and advective transport of materials and organisms, dilution or mobilization of contaminants, compression of the estuarine salinity field and density gradient, increase in stratification, and decrease in residence time for water while increasing it for some particles and biota. In the San Francisco Estuary, freshwater flow is highly variable, and has been altered by shifts in seasonal patterns of river flow and increases in diversions from tidal and non-tidal regions, entraining fish of several species of concern. Abundance or survival of several estuarine-dependent species also increases with freshwater outflow. These relationships to flow may be due to several potential mechanisms, each with its own locus and period of effectiveness, but no mechanism has been conclusively shown to underlie the flow relationship of any species. Several flow-based management actions were established in the mid-1990s, including a salinity standard based on these flow effects, as well as reductions in diversion pumping during critical periods for listed species of fish. The effectiveness of these actions has not been established. To make the salinity standard more effective and more applicable to future estuarine conditions will require investigation to determine the underlying mechanisms. Effects of entrainment at diversion facilities are more straightforward conceptually but difficult to quantify, and resolving these may require experimental manipulations of diversion flow.

Introduction

Freshwater flow defines an estuary. Variability in freshwater flow is the predominant source of seasonal and interannual variability in estuaries (Skreslet 1986), and freshwater flow influences the physics, geology, chemistry, and biology of estuaries through a variety of pathways (Skreslet 1986; Sklar and Browder 1998). Human uses of an estuary are therefore profoundly influenced by the quantity of freshwater entering the estuary and its variability. Many estuaries are subject to the diversion of water for agriculture and other uses, resulting in degradation due to alteration in the amount or timing of flow (e.g., Herbold et al. 1992; Dynesius and Nilsson 1994; McIvor et al. 1994). Diversions have led to severe depletion or even cessation of flow with severe consequences for some estuaries (e.g., Aleem 1972; Micklin 1988; Whitfield and Wooldridge 1994).

The inherent conflict between human demand for freshwater and for other ecosystem services of an estuary results in a requirement to manage freshwater flow to protect these services. In some cases this management has been framed by perceived needs of estuaries for freshwater flow (e.g., Longley 1994), but estuarine responses to fresh-

water flow may not provide clear guidance to those needs (Kimmerer and Schubel 1994; Jassby et al. 1995). The concept of the need of an estuary for freshwater flow cannot be separated from the numerous demands that humans place on estuaries. Practical management of inflow to an estuary must address a variety of goals, each of which may imply different strategies for setting the timing and quantity of inflow or diversion flow.

It is timely to examine the management implications of estuarine responses to freshwater flow. The projected course of climate change may result in lower precipitation in some watersheds and higher in others, but at the very least seasonal changes are expected (Dettinger and Cayan 1995). In seasonally dry climates such as that of central California, this may take the form of lower availability of freshwater during the dry season. This pattern is likely to interact with increasing demand due to growing human populations (Vörösmarty et al. 2000). It is essential to understand the physical, biological, and management context into which long-term trends in flow are projected.

In this paper I present a case study of the San Francisco Estuary to illustrate some key influences of freshwater flow, identify some potential mechanisms for flow effects on biota, and discuss how alternative assumptions about these mechanisms can and should influence management actions tak-

* Tele: 415/338-3515; fax: 415/435-7120; e-mail: kimmerer@sfsu.edu.

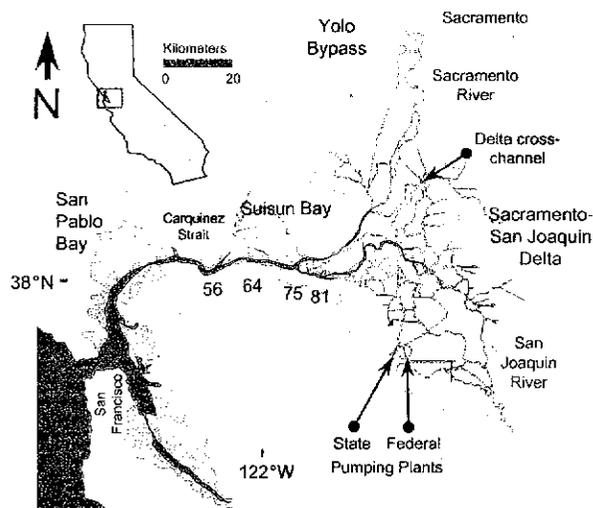


Fig. 1. Map of the San Francisco Estuary showing key features discussed in the text. Heavy shading indicates depths greater than 10 m. Numbers indicate river kilometer (distance from the mouth of the estuary) for identification of locations in the text.

en for environmental protection. This paper focuses on the river-dominated northern part of San Francisco Estuary (Walters et al. 1985), including the Sacramento-San Joaquin Delta and several shallow embayments (Fig. 1), primarily in spring to summer when larval and early juvenile stages of many nekton species are present. I use available data from several monitoring programs to demonstrate the physical, chemical, and biological consequences of flow, and to explore several mechanisms by which biological populations may be affected by flow, then discuss briefly the management actions that use flow to achieve environmental goals.

The San Francisco Estuary is well established in the literature showing severe effects of freshwater diversions (e.g., Stevens et al. 1985; Nichols et al. 1986). Because of variation in precipitation in the watershed, outflow had no trend over the period from 1921–1986 (Fox et al. 1990). Construction and operation of reservoirs has altered the hydrograph more through a change in seasonal pattern than through a change in total flow; thus, in contrast to freshwater-starved estuaries such as the Nile (Aleem 1972) or the Sea of Azov (Micklin 1988), management of the San Francisco Estuary must be based on more subtle effects of flow.

Study Site and Methods

Several volumes on the geography, hydrology, environmental conditions, and general biology of the San Francisco Estuary provide valuable background information (e.g., Conomos 1979; Cloern

and Nichols 1985; Nichols et al. 1986; Hollibaugh 1996). Extensive human modifications to the estuary have included diking and isolation of about 95% of the estuary's wetlands, establishment of numerous exotic species; reduction or elimination of many stocks of fish and invertebrates, alteration of bathymetry and introduction of contaminated sediment through hydraulic mining in the watershed, disposal and accumulation of agricultural and urban waste including numerous toxic substances, reduction in sediment supply due to damming of all of the major rivers in the watershed, and alteration of the seasonal pattern and quantity of freshwater flowing into the estuary (Nichols et al. 1986).

The San Francisco Estuary (Fig. 1) receives nearly all of its freshwater from the Sacramento-San Joaquin River system, which drains approximately 100,000 km² (40% of the area of California). Water enters the estuary through the Sacramento-San Joaquin Delta, a complex network of tidal channels and islands, former marshes that were diked and drained for conversion to farms during and after the Gold Rush of the mid-19th century. Freshwater flow into the estuary has been altered by extensive development of dams, diversions, and canals upstream on the major rivers and tributaries, particularly the large dams and diversions of the federal Central Valley Project (CVP) and State Water Project (SWP). Most of the precipitation falls to the north of the Delta during winter-spring, and most of the demand is to the south during summer. During the summer-fall dry season the river-Delta system is essentially a conveyance system for moving water from reservoirs in the north to farms and cities in the San Joaquin valley or southern California and other areas outside the watershed. Water is exported from the Delta by large diversion pumps of the CVP and SWP, and the smaller Contra Costa Water District facility. Managers release water from reservoirs both to supply water for export from the Delta and to keep the Delta fresh by opposing tidal encroachment of salt water.

In addition to the water export facilities, over 2,200 pumps and siphons throughout the Delta take water for irrigation (Herren and Kawasaki 2001). Some of this water is lost through evapotranspiration, and some agricultural drainage is pumped back into the Delta channels. On an annual average basis, about 2 km³ is estimated to flow through these diversions, compared with about 4.5 km³ through the major export facilities and 26 km³ to the lower estuary as outflow (unpublished data from California Department of Water Resources, DWR, for 1956–2001).

The Sacramento-San Joaquin Delta (Fig. 1), the keystone of water management in California, is home to several species of fish that have been in a

state of decline in recent decades (Herbold et al. 1992; Moyle 2002). Concern over the effects of freshwater diversions on these fish species, particularly five that are listed as threatened or endangered, has resulted in curtailed freshwater exports, with resulting conflict between resource advocates and water users. Dissatisfaction with an adversarial approach to resource management (Kimmerer and Schubel 1994), as well as concerns over conflicting goals for the estuary and watershed, led to formation in 1995 of the CALFED (California-Federal) Bay-Delta program (<http://calfed.water.ca.gov>), an ambitious joint state and federal effort to restore ecosystems, improve water quality and reliability of supply, and reduce risks of levee failures.

Data and analytical methods for analyzing responses of biota to flow were described by Jassby et al. (1995) and Kimmerer (2002) and are summarized here and in figure captions. Data on freshwater flow were obtained from DWR (<http://www.iep.water.ca.gov/dayflow/>). Data on water quality and biological abundance for time periods of 20–31 years were obtained from the Interagency Ecological Program for the San Francisco Estuary (<http://www.iep.water.ca.gov>). Biological variables included abundance indices for a variety of fish and bay shrimp (Turner and Chadwick 1972; Armor and Herrgesell 1985; Kimmerer et al. 2000), and estimates averaged over months or seasons for zooplankton abundance (Orsi and Mecum 1986) and chlorophyll concentration (Lehman 2000). Chlorophyll data were also obtained from the U.S. Geological Survey (USGS; Cloern et al. 1985; <http://sfbay.wr.usgs.gov/access/quality.html>). Nutrient data were from DWR (Lehman 2000). Abundance of young striped bass and Pacific herring are influenced by egg production, so indices of early survival were calculated as the ratio of young abundance to estimates of egg production (Kimmerer et al. 2000; Kimmerer 2002). Sediment concentration and flux data are from the USGS (Schemel et al. 1996). Analyses consisted mainly of least-squares regressions or analyses of covariance, with robust procedures used in a few cases where outliers were apparent (Venables and Ripley 1997). In all analyses, diagnostic plots were used to ensure that assumptions of the methods were met.

DWR provides several estimated flow variables useful in examining the patterns of freshwater flow in the estuary. These variables include daily or monthly average flows in the Delta for water years 1956–2000: freshwater inflow, the sum of all the river flows into the Delta; export flow, the total of diversion flows by the major export facilities; and calculated net Delta outflow, the difference between inflow and export flows less net consumption in the Delta. Outflow measured using ultra-

sonic velocity meters at four stations in 1996–1998 was close to the calculated value at high freshwater flow, but diverged substantially at low flow because of spring-neap tidal and meteorological effects on water level (Olmann 1998). An additional calculated quantity is monthly unimpaired flow for 1908–1994, which is inflow that would exist if the reservoirs retained no water, but all other uses of water in the watershed were unchanged (DWR 1994). Pre-development natural flow may have been lower than unimpaired flow in the dry season because of higher evapotranspiration in the watershed before extensive development (Fox et al. 1990). On an annual (water year) basis unimpaired flow, inflow, and outflow have no time trend over their respective periods of record.

An additional flow-related variable used extensively in the San Francisco Estuary is X_2 , the distance up the axis of the estuary to where the daily average near-bottom salinity is 2 psu. This variable is used as a measure of the physical response of the estuary to freshwater flow, partly because of the difficulties of estimating outflow at low values (Jassby et al. 1995). X_2 has a lagged linear relationship to the log of freshwater outflow with a time constant of about 2 weeks. It was determined by interpolation among a set of continuous salinity monitoring stations for 1968 to 1992, and by time-series regression on the log of net Delta outflow for other years (Jassby et al. 1995). For most of the years in this analysis, under low-flow conditions X_2 gives a more accurate measure of flow conditions in the estuary west of the Delta than does Delta outflow.

Results and Discussion

FLOW PATTERNS IN THE SAN FRANCISCO ESTUARY

California's Mediterranean climate controls seasonal patterns of freshwater flow into the estuary. Nearly all of the precipitation falls during the winter-spring wet season, resulting in a > 10-fold seasonal range of daily freshwater flow into the estuary (Fig. 2). Annual flow is generally defined in terms of water year, which begins on October 1, so that the high-flow period is nearly always contained within a single year. Interannual variability in flow results from variability in regional climate, and annual runoff can also range over 10-fold (Fig. 2).

The Sacramento River provided 85% (median; range 69–95%) and the San Joaquin River 11% (4–25%) of annual total flow into the Delta during 1956–2000. Total annual export volume from the two major and one minor water export facilities increased up to the mid-1970s, after which annual export volume remained roughly steady, with a median of about 5.7 km³ or 29% of inflow since 1974 (Fig. 3). Export flow rate from the south Delta usu-

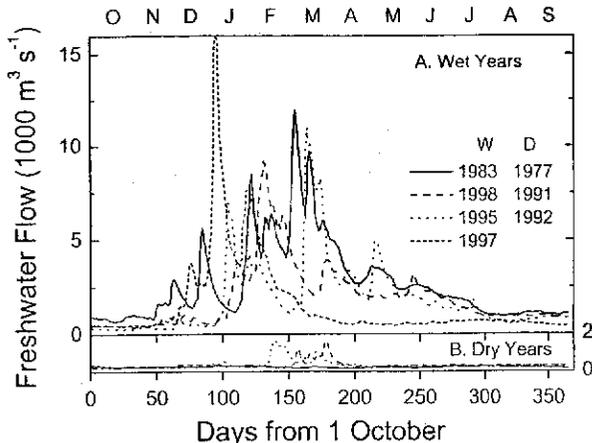


Fig. 2. Daily average freshwater flow entering the Sacramento-San Joaquin Delta (Inflow) calculated as the sum of gaged and estimated ungaged flows of rivers entering the Delta. A) three wettest years in the record (1956–2000) plus 1997, the year of the highest daily flow; B) three driest years on record on the same scale as A (right scale). Water years begin on October 1, near the end of the dry season.

ally exceeds flow in the San Joaquin River, with the result that the Sacramento River must provide the balance. This requires a net flow either southward or eastward through the Delta toward the export pumps, which is facilitated by the Delta Cross Channel (Fig. 1), a short, artificial canal with a pair of gates that can be opened to allow water to flow from the Sacramento River into the central Delta. These gates must often be open during dry periods to minimize saltwater intrusion into the southern Delta, but are closed during periods when juvenile salmonids are migrating down the Sacramento River, particularly in winter and spring.

The ratio of calculated inflow to estimated unimpaired flow for 1956–1994 shows that capture of runoff in reservoirs in the major rivers results in net storage and diversion of freshwater in spring and net release in late summer to early fall (Fig. 4a). Long-term trends in this ratio show an increasing trend toward more storage early in spring and more release in summer (Fig. 4b), presumably due to increasing demand and upstream storage capacity (Fig. 2 in Arthur et al. 1996). During wet winters, much of the inflow to reservoirs is essentially passed through the reservoirs to maintain capacity for flood control.

EFFECTS OF FRESHWATER FLOW

The effects of freshwater inflow on the physical, chemical, and biological conditions in an estuary are numerous and complex (Skreslet 1986; Drinkwater and Frank 1994). A simplified conceptual model shows some of the prominent effects of

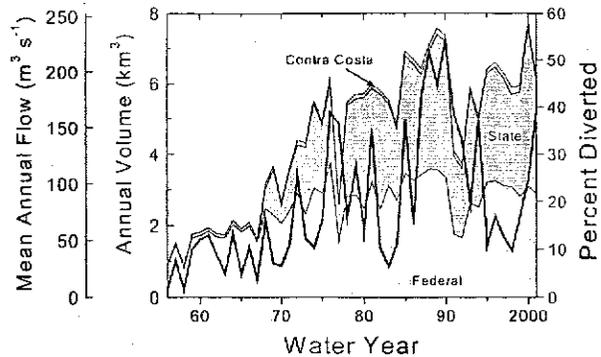


Fig. 3. Historical record of monthly export flow from major diversion facilities in the southern Sacramento-San Joaquin Delta. The heavy line gives the mean annual proportion of flow into the Delta that is diverted (right axis).

freshwater flow, using an increase in flow as an example (Fig. 5). In the discussion here, flow generally refers to inflow for events occurring in the Delta and Delta outflow for the remainder of the estuary; they are closely correlated. Numbers below refer to specific quantities in Fig. 5 which are ordered according to mechanisms discussed in Table 1.

Starting from the right side of the diagram, freshwater flow covaries with river stage and velocity. When river stage increases above a threshold, floodplains such as the Yolo Bypass are inundated (Figs. 1, 5, and 6a, #10). The proportion of inflow that is exported decreases as inflow increases (Fig. 6b, #9), so Delta outflow begins to approach inflow closely (Fig. 6c). The correlation between raw inflow and outflow values in Fig. 6c is 0.99, mainly because of the influence of flow values above $1,000 \text{ m}^3 \text{ s}^{-1}$, but also because inflow is adjusted to accommodate changes in export flow. An increase in river stage enhances the tidally-averaged water level gradient through the estuary, forcing a larger seaward residual or net flow at all points in the estuary, and compressing the salinity gradient (Fig. 6d). Residence time of water (Walters et al. 1985) and of conservative scalars decreases throughout the estuary as flow increases.

Increased inflow implies an increase in flux into the estuary of any scalar whose concentration decreases more slowly than $1/\text{flow}$ as flow increases (#1, 3, 6, 7, 8). In most estuaries, loadings of sediment, organic matter, and nutrients increase with increasing flow (e.g., Day et al. 1994). In the San Francisco Estuary, many material fluxes increase with increasing flow, including sediment (Fig. 7a), nutrients (nitrate plus nitrite in Fig. 7b, also phosphate and dissolved silica), chlorophyll (Fig. 7c), total organic carbon (Krone 1979; Schemel et al. 1996), and abundance of various zooplankton taxa

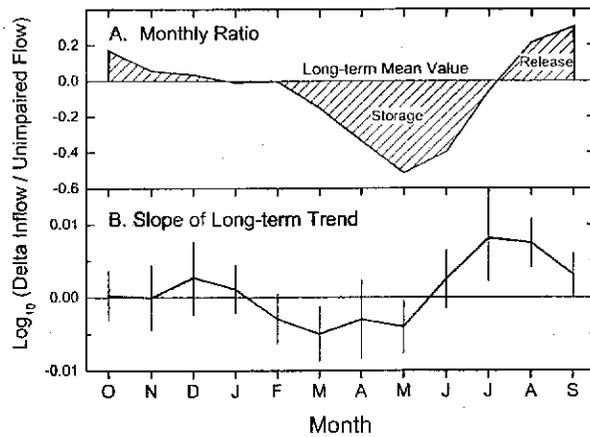


Fig. 4. Ratio of monthly total Delta inflow to unimpaired flow for water years 1956-1994. A) Mean log ratio by month, showing periods of storage (in natural or human-made contrivances) and release; B) Slope of the log ratio versus year with 95% C.I., showing how these ratios have changed over time.

including rotifers (Fig. 7d) and cladocerans (not shown). The increasing sediment load causes an increase in turbidity which can be seen throughout the estuary under high-flow conditions and can result in a low-density plume that is often clearly visible in the nearby coastal ocean (Largier 1996).

The landward density gradient opposes the seaward mean pressure gradient to determine the landward extent of the salt field, indexed in the San Francisco Estuary by X_2 , (Jassby et al. 1995). Vertical mixing, and therefore water depth and tidal velocities, are important in determining how readily the salt field moves (Festa and Hansen 1978; Geyer 1993; Monismith et al. 2002). The seaward limit of the salt field cannot move much beyond the mouth of the estuary because the sharp increase in cross-sectional area outside the mouth allows for a compensating increase in landward salt flux. The landward limit of the salt field varies as $Q^{-0.14}$ where Q is daily estimated net Delta outflow (Monismith et al. 2002). Apparently seaward compression of the salt field moves the steepening density gradient over areas of increasing depth, allowing for more frequent stratification which enhances the landward salt flux through gravitational circulation. The incidence of stratification and gravitational circulation, or other asymmetrical residual circulation, should increase with increasing flow partly because of compression of the density gradient and partly because of changes in depth of channels (Monismith et al. 1996, 2002, #2, 11). This theoretically-based covariation has not yet been confirmed by measurements. If it occurs, it provides a mechanism by which organisms or particles that remain near the bottom may be retained

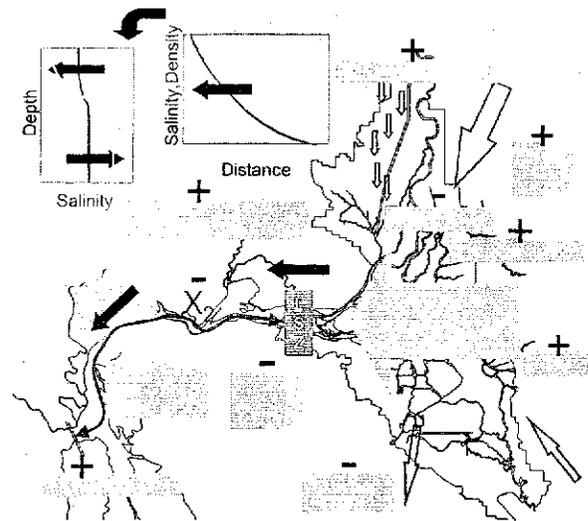


Fig. 5. Schematic diagram illustrating how fluxes into the estuary and physical attributes of the estuary change with increasing freshwater flow. Open arrow indicates direction of water flow, and filled arrows and plus and minus signs indicate direction of change with increasing flow. Numbers correspond to mechanisms listed in Table 1 and discussed in the text. 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.

more effectively, or move further or more rapidly into the estuary, at high flow than low.

In addition to changes in stratification and circulation patterns, a variety of changes in physical habitat accompany a seaward shift of the salt field. The area and volume of tidal and non-tidal freshwater habitat increases, particularly when floodplains are inundated (#10). The total area and volume of brackish to saline habitat must therefore decrease, but the area encompassed by two particular isohalines may increase or decrease because of the variable shape of the estuary. However, the mean distance between two isohalines, measured along the axis of the estuary, scales with X_2 (Monismith et al. 1996).

BIOTIC RESPONSES TO FLOW CONDITIONS

Estuarine biota may respond directly or indirectly to the diversion of water from the Delta, or to freshwater outflow. The diversion of a substantial amount of water from the tidal freshwater reach appears to be a peculiar feature of the San Francisco Estuary. During low-flow periods as much as 70% of the freshwater entering the estuary is subsequently exported (Fig. 6b), and although the daily export flow is only about 2-3% of the volume of the Delta, its cumulative effect could be substantial. The principal concern over ecological effects of the water diversion facilities is

TABLE 1. Summary of likely mechanisms for effects of flow on estuarine biota. Mechanisms are identified by type (i.e., whether bottom-up, direct, or indirect through other foodweb effects), and index to numbers in Fig. 5. Some mechanisms are broken into parts with references in the right-hand column indicating support for each part. References in bold are from the San Francisco Estuary, including figures in this paper. References in italics either refute or fail to support the mechanism indicated.

Type and Index	Mechanism	References
Bottom-up 1	Nutrient loading increases with flow. Stimulating primary production, Which is passed up the food web.	Riley 1937; Nixon et al. 1986; Fig. 6 <i>Ball and Arthur 1979; Cole and Cloern 1984, 1987;</i> Nixon et al. 1986; Malone et al. 1988; Boynton et al. 1982; Mallin et al. 1993; Rudnick et al. 1999; Fig. 8 Aleem 1972; Fig. 8
Bottom-up 2	Stratification increases with freshwater flow due to compression of the salinity gradient, Stimulating primary production, Which is passed up the food web.	Geyer 1993; Monismith et al. 1996, 2002 McCulloch et al. 1970; Cloern and Jassby 1994; Lucas et al. 1998 Fig. 8
Bottom-up 3	Loading of organic matter increases with flow, Stimulating bacterial production, Which is passed up the food web.	Smith and Hollibaugh 1993; Day et al. 1994; Howarth et al. 1996; Schemel et al. 1996; Kemp et al. 1997; Jassby and Cloern 2000 Hollibaugh and Wong 1996 Fig. 8
Bottom-up 4	Osmotic stress shifts benthic community from salt-tolerant to freshwater when flow is high, Resulting in suppression of predators or grazers.	Kaartvedt and Aksnes 1992; <i>Laprise and Dodson 1993</i> Nichols 1985; <i>Alpine and Cloern 1992</i> ; Wilber 1992; Livingston et al. 2000
Direct 5	High flow provides clearer cues to guide migration.	None
Indirect 6	Loading of sediment increases with increasing flow increasing turbidity, reducing rates of capture by visual predators, increasing survival of larvae and juveniles.	Krone 1979; Schemel et al. 1996 Breitburg 1988; Monteleone and Houde 1992; Gregory and Levings 1998
Direct or Indirect 7	Freshwater flow dilutes contaminants resulting in higher survival with high flow either directly or through food web. Available evidence suggests loading of contaminants increases with increasing rainfall and freshwater flow. High flow transports biota more rapidly to rearing areas, e.g., low-salinity zone.	<i>Luoma and Cain 1979; Kuivila and Foe 1995; Bergamaschi et al. 2001</i> Turner and Chadwick 1972
Direct 8	Where daily growth rate is higher or mortality is lower than elsewhere	Dodson et al. 1989; Moon and Dunstan 1990; Frenette et al. 1995; <i>Schoellhamer 1996, 2001</i> ; Wainwright et al. 1996; <i>Kimmerer et al. 1998</i> ; Sirois and Dodson 2000
Direct 9	Influence of export pumping decreases as the fraction of freshwater pumped decreases, or as habitat moves seaward away from pumps.	Turner and Chadwick 1972; Stevens et al. 1985; <i>Kimmerer et al. 2001</i>
Indirect 10	Physical area of, or access to, suitable spawning or rearing habitat increases with increasing flow or seaward X_2 .	Gammelsrød 1992; Sommer et al. 1997; Sklar and Browder 1998; <i>Kimmerer et al. 2001; Fig. 10</i>
Direct 11	Asymmetric residual (e.g., gravitational) circulation increases with flow, And interacts with vertical position to reduce seaward losses or increase landward movement to rearing areas.	Postuna and Kalle 1955; <i>Schoellhamer 2001; Monismith et al. 2002</i> Cronin and Forward 1979; Harden Jones et al. 1979; Christy and Morgan 1998; Kimmerer et al. 1998, 2002; Bennett et al. 2002

the entrainment of fish and other aquatic organisms into these facilities (Arthur et al. 1996; Brandes and McLain 2001), although there is also a belief that the net flow rates due to water exports alter the hydrodynamics of the Delta in as yet undefined ways (Brandes and McLain 2001). Screening facilities allow for many fish longer than ~38 mm to be salvaged and returned to the estuary, but considerable mortality of these fish is believed to occur, and smaller fish are not screened effectively (Brown et al. 1996).

Despite concern about the effects of these diversion facilities, and the likelihood that a substan-

tial fraction of some fish populations may be entrained there (Stevens et al. 1985), few studies have attempted to document population-level effects. Although striped bass are entrained in large numbers during larval and juvenile stages, the effect of this entrainment on recruitment to the adult population appears to be negligible (Kimmerer et al. 2001). Mark-recapture experiments with salmon smolts released in the Sacramento River revealed little effect of export pumping rates (Rice and Newman 1997). Export of water from the Delta appears to remove a substantial fraction of phytoplankton biomass daily, but this effect appears to

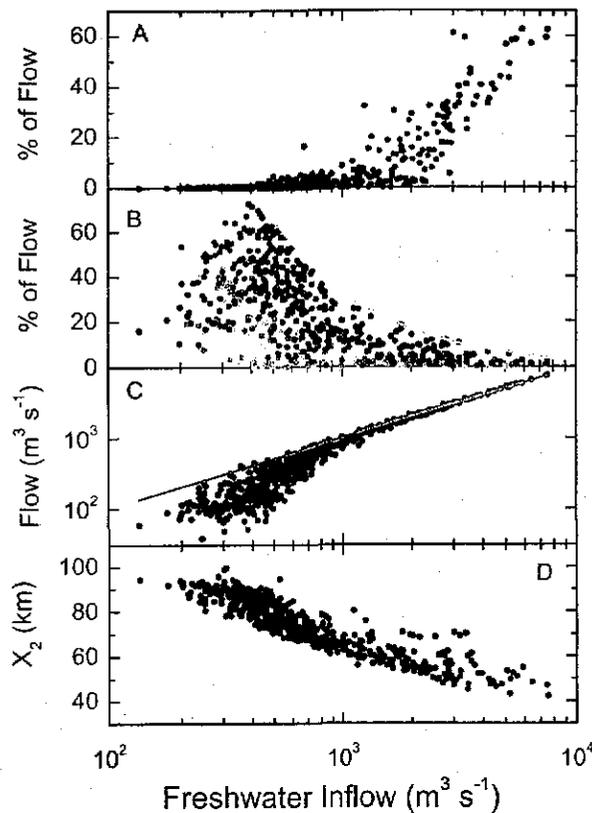


Fig. 6. Key variables that covary with inflow, monthly means: A) proportion of Sacramento River flow diverted into the Yolo Bypass; B) Proportion of inflow that is exported by the major diversion facilities in the south Delta with more recent points darker to account for the decade-scale change in export flow (Fig. 3) and a line indicating the maximum allowable export flow ($331 \text{ m}^3 \text{ s}^{-1}$); C) net Delta outflow with the 1:1 line, the difference being the sum of export flow and net consumption in the Delta; and D) X_2 , the distance up the axis of the estuary to where the tidally-averaged near-bottom salinity is 2.

be overwhelmed by interannual variability possibly due to benthic grazing (Jassby et al. 2002).

The smaller agricultural diversions are largely unscreened, but their cumulative impact on fishes of concern is unknown. Relatively few individuals of species of concern were collected in the only experimental studies of unscreened diversions to date (Cook and Buffaloe 1998; Nobriga and Matica 2000).

Several estuarine-dependent nekton populations in the San Francisco Estuary responded positively to interannual variability in freshwater outflow (Jassby et al. 1995; Kimmerer 2002, Fig. 8). Notable exceptions to this pattern were delta smelt, a threatened fish, and most organisms in lower trophic levels (Fig. 8). Relationships of abundance of copepods and mysids to flow changed after 1987, when the clam *Potamocorbula amurensis* became

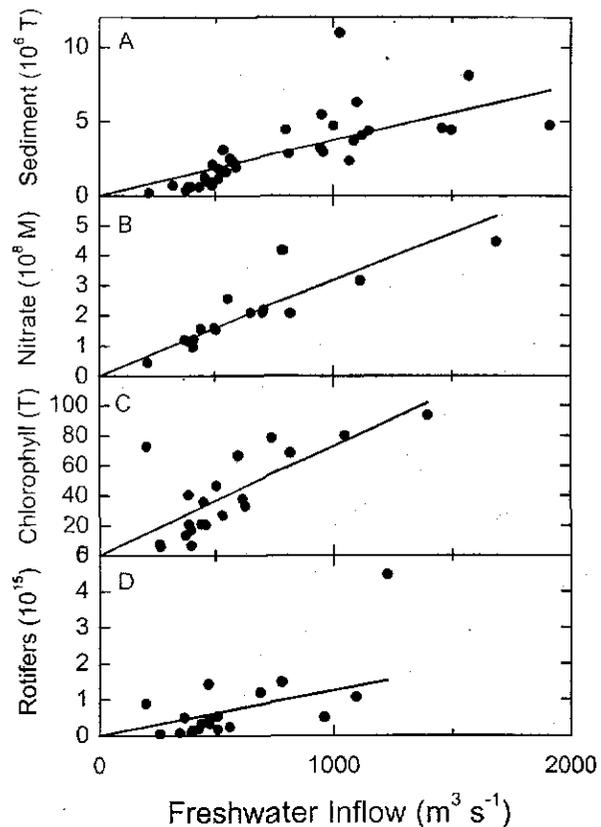


Fig. 7. Annual fluxes into the estuary from the Sacramento River as a function of flow. A) sediment; B) nitrate plus nitrite; C) chlorophyll; and D) rotifer numbers. Lines are from significant ($p < 0.01$) regressions except for rotifers, which is from a robust regression ($p < 0.01$) which gives points far from the line a lower weighting (Venables and Ripley 1997). Nutrient, chlorophyll, and rotifer data were for a station at Hood on the Sacramento River (river kilometer 139), while sediment data were either from Sacramento (Fig. 1, river kilometer 160) or Freeport (river kilometer 155).

abundant. This clam apparently had a substantial grazing impact on phytoplankton and reduced zooplankton abundance through both predation and competition (Alpine and Cloern 1992; Kimmerer et al. 1994; Kimmerer and Orsi 1996; Orsi and Mecum 1996).

A few fish species not shown in Fig. 8 have apparent positive responses to flow but the data are not suitable for the same model. White sturgeon have strong year-classes following years of exceptionally high flow (Kohlhorst et al. 1991). The number of adult salmon returning to the San Joaquin basin to spawn is strongly related to flow conditions when the salmon left the estuary (Speed 1993), and abundance of juvenile salmon migrating out of the Delta increases with increasing flow (Brandes and McLain 2001), but these effects probably occur in the rivers rather than the estu-

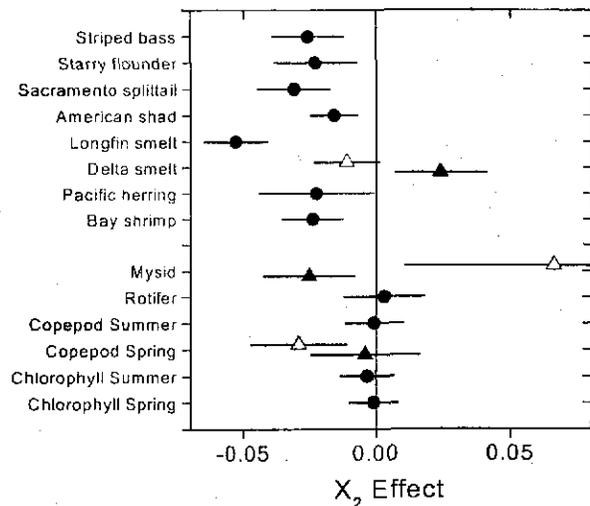


Fig. 8. Results of analyses of covariance or regressions of abundance or survival indices or estimates versus X_2 (Kimmerer 2002). Symbols indicate slopes and 95% confidence intervals; negative slopes indicate taxa whose abundance or survival is higher under high-flow than low-flow conditions. The upper 8 taxa are species of fish and bay shrimp, whose life histories encompass a variety of habitats; the bottom 6 are taxa from lower trophic levels in the low-salinity zone, including the rotifer *Synchaeta bicornis*, the copepod *Eurytemora affinis*, and the mysid *Neomysis mercedis* plus chlorophyll. Circles indicate variables for which slopes did not change in 1987-1988. Triangles indicate slopes that changed between the earlier (filled) and later (open symbols) period. The exception is Delta smelt, for which the breakpoint was 1981-1982. Data for striped bass and Pacific herring are egg-juvenile survival, and the remainder are abundance indices or estimates.

ary. High freshwater flow is associated with higher abundance of chinook salmon fry rearing in the Delta (Kjelson and Raquel 1981; Brandes and McLain 2001), but the contribution of these fish to the adult population, in relation to those that remain to rear in rivers, is unknown. Net flow conditions in the estuary have at most a small effect on survival of salmon smolts migrating seaward through the estuary (Rice and Newman 1997).

Classes of mechanisms that may contribute to the flow relationships in Fig. 8 are summarized in Table 1 with reference to numbers in Fig. 5. With the possible exception of entrainment into diversions, these mechanisms probably operate in other estuaries (Drinkwater and Frank 1994). Since the evidence that any of these mechanisms operate in the San Francisco Estuary is strong for only a few taxa, only a few examples are discussed here, for the purpose of illustrating some management implications.

The first 3 mechanisms in Table 1 presume bottom-up effects by which flow stimulates production of phytoplankton or bacteria, and this stimulation propagates through the food web. These mecha-

nisms appear to be important in many estuaries (e.g., Riley 1937; Malone et al. 1988; Mallin et al. 1993; Rudnick et al. 1999). Phytoplankton biomass was related to nutrient loading in a comparison among estuaries (Boynton et al. 1982). Bottom-up effects of flow on estuarine food webs, by which production in higher trophic levels was stimulated by flow through phytoplankton production, have been inferred for several estuaries (e.g., Alecm 1972; Nixon et al. 1986). These mechanisms, particularly #1, may not be very important in the San Francisco Estuary. First, available evidence does not support flow responses of lower trophic levels (Figs. 8 and 9). Stimulation of either phytoplankton or bacterial production, or simply loading of organic matter to the brackish estuary, can be passed to higher trophic levels only through an increase in intermediate steps such as rotifers, copepods, and mysids, which was not observed. Phytoplankton production is generally light limited in the northern San Francisco Estuary (Cole and Cloern 1984; Cloern 1987), and nutrient concentrations are at limiting levels only during strong blooms (Ball and Arthur 1979), meaning that increases in nutrient loading are unlikely to produce blooms. Turbidity in an estuary generally increases with increasing flow (Uncles et al. 1992) due to increased sediment loading (Schemel et al. 1996; Fig. 7a), reducing light penetration and primary production (Cole and Cloern 1984; Cloern 1987). In freshwater to brackish regions of the San Francisco Estuary, high flow is associated with low phytoplankton biomass, apparently because of reductions in residence time (Jassby and Cloern 2000).

According to mechanism 10, abundance increases because of an increase in physical habitat with increasing flow. Physical habitat is a useful concept for terrestrial or benthic organisms but mechanisms for space limitation are less clear for plankton or nekton. Habitat for some species could be defined by the overlap of favorable water quality characteristics such as salinity and temperature, favorable dynamic characteristics such as flow velocity, and favorable bathymetric regimes (Sklar and Browder 1998). If that is true the amount of suitable habitat having some suite of characteristics, and therefore abundance of a species that responds to those characteristics, may covary with flow.

In the San Francisco Estuary the area of freshwater habitat clearly increases with flow, particularly when floodplains are inundated (Fig. 6a). The resulting increase in habitat may benefit species that use floodplains when available. The area of spawning and rearing habitat for Sacramento splittail increases sharply as floodplains are inundated (Sommer et al. 1997). The total area and volume

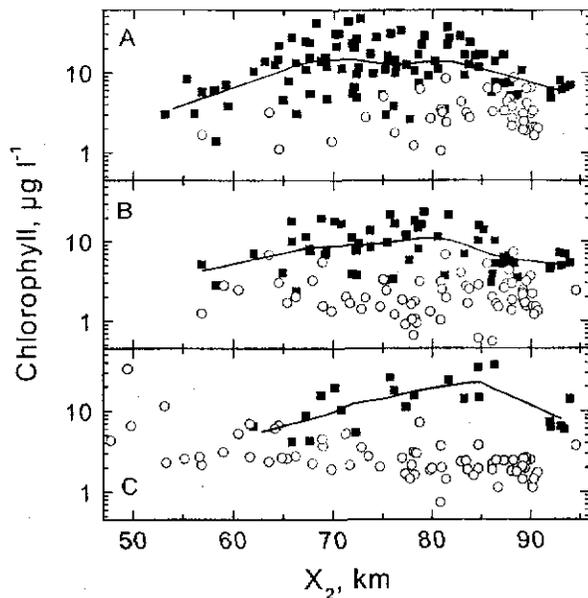


Fig. 9. Chlorophyll concentration versus X_2 from three independent sampling surveys. Data are monthly means for April through September of all samples taken in the low-salinity zone (salinity 0.5–6 psu). Filled symbols, data through 1987, open symbols, data after 1987. Lines are locally-weighted regressions fit to data from before 1987 (Venables and Ripley 1997). Data from A) Department of Water Resources for 1969–1993; B) Department of Fish and Game, 1976–1999; and C) U.S. Geological Survey, 1977–1980 and 1988–2000.

of habitat seaward of 2 psu must decrease as flow increases, but the area or volume of habitat in a selected salinity range could either increase or decrease. For example, the area of low-salinity habitat could increase when X_2 moves from the Delta into the broad shoals of Suisun Bay (Fig. 1). Available data from shoals are insufficient to delineate the distribution of salinity and other properties.

Distributions of young striped bass, which inhabit the low-salinity zone, are actually broader when X_2 is landward than when it is seaward, suggesting that the extent of habitat for this species does not increase with increasing flow (Kimmerer et al. 2001). Juvenile longfin smelt also inhabit most of the estuary seaward of about 2 psu salinity. Although they are found in the coastal ocean (Emmett et al. 1991), the abundance per tow of longfin smelt drops off at salinity above 30 psu (data from California Department of Fish and Game). Their in-bay habitat must be compressed as freshwater flow increases, and this compression can be seen in their distribution. The distance between 10th and 90th percentiles of their distribution along the axis of the estuary is strongly and positively related to X_2 (Fig. 10), suggesting that their habitat extends from about 2 psu salinity to the mouth of

the bay and decreases as X_2 moves seaward. Data for striped bass and longfin smelt both fail to support a mechanism by which habitat area increases with flow.

The circulation patterns of estuaries include a net seaward residual flow equal to river flow, and residence time of water in the estuary declines as flow increases (Walters et al. 1985). Passive scalars and neutrally- or positively-buoyant particles would also have a lower residence time with high flow. Residual circulation including gravitational flow (Postma and Kalle 1955) can cause retention of negatively-buoyant particles and organisms as in an estuarine turbidity maximum (ETM; Festa and Hansen 1978). Many organisms recruit to estuaries as larvae or juveniles using selective tidal stream transport (Cronin and Forward 1979; Harden Jones et al. 1979; Christy and Morgan 1998), which could be enhanced by landward net bottom currents. If the increase in residual circulation with increasing flow is large (Monismith et al. 2002) the more efficient retention or landward transport may result in higher survival or recruitment and therefore larger populations.

There is only indirect evidence to support the contribution of this mechanism to the observed flow effects. Landward net bottom currents are common in deeper channels (Conomos et al. 1970; Peterson et al. 1975). A typical ETM is not usually observed in the San Francisco Estuary but gravitational circulation cells are seen in deeper parts of the estuary where salinity is above about 2 (Schoellhamer 2001). Mesozooplankton and larval fish in the low-salinity zone migrated in synchrony with tides much of the time (Kimmerer et al. 1998, 2002; Bennett et al. 2002). Macrozooplankton migrated under low-flow conditions but remained near the bottom at intermediate freshwater flow, possibly because gravitational circulation was sufficient for position maintenance (Kimmerer et al. 2002). The bay shrimp *Crangon franciscorum*, which recruits from the ocean (Emmett et al. 1991), remained near the bottom where it would be subjected to landward movement in deeper channels (Kimmerer et al. 2002).

The mechanisms underlying effects of freshwater flow on higher trophic levels are uncertain, but probably differ among species. This implies that the location and timing of freshwater flow effects differ among species as well. The effects of diversions on fish and other aquatic species are not well documented.

MANAGEMENT RESPONSES

To manage an ecosystem is to manage the activities of people that affect the ecosystem. In many estuaries and their watersheds management is

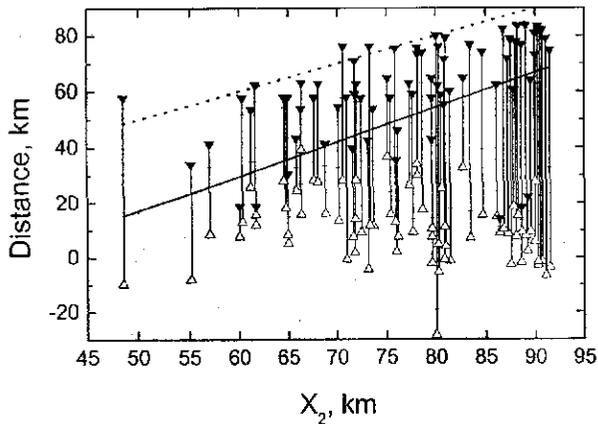


Fig. 10. Distribution patterns of age-0 longfin smelt during June through December. Each pair of symbols, connected by a vertical line, shows the 10th and 90th percentiles of the position of the population along the axis of the estuary from a single survey of the San Francisco Bay Study (Armor and Herrgesell 1985). The dotted line is the 1:1 line. The solid line indicates the relationship of X_2 to the difference between the 10th and 90th percentiles using a robust regression to allow for apparent outliers (90th-10th percentiles = $-45 + X_2 \times 1.2 \pm 0.35$, 95% confidence limits).

aimed at conceptually straightforward goals such as reducing loading of anthropogenic nutrients (Jaworski 1981) or contaminants, fishery management (Richards and Rago 1999), or enhancing seagrass or other valued habitat (Fourqurean and Robblee 1999). Management and restoration goals for the San Francisco Estuary's ecosystem are more varied than these, and are intertwined with other, potentially conflicting, goals such as improving reliability and quality of water supply for human uses. A substantial effort is underway toward resolving these conflicts and achieving these goals. Here I consider only those activities intended for environmental protection that influence estuarine freshwater flow patterns either directly or indirectly.

Current management actions using flow for environmental protection in the estuary include standards for salinity and therefore net Delta outflow, restrictions on export flow rates, and the installation and removal of barriers in Delta channels (Table 2). The principal goal of most of these actions is the protection of species of fish listed under endangered-species legislation, although the salinity standard is designed for protection of the estuarine ecosystem as a whole, including listed species. Installing barriers at various locations in the Delta can require additional releases of freshwater from reservoirs to counteract intrusion of salt, but barriers are not considered further here. Actions taken using flow have a basis in analytical results, in the case of the salinity standard, and in logic in the case of export restrictions, but in neither case have

analyses been made of the effectiveness of these actions in supporting biological populations or the estuarine ecosystem.

The centerpiece of current flow management is the X_2 standard, using salinity to maintain flow with the goal of broad ecosystem protection. Originally suggested by Williams (1989), the standard as implemented requires salinity at a control point at 81 km not to exceed 2 psu continuously, and at two control points (64 and 75 km) not to exceed 2 psu for a set number of days during January-June each year. The number of days when salinity must be ≤ 2 psu at each control point is determined using a sliding scale that depends on precipitation in the watershed and the amount of water stored in the reservoirs. Water for the environment is allocated on the same basis by which the federal and state water managers meet contractual obligations to supply water for human use. The actual standard incorporates operational flexibility to account for the lag between changes in flow and response of the salt field.

The salinity standard is a rare example of ecosystem-level management, and its design is consistent with the response of the ecosystem to flow. The amount of water required to move the salt field seaward can be high, particularly at high initial flow, because of the flat power-law dependence of X_2 on flow. The standard is in effect from February to June, a long period made necessary by uncertainty about how and when flow influences biological populations. The cost of water to move X_2 seaward a selected amount increases sharply as the initial position moves seaward (Fig. 11). Note that the examples in this figure are generally less than the tidal excursion (5-25 km) and small relative to the historical range of X_2 (Fig. 6d).

The high cost of the water to move the salt field raises the question: Can these actions be made more effective with the same quantity of water, or equally effective with less water? The answer to these questions depends on the mechanisms of response and the biology of the species being managed, which determine the location, timing, and duration of the flow effect (Fig. 5). The further seaward the locus of a flow effect, the less controllable the effect is likely to be, and the greater the lag between the initiation of a change in flow and the ecosystem response. The greatest benefits of flow enhancement may occur during different seasons, and for different durations, for each species. Revising the salinity standards to target individual species more effectively would require resolving conflicts among species that need not be resolved under the current management scheme.

Even for a single species the timing and duration of flow-based management should coincide with

TABLE 2. Summary of ecosystem management or restoration actions taken in the San Francisco Estuary or watershed using freshwater flow.

Action	Started	Description
Flow standard	1978	Flow was regulated to support production of young striped bass (supplanted in 1994).
Salinity standard (X_2 standard)	1994	Freshwater flow is regulated so that salinity at 3 control points is not over 2 psu for a number of days depending on precipitation, during February–June.
Export: Inflow Ratio (E:1 Ratio)	1994	The ratio of total export from water diversions in the Delta to total inflow may not exceed 35% during February–June or 65% the rest of the year.
Environmental Water (GVPIA)	1992	Up to 800,000 acre-feet (988 km ³) or yield from the federal Central Valley Project is to be used for environmental purposes, mainly in the watershed.
Environmental Water (EWA)	2001	Up to \$50M is to be spent to purchase water on the open market for environmental purposes as an alternative to export restrictions necessitated by take of endangered fish at export facilities; also provides for reliability of water supply.
Environmental Water (EWP)	2003?	Water is to be purchased on the open market for environmental purposes and used predominantly in the watershed.
Flow barriers including Delta Cross Channel (DDC) gates	1996	DDC gates are closed to keep migrating juvenile salmonids in the lower Sacramento River; gates must be opened at times to limit salt penetration into the south Delta to protect drinking water quality. Although this does not influence flow directly, it can have indirect effects because when the gates are closed, export flows may be restricted to prevent salt penetration. Other temporary barriers have been installed in the southern Delta to keep migrating juvenile salmonids in the lower San Joaquin River away from the export pumping facilities.

the mechanism by which the species responds to flow. This implies knowledge of the specific mechanism. A mechanism involving an increase in brackish habitat during the rearing season (mechanism 10, Table 1) may require a long period of increased flow, and opportunities for efficiency will be limited; a mechanism involving tidal stream transport and gravitational circulation in the lower estuary (mechanism 11) may occur over a relatively brief period of larval or juvenile recruitment into the estuary.

As a more specific example, Sacramento splittail clearly respond to increasing flow through inundation of floodplains during early spring (Sommer et al. 1997). This effect may occur through access to spawning habitat, in which case the period of effectiveness would be fairly brief, or rearing hab-

itat, which would require a longer period of inundation. Distinguishing between these mechanisms and determining their importance to overall abundance of the species are important research objectives that may require experimental manipulation of the floodplain habitat (Sommer et al. 2002) or flows in the floodplain.

Among the restoration projects to be considered by the CALFED Bay-Delta Program is the construction of various alternative methods for moving water from the source through the Sacramento River and to users south of the Delta. Because of previous failures to garner public approval for such projects (Arthur et al. 1996), there is considerable public sensitivity to the likely environmental effects of large-scale alterations to the water conveyance facilities. The flow relationships that form the basis of the current salinity standard (Fig. 8) provide no guidance about how they may respond to such a major change in configuration of the estuary. Predicting these responses is contingent on understanding the mechanisms underlying the flow relationships. The wide natural range of flow in the estuary (Fig. 6) provides sufficient contrast among years to allow for insights into at least some of these mechanisms. The mechanisms should be amenable to a research approach including modeling and specific field studies, layered on the extensive monitoring programs already in place; some of this research has already begun (e.g., Benner et al. 2002; Kimmerer et al. 2002).

In contrast to the salinity standard, which is based on clear relationships to population parameters, restrictions on export flow are based mainly on observations that large numbers of fish are entrained in export pumping facilities (Brown et al.

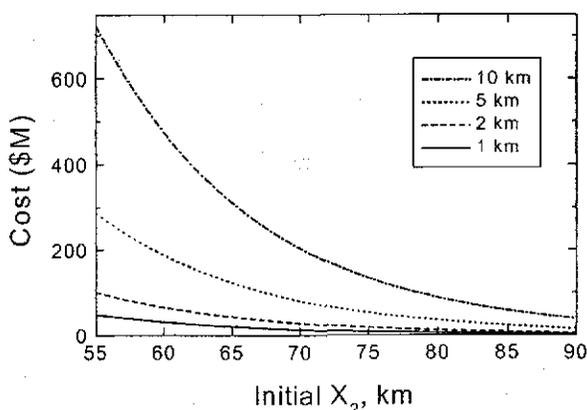


Fig. 11. Estimated cost of moving X_2 seaward by selected amounts, starting from an assumed initial position (x axis). Estimates use an assumed water cost of $\$0.10 \text{ m}^{-3}$, which is intermediate among recent market costs for water.

1996), and equivocal results of mark-recapture experiments using hatchery-reared juvenile salmon (Rice and Newman 1997; Brandes and McLain 2001). Current limitations on export flows at the major diversion facilities, particularly in springtime, were prompted mainly by concerns over threatened and endangered species of fish. The principal limit takes the form of a maximum ratio of export flow to inflow into the Delta. This limit was established on the basis of logic rather than data, since there is little clear evidence of effects of export flows on abundance or survival of species resident in or migrating through the Delta (Rice and Newman 1997; Kimmerer et al. 2001). The observation of large numbers of fish being entrained provided "credible evidence" (Walters and Holling 1990, p. 2067) supporting these actions, but for at least some species this evidence may be misleading.

I do not suggest that the lack of evidence of export effects should be construed as evidence of no effect. Much of the difficulty with determining effects of export pumping is the low abundance of the species of greatest concern, resulting in low signal-to-noise ratio in the analyses and poor constraints on statistical estimates of population parameters. Monitoring is already intense, particularly in the Delta, with expenditures of several million dollars annually. There is little prospect that increased monitoring will substantially improve the estimates of export effects. Experimental manipulations, with export pumping alternated between high and low levels, may be the only way that these effects can be teased out of the noisy data.

Three programs are now in place to acquire water to be used for environmental purposes (Table 2). All three can use this water to improve conditions in the estuary. Environmental water was used in spring 2001 to curtail export flow when juveniles of endangered winter-run salmon were migrating through the Delta. The population-level impacts of these actions appear to be small, raising questions about the cost-benefit ratio of these actions compared with other uses of environmental water. Critical assumptions used to justify these actions have not been tested, in spite of the high cost of the water used for this purpose (Table 2). These programs can purchase only a small fraction of the water needed for a substantial change in outflow and X_2 (Fig. 11), so use of this water would be most effective either in the Delta or upstream.

The management actions that manipulate flow conditions in the estuary can be seen as an uncontrolled, unreplicated experiment (Walters 1986; Walters and Holling 1990). Except for clear evidence of effects of outflow on the estuarine ecosystem (Fig. 8), support for other flow-related ac-

tions in the estuary is weak. The high cost of these actions, and the opportunity cost associated with failure to take alternative actions that could be more effective, indicate a need for alternative approaches to this problem. Using environmental water in an experimental context could yield valuable insights into the effects of export pumping (as separate from the effects of outflow).

The management of freshwater flow in the San Francisco Estuary has proceeded under assumptions about the frequency of droughts and the seasonal timing of runoff. These assumptions may not hold in a regime of climate change, in which one likely scenario may be earlier snowmelt and runoff (Dettinger and Cayan 1995). This would limit the capability of the water management system to retain runoff because of the need to anticipate flood conditions in winter and store water in spring (Fig. 4). Together with projected increases in population and therefore demand, this foretells a decreasing supply of water during spring and summer. This situation will place greater emphasis on accurate analyses of the effects of freshwater flow and diversions on the estuarine ecosystem, and on the efficiency of measures for environmental protection using freshwater.

Conclusions

Considerable resources, both money and water, are being used to establish flow conditions in the estuary that are believed to benefit the estuarine ecosystem and particularly threatened and endangered species of fish. The estuarine ecosystem responds to increased flow with increased abundance of some species, and the current salinity standard was designed to address that response. The current state of knowledge about flow effects does not provide adequate support to decision making. The salinity standard is a crude tool that could possibly be made more effective. Major changes in configuration of the Delta or regional climate could result in unanticipated changes in flow response of the estuarine ecosystem. Reductions in export flow are inadequately supported by evidence, and there is little understanding of population-level effects of entrainment in export pumping facilities. The effectiveness of export reductions using environmental water has not been put in a population-level context or compared with alternative actions in the watersheds. All of these problems are shortfalls of knowledge that can be addressed through a program of research coupled with experimental manipulation of some aspects of freshwater flow.

ACKNOWLEDGMENTS

Funding for this study was provided by the CALFED Bay-Delta Program. The ideas in this paper were developed over the years

in discussions with members of the Estuarine Ecology Team of the Interagency Ecological Program for the San Francisco Estuary, and other colleagues, particularly Alan Jassby. I thank Randy Brown for helpful discussions and comments on the manuscript, and Meryll Alber and Paul Montagna for organizing the Flows session at the 2001 Estuarine Research Federation meeting.

LITERATURE CITED

- ALEEM, A. A. 1972. Effect of river outflow management on marine life. *Marine Biology* 15:200-208.
- ALPINE, A. E. AND J. E. CLOERN. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37:946-955.
- ARMOR, C. AND P. L. HERRGSELL. 1985. Distribution and abundance of fishes in the San Francisco Bay estuary between 1980 and 1982. *Hydrobiologia* 129:211-227.
- ARTHUR, J. F., M. D. BALL, AND S. Y. BAUGHMAN. 1996. Summary of federal and state water project environmental impacts in the San Francisco Bay-Delta estuary, California, p. 445-495. In J. T. Hollibaugh (ed.), *San Francisco Bay: The Ecosystem*. AAAS, San Francisco, California.
- BALL, M. D. AND J. F. ARTHUR. 1979. Planktonic chlorophyll dynamics in the northern San Francisco Bay and Delta, p. 265-285. In T. J. Conomos (ed.), *San Francisco Bay: The Urbanized Estuary*. Pacific Division, American Association for the Advancement of Science, San Francisco, California.
- BENNETT, W. A., W. J. KIMMERER, AND J. R. BURAU. 2002. Plasticity in vertical migration by native and exotic fishes in a dynamic estuarine low-salinity zone. *Limnology and Oceanography* 47:1496-1507.
- BERGAMASCHI, B. A., K. M. KUIVILA, AND M. S. FRAM. 2001. Pesticides associated with suspended sediments entering San Francisco Bay following the first major storm of Water Year 1996. *Estuaries* 24:368-380.
- BOYNTON, W. R., W. M. KEMP, AND C. W. KEEFE. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton, p. 69-90. In V. S. Kennedy (ed.), *Estuarine Comparisons*. Academic Press, New York.
- BRANDES, P. L. AND J. S. MCLAIN. 2001. Juvenile chinook salmon abundance, distribution, and survival in the Sacramento-San Joaquin estuary, p. 39-136. In R. L. Brown (ed.), *Fish Bulletin 179: Contributions to the Biology of Central Valley Salmonids*, Volume 2. California Department of Fish and Game, Sacramento, California.
- BREITBURG, D. L. 1988. Effects of turbidity on prey consumption by striped bass larvae. *Transactions of the American Fisheries Society* 117:72-77.
- BROWN, R., S. GREENE, P. COULSTON, AND S. BARROW. 1996. An evaluation of the effectiveness of fish salvage operations at the intake to the California Aqueduct, 1979-1993, p. 497-518. In J. T. Hollibaugh (ed.), *San Francisco Bay: The Ecosystem*. AAAS, San Francisco, California.
- CHRISTY, J. H. AND S. G. MORGAN. 1998. Estuarine immigration by crab postlarvae: Mechanisms, reliability and adaptive significance. *Marine Ecology Progress Series* 174:51-65.
- CLOERN, J. E. 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. *Continental Shelf Research* 7:1367-1381.
- CLOERN, J. E., B. E. COLE, R. L. J. WONG, AND A. E. ALPINE. 1985. Temporal dynamics of estuarine phytoplankton: A case study of San Francisco Bay. *Hydrobiologia* 129:153-176.
- CLOERN, J. E. AND A. D. JASSBY. 1994. Year-to-year fluctuation in the spring phytoplankton bloom in South San Francisco Bay: An example of ecological variability at the land-sea interface, p. 139-149. In J. H. Steele, T. M. Powell, and S. Levin (eds.), *Ecological Time Series*. Chapman Hall, London, U.K.
- CLOERN, J. E. AND F. H. NICHOLS. 1985. Temporal Dynamics of an Estuary: San Francisco Bay. Junk, Dordrecht, The Netherlands.
- COLE, B. E. AND J. E. CLOERN. 1984. Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. *Marine Ecology Progress Series* 17:15-24.
- COLE, B. E. AND J. E. CLOERN. 1987. An empirical model for estimating phytoplankton productivity in estuaries. *Marine Ecology Progress Series* 36:299-305.
- CONOMOS, T. J. 1979. San Francisco Bay: The Urbanized Estuary. Pacific Division, American Association for the Advancement of Science, San Francisco, California.
- CONOMOS, T. J., D. H. PETERSON, P. R. CARLSON, AND D. S. MCCULLOCH. 1970. Movement of seabed drifters in the San Francisco Bay estuary and the adjacent Pacific Ocean: A preliminary report. Circular 637-B. U.S. Geological Survey, Menlo Park, California.
- COOK, L. AND L. D. BUFFALO. 1998. Delta agricultural diversion evaluation summary report, 1993-1995. Technical Report 61. Interagency Ecological Program for the San Francisco Bay/Delta estuary. Sacramento, California.
- CRONIN, T. W. AND R. B. FORWARD, JR. 1979. Tidal vertical migration: An endogenous rhythm in estuarine crab larvae. *Science* 205:1020-1022.
- DAY, JR., J. W., C. J. MADDEN, R. R. TWILLEY, R. F. SHAW, B. A. MCKEE, M. J. DAGG, D. L. CHILDERS, R. C. RAYNIE, AND L. J. ROUSE. 1994. The influence of Atchafalaya River discharge on Fourleague Bay, Louisiana (USA), p. 151-160. In K. R. Dyer and R. J. Orth (eds.), *Changes in Fluxes in Estuaries: Implications from Science to Management*. Olsen & Olsen, Fredensborg, Denmark.
- DEPARTMENT OF WATER RESOURCES (DWR). 1994. California Central Valley Unimpaired Flow Data. California Department of Water Resources, Sacramento, California.
- DETTINGER, M. D. AND D. R. CAYAN. 1995. Large-scale atmospheric forcing of recent trends toward early snowmelt runoff in California. *Journal of Climate* 8:606-623.
- DODSON, J. J., J.-C. DAUVIN, R. INGRAM, AND B. D'ANGLEJAN. 1989. Abundance of larval rainbow smelt (*Osmerus mordax*) in relation to the maximum turbidity zone and associated macroplanktonic fauna of the middle St. Lawrence estuary. *Estuaries* 12:66-81.
- DRINKWATER, K. F. AND K. T. FRANK. 1994. Effects of river regulation and diversion on marine fish and invertebrates. *Aquatic Conservation: Freshwater and Marine Ecosystems* 4:135-151.
- DYNESIUS, M. AND C. NILSSON. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266:753-762.
- EMMETT, R. L., S. L. STONE, S. A. HINTON, AND M. E. MONACO. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Volume II: Species life history summaries. ELMR Report No. 8. NOAA/NOS Strategic Environmental Assessments Division, Rockville, Maryland.
- FESTA, J. F. AND D. V. HANSEN. 1978. Turbidity maxima in partially mixed estuaries: A two-dimensional numerical model. *Estuarine and Coastal Marine Science* 7:347-359.
- FOURQUREAN, J. W. AND M. B. ROBBLEE. 1999. Florida Bay: A history of recent ecological changes. *Estuaries* 22:345-357.
- FOX, J. P., T. R. MORGAN, AND W. J. MILLER. 1990. Trends in freshwater inflow to San Francisco Bay from the Sacramento-San Joaquin Delta. *Water Resources Bulletin* 26:1-16.
- FRENETTE, J. J., W. F. VINCENT, J. J. DODSON, AND C. LOVEJOY. 1995. Size-dependent variations in phytoplankton and protozoan community structure across the St. Lawrence River transition region. *Marine Ecology Progress Series* 120:99-110.
- GAMMELSRØD, T. 1992. Variation in shrimp abundance on the Sofala Bank, Mozambique, and its relation to the Zambezi River runoff. *Estuarine, Coastal and Shelf Science* 35:91-103.
- GEYER, W. R. 1993. The importance of suppression of turbu-

- lence by stratification on the estuarine turbidity maximum. *Estuaries* 16:113-125.
- GREGORY, R. S. AND C. D. LEVINGS. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. *Transactions of the American Fisheries Society* 127:275-285.
- HARDEN JONES, F. R., G. P. ARNOLD, M. GREER WALKER, AND P. SCHOLLS. 1979. Selective tidal stream transport and the migration of plaice (*Pleuronectes platessa* L.) in the southern North Sea. *Journal du Conseil internationale pour l'Exploration de la Mer* 38:331-337.
- HERBOLD, B., A. D. JASSBY, AND P. B. MOYLE. 1992. Status and trends report on aquatic resources in the San Francisco estuary. San Francisco Estuary Project. U.S. Environmental Protection Agency, Oakland, California.
- HERREN, J. R. AND S. S. KAWASAKI. 2001. Inventory of water diversions in four geographic areas in California's Central Valley, p. 343-355. In R. L. Brown (ed.), *Fish Bulletin 179: Contributions to the Biology of Central Valley Salmonids*, Volume 2. California Department of Fish and Game, Sacramento, California.
- HOLLIBAUGH, J. T. 1996. San Francisco Bay: The Ecosystem. Further Investigations into the Natural History of San Francisco Bay and Delta with Reference to the Influence of Man. American Association for the Advancement of Science, San Francisco, California.
- HOLLIBAUGH, J. T. AND P. S. WONG. 1996. Distribution and activity of bacterioplankton in San Francisco Bay, p. 263-288. In J. T. Hollibaugh (ed.), *San Francisco Bay: The Ecosystem*. AAAS, San Francisco, California.
- HOWARTH, R. W., R. SCHNEIDER, AND D. SWANEY. 1996. Metabolism and organic carbon fluxes in the tidal freshwater Hudson River. *Estuaries* 19:848-865.
- JASSBY, A. D. AND J. E. CLOERN. 2000. Organic matter sources and rehabilitation of the Sacramento-San Joaquin Delta (California, USA). *Aquatic Conservation: Marine and Freshwater Ecosystems* 10:323-352.
- JASSBY, A. D., J. E. CLOERN, AND B. E. COLE. 2002. Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal estuary. *Limnology and Oceanography* 47:698-712.
- JASSBY, A. D., W. J. KIMMERER, S. G. MONISMITH, C. ARMOR, J. E. CLOERN, T. M. POWELL, J. R. SCHUBEL, AND T. J. VENDLINSKI. 1995. Isohaline position as a habitat indicator for estuarine populations. *Ecological Applications* 5:272-289.
- JAWORSKI, N. A. 1981. Sources of nutrients and the scale of eutrophication problems in estuaries, p. 83-110. In B. J. Neilson and L. E. Cronin (eds.), *Estuaries and Nutrients*. Humana, Clifton, New Jersey.
- KAARTVEDT, S. AND D. L. ARSNES. 1992. Does freshwater discharge cause mortality of fjord-living zooplankton. *Estuarine, Coastal and Shelf Science* 34:305-313.
- KEMP, W. M., E. M. SMITH, M. MARVIN-DIPASQUALE, AND W. R. BOYNTON. 1997. Organic carbon balance and net ecosystem metabolism in Chesapeake Bay. *Marine Ecology Progress Series* 150:229-248.
- KIMMERER, W. J. 2002. Effects of freshwater flow on abundance of estuarine organisms: Physical effects or trophic linkages? *Marine Ecology Progress Series* 243:39-55.
- KIMMERER, W. J., W. A. BENNETT, AND J. R. BURAU. 2002. Persistence of tidally-oriented vertical migration by zooplankton in a temperate estuary. *Estuaries* 25:359-371.
- KIMMERER, W. J., J. R. BURAU, AND W. A. BENNETT. 1998. Tidally-oriented vertical migration and position maintenance of zooplankton in a temperate estuary. *Limnology and Oceanography* 43:1697-1709.
- KIMMERER, W. J., J. H. COWAN, JR., L. W. MILLER, AND K. A. ROSE. 2000. Analysis of an estuarine striped bass population: Influence of density-dependent mortality between metamorphosis and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 57:478-486.
- KIMMERER, W. J., J. H. COWAN, L. W. MILLER, AND K. A. ROSE. 2001. Analysis of an estuarine striped bass population: Effects of environmental conditions during early life. *Estuaries* 24:556-574.
- KIMMERER, W. J., E. GARTSIDE, AND J. J. ORSI. 1994. Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. *Marine Ecology Progress Series* 113:81-93.
- KIMMERER, W. J. AND J. J. ORSI. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987, p. 403-424. In J. T. Hollibaugh (ed.), *San Francisco Bay: The Ecosystem*. AAAS, San Francisco, California.
- KIMMERER, W. J. AND J. R. SCHUBEL. 1994. Managing freshwater flows into San Francisco Bay using a salinity standard: Results of a workshop, p. 411-416. In K. R. Dyer and R. J. Orth (eds.), *Changes in Fluxes in Estuaries: Implications from Science to Management*. Olsen and Olsen, Fredensborg, Denmark.
- KJELSON, M. A. AND P. F. RAQUEL. 1981. The life history of fall run juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin estuary of California. *Estuaries* 4:285.
- KOHLHORST, D. W., L. W. BOYTFORD, J. S. BRENNAN, AND G. M. CHILLET. 1991. Aspects of the structure and dynamics of an exploited central California population of white sturgeon (*Acipenser transmontanus*), p. 277-293. In P. Williot (ed.), *Acipenser*. CEMAGREF Publ., Bordeaux, France.
- KRONE, R. B. 1979. Sedimentation in the San Francisco Bay system, p. 85-95. In T. J. Conomos (ed.), *San Francisco Bay: The Urbanized Estuary*. Pacific Division, American Association for the Advancement of Science, San Francisco, California.
- KUUVILA, K. M. AND C. G. FOE. 1995. Concentrations, transport and biological effects of dormant spray pesticides in the San Francisco estuary, California. *Environmental Toxicology and Chemistry* 14:1141-1150.
- LAPRISE, R. AND J. J. DOBSON. 1993. Nature of environmental variability experienced by benthic and pelagic animals in the St. Lawrence estuary, Canada. *Marine Ecology Progress Series* 94:129-139.
- LARGIER, J. L. 1996. Hydrodynamic exchange between San Francisco Bay and the ocean: The role of ocean circulation and stratification, p. 69-104. In J. T. Hollibaugh (ed.), *San Francisco Bay: The Ecosystem*. AAAS, San Francisco, California.
- LEHMAN, P. W. 2000. Phytoplankton biomass, cell diameter, and species composition in the low salinity zone of Northern San Francisco Bay estuary. *Estuaries* 23:216-230.
- LIVINGSTON, R. J., F. G. LEWIS, G. C. WOODSUM, X. NIU, B. GALPERIN, W. HUANG, J. D. CHRISTENSEN, M. E. MONACO, T. A. BATTISTA, C. J. KLEIN, R. L. HOWELL, AND G. L. RAY. 2000. Modelling oyster population response to variation in freshwater input. *Estuarine, Coastal and Shelf Science* 50:655-672.
- LONGLEY, W. L. 1994. Freshwater inflows to Texas bays and estuaries: Ecological relationships and methods for determination of needs. Texas Water Development Board, Austin, Texas.
- LUCAS, L. V., J. E. CLOERN, J. R. KOSEFF, S. G. MONISMITH, AND J. K. THOMPSON. 1998. Does the Sverdrup critical depth model explain bloom dynamics in estuaries? *Journal of Marine Research* 56:375-415.
- LUOMA, S. N. AND D. J. CAIN. 1979. Fluctuations of copper, zinc, and silver in tellinid clams as related to freshwater discharge—south San Francisco Bay, p. 231-246. In T. J. Conomos (ed.), *San Francisco Bay: The Urbanized Estuary*. Pacific Division, American Association for the Advancement of Science, San Francisco, California.
- MALIN, M. A., H. W. PAERI, J. RUDEK, AND P. W. BATES. 1993. Regulation of estuarine primary production by watershed rainfall and river flow. *Marine Ecology Progress Series* 93:199-203.
- MALONE, T. C., L. H. CROCKER, S. E. PIKE, AND B. W. WENDLER.

1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. *Marine Ecology Progress Series* 48:235-249.
- MCCULLOCH, D. S., D. H. PETERSON, P. R. CARLSON, AND T. J. CONOMOS. 1970. Some effects of freshwater inflow on the flushing of south San Francisco Bay: A preliminary report. U.S. Geological Survey Circular 637-A. U.S. Geological Survey, Menlo Park, California.
- MCIVOR, C. C., J. A. LEY, AND R. D. BJORK. 1994. Changes in freshwater inflow from the Everglades to Florida Bay including effects on biota and biotic processes: A review, p. 117-146. In S. Davis and J. Ogden (eds.), *Everglades: The Ecosystem and Its Restoration*. St. Lucie Press, Boca Raton, Florida.
- MICKLIN, P. P. 1988. Desiccation of the Aral Sea: A water management disaster in the Soviet Union. *Science* 241:1170-1176.
- MONISMITH, S. G., J. R. BURAU, AND M. STACEY. 1996. Stratification dynamics and gravitational circulation in northern San Francisco Bay, p. 123-153. In J. T. Hollibaugh (ed.), *San Francisco Bay: The Ecosystem*. AAAS, San Francisco, California.
- MONISMITH, S. G., W. J. KIMMERER, J. R. BURAU, AND M. T. STACEY. 2002. Structure and flow-induced variability of the subtidal salinity field in northern San Francisco Bay. *Journal of Physical Oceanography* 32:3003-3019.
- MONTELLONE, D. M. AND E. D. HOUBE. 1992. Vulnerability of striped bass *Morone saxatilis* Waldbaum eggs and larvae to predation by juvenile white perch *Morone americana* Gmelin. *Journal of Experimental Marine Biology and Ecology* 158:93-104.
- MOON, C. AND W. M. DUNSTAN. 1990. Hydrodynamic trapping in the formation of the chlorophyll- α peak in turbid, very low salinity water of estuaries. *Journal of Plankton Research* 12:323-336.
- MOYLE, P. B. 2002. *Inland Fishes of California*, 2nd edition. University of California Press, Berkeley, California.
- NICHOLS, F. H. 1985. Increased benthic grazing: An alternative explanation for low phytoplankton biomass in northern San Francisco Bay during the 1976-1977 drought. *Estuarine, Coastal and Shelf Science* 21:379-388.
- NICHOLS, F., J. CLOERN, S. LUOMA, AND D. PETERSON. 1986. The modification of an estuary. *Science* 231:567-573.
- NIXON, S. W., C. A. OVIATT, J. FRITHSEN, AND B. SULLIVAN. 1986. Nutrients and the productivity of estuarine and coastal marine systems. *Journal of the Limnological Society of South Africa* 12:43-71.
- NOBRIGA, M. AND Z. MAUTICA. 2000. Sherman island agricultural diversion evaluation. Interagency Ecological Program. *San Francisco Estuary Newsletter* 13:11.
- OLTMANN, R. N. 1998. Indirect measurement of Delta outflow using ultrasonic velocity meters and comparison with mass-balance calculated outflow. Interagency Ecological Program for the *San Francisco Estuary Newsletter* 11:5-8.
- ORSI, J. AND W. MECUM. 1986. Zooplankton distribution and abundance in the Sacramento-San Joaquin Delta in relation to certain environmental factors. *Estuaries* 9:326-339.
- ORSI, J. J. AND W. L. MECUM. 1996. Food limitation as the probable cause of a long-term decline in the abundance of *Neomysis mercedis* the opossum shrimp in the Sacramento-San Joaquin estuary, p. 375-401. In J. T. Hollibaugh (ed.), *San Francisco Bay: The Ecosystem*. AAAS, San Francisco, California.
- PETERSON, D. H., T. J. CONOMOS, W. W. BROENKOW, AND P. C. DOHERTY. 1975. Location of the non-tidal current null zone in northern San Francisco Bay. *Estuarine and Coastal Marine Science* 3:1-11.
- POSTMA, V. H. AND K. KALLE. 1955. On the development of turbid zones in the lower course of rivers with special consideration of conditions in the lower Elbe. *Deutsche Hydrographische Zeitschrift* 8:137-144.
- RICE, J. AND K. NEWMAN. 1997. Statistical model for survival of chinook salmon smolts outmigrating through the lower Sacramento-San Joaquin system. Interagency Ecological Program for the San Francisco Bay/Delta Estuary. Technical Report 59. Sacramento, California.
- RICHARDS, R. A. AND P. J. RAGO. 1999. A case history of effective fishery management: Chesapeake Bay striped bass. *North American Journal of Fisheries Management* 19:356-375.
- RILEY, G. A. 1937. The significance of the Mississippi River drainage for biological conditions in the northern Gulf of Mexico. *Journal of Marine Research* 1:60-74.
- RUDNICK, D. T., Z. CHEN, D. L. CHILDERS, J. N. BOYER, AND T. D. FONTAINE, III. 1999. Phosphorus and nitrogen inputs to Florida Bay: The importance of the Everglades watershed. *Estuaries* 22:398-416.
- SCHEMEL, L. E., S. W. HAGER, AND D. CHILDERS, JR. 1996. The supply and carbon content of suspended sediment from the Sacramento River to San Francisco Bay, p. 237-260. In J. T. Hollibaugh (ed.), *San Francisco Bay: The Ecosystem*. AAAS, San Francisco, California.
- SCHOELLHAMER, D. H. 1996. Factors affecting suspended-solids concentrations in south San Francisco Bay, California. *Journal of Geophysical Research* 101:12087-12095.
- SCHOELLHAMER, D. H. 2001. Influence of salinity, bottom topography, and tides on locations of estuarine turbidity maxima in northern San Francisco Bay, p. 343-356. In W. H. McAnally and A. J. Mehta (eds.), *Coastal and Estuarine Fine Sediment Processes*. Elsevier, Amsterdam, The Netherlands.
- SIROIS, P. AND J. J. DODSON. 2000. Critical periods and growth-dependent survival of larvae of an estuarine fish, the rainbow smelt *Osmerus mordax*. *Marine Ecology Progress Series* 203:233-245.
- SKLAR, F. H. AND J. A. BROWDER. 1998. Coastal environmental impacts brought about by alterations to freshwater flow in the Gulf of Mexico. *Environmental Management* 22:547-562.
- SKRESLET, S. 1986. *The Role of Freshwater Outflow in Coastal Marine Ecosystems*. NATO ASI Series, G edition. Springer-Verlag, Berlin, Germany.
- SMITH, S. V. AND J. T. HOLLIBAUGH. 1993. Coastal metabolism and the oceanic organic carbon balance. *Reviews of Geophysics* 31:75-89.
- SOMMER, T., R. BAXTER, AND B. HERBOLD. 1997. Resilience of splittail in the Sacramento-San Joaquin estuary. *Transactions of the American Fisheries Society* 126:961-976.
- SOMMER, T. R., L. CONRAD, G. O'LEARY, F. FEYRER, W. C. HARRELL, AND D. FELIZ. 2002. Spawning and rearing of splittail in a model floodplain wetland. *Transactions of the American Fisheries Society* 131:966-974.
- SPEED, T. 1993. Modelling and managing a salmon population, p. 268-290. In V. Barnett and K. Feridun Turkman (eds.), *Statistics for the Environment*. Wiley, New York.
- STEVENS, D. E., D. W. KOHLHORST, L. W. MILLER, AND D. W. KELLEY. 1985. The decline of striped bass in the Sacramento-San Joaquin estuary, California. *Transactions of the American Fisheries Society* 114:12-30.
- TURNER, J. L. AND H. K. CHADWICK. 1972. Distribution and abundance of young-of-the-year striped bass, *Morone saxatilis*, in relation to river flow in the Sacramento-San Joaquin estuary. *Transactions of the American Fisheries Society* 101:442-452.
- UNCLES, R. J., J. A. STEPHENS, AND M. L. BARTON. 1992. Observations of fine-sediment concentrations and transport in the turbidity maximum region of an estuary, p. 255-276. In D. Prandle (ed.), *Dynamics and Exchanges in Estuaries and the Coastal Zone*. American Geophysical Union, Washington, D.C.
- VENABLES, W. N. AND B. N. RIPLEY. 1997. *Modern Applied Statistics with S-plus*, 2nd edition. Springer-Verlag, New York.
- VÖRÖSMARTY, C. J., P. GREEN, J. SALISBURY, AND R. B. LAMMERS. 2000. Global water resources: Vulnerability from climate change and population growth. *Science* 289:284-288.
- WAINRIGHT, S. C., C. M. FULLER, R. H. MICHELER, AND R. A. RICHARDS. 1996. Spatial variation of trophic position and

- growth rate of juvenile striped bass (*Morone saxatilis*) in the Delaware River. *Canadian Journal of Fisheries and Aquatic Sciences* 53:685-692.
- WALTERS, C. J. 1986. Adaptive Management of Renewable Resources. MacMillan, New York.
- WALTERS, C. J. AND C. S. HOLLING. 1990. Large-scale management experiments and learning by doing. *Ecology* 71:2060-2068.
- WALTERS, R. A., R. T. CHENG, AND T. J. CONOMOS. 1985. Time scales of circulation and mixing processes of San Francisco Bay waters. *Hydrobiologia* 129:13-36.
- WHITFIELD, A. K. AND T. H. WOOLDRIDGE. 1994. Changes in freshwater supplies to southern African estuaries: Some theoretical and practical considerations, p. 41-50. In K. R. Dyer and R. J. Orth (eds.), *Changes in Fluxes in Estuaries: Implications from Science to Management*. Olsen & Olsen, Fredensborg, Denmark.
- WILBER, D. H. 1992. Associations between freshwater inflows and oyster productivity in Apalachicola Bay, Florida. *Estuarine, Coastal and Shelf Science* 35:179-190.
- WILLIAMS, P. B. 1989. Managing freshwater inflow to the San Francisco Bay estuary. *Regulated Rivers—Research and Management* 4:285-298.

Received for consideration, January 30, 2002
Accepted for publication, September 24, 2002