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Factors Affecting Fish Entrainment into Massive Water Diversions in a Tidal Freshwater Estuary: Can Fish Losses be Managed?

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Abstract.—We examined factors affecting fish entrainment at California's State Water Project and Central Valley Project, two of the largest water diversions in the world. Combined, these diversions from the upper San Francisco Estuary support a large component of the municipal and agricultural infrastructure for California. However, precipitous declines in the abundance of several estuarine fish species, notably the threatened delta smelt Hypomesus transpacificus, have generated major concern about entrainment as a possible cause of the declines. We examined a 13-year data set of export pumping operations and environmental characteristics to determine factors affecting entrainment (as indexed by salvage at fish screens) and the potential for manipulation of these factors to improve conditions for fish. Entrainment of three migratory pelagic species-delta smelt, longfin smelt Spirinchus thaleichthys, and striped bass Morone saxatilis—was primarily determined by the seasonal occurrence of particular life stages close to the export facilities. We also found that the direction and magnitude of flows through the estuary and to the export facilities were reasonable predictors of pelagic fish entrainment. Entrainment of resident demersal species (prickly sculpin Cottus asper and white catfish Ameiurus catus) and littoral species (Mississippi silverside Menidia audens and largemouth bass Micropterus salmoides) was not explained by diversion flows, although large numbers of individuals from these species were collected. Our study suggests that entrainment of pelagic species can be effectively reduced by manipulating system hydrodynamics.

Worldwide, more than 50% of freshwater runoff is diverted from natural waterways, producing substantial impacts on aquatic resources (Postel 1992, 2000, 2005; Kingsford 2000). Estuaries are particularly sensitive to water diversions because reduced freshwater inflows can alter sediment budgets (Wright and Schoellhamer 2005), water quality (Lane et al. 1999; Monsen et al. 2007), biological productivity (Jassby and Cloern 2000; Jassby 2005), and distribution of invertebrates (Stora and Arnoux 1983; Rodriguez et al. 2001; Kimmerer 2002a; Massengill 2004) and fishes (Kimmerer 2002a; Feyrer et al. 2007). Natural mortality for young fishes is very high (Houde 1987); entrainment adds additional mortality that can compromise population resilience (Barnthouse et al. 1983; Stevens et al. 1985; Boreman and Goodyear 1988; Pawson and Eaton 1999; Bennett 2005; Kimmerer 2008). A better understanding of how the timing and magnitude of water diversions influence fish entrainment can help managers reduce entrainment of fish and any impacts

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diversions may have on fish populations (Barnthouse et al. 1988).

The tidal freshwater region of the San Francisco Estuary, the Sacramento–San Joaquin Delta (hereafter, the Delta), is a key nursery area for many resident and migratory fishes. The Delta also contains two of the largest water diversions in the world: the pumps of the State Water Project (SWP) and the federally operated Central Valley Project (CVP), which can jointly export 28×10^6 m³ of water/d from the Delta and up to 8×10^9 m³ of water/year. The SWP provides drinking water for over 23 million Californians. Water exports from the Delta also help fuel an estimated US\$25 billion annual agricultural economy, the largest agricultural economy in North America and one of the largest in the world.

Water demands often exceed supplies in California, resulting in conflicts over the allocation of freshwater among beneficial uses (Mount 1995; Service 2007). In recent years, these conflicts have increased because many pelagic fishes in the estuary have dropped to record low abundances while demands for water have increased (Sommer et al. 2007). Historically, many fishes in the estuary responded favorably to wetter years because high inflows usually improved spawning and rearing conditions in the estuary (Stevens and Miller 1983; Sommer et al. 1997; Kimmerer et al. 2001; Bennett 2005; Feyrer et al. 2007; Rosenfield and Baxter 2007). The strength of these relationships has diminished during the last few years for several possible reasons, including habitat changes, water diversions, food web alterations, and stock-recruitment effects (Sommer et al. 2007). As a consequence of declining pelagic fish populations and the resulting conflicts over water use, resource managers face a major crisis in the upper San Francisco Estuary (Service 2007).

The biological focus of water conflicts in the estuary is the native delta smelt Hypomesus transpacificus, a small, near-annual fish (Family Osmeridae) that is listed as threatened under the California Endangered Species Act (CESA) and the federal Endangered Species Act (ESA). Although many factors have been identified as stressors for delta smelt in the estuary (Bennett and Moyle 1996; Bennett 2005; Sommer et al. 2007), water diversions are perhaps the most readily "manageable" because export operations can be altered to reduce losses of fish or improve habitat conditions. For example, freshwater flow to the estuary is managed so that salinity is less than 2 practical salinity units at three control points in the estuary (Jassby et al. 1995) for a varying number of days between February and June (Kimmerer 2002b). This salinity standard, known as X_2 , was implemented because many species show increased abundance, survival, or other positive responses to freshwater flows (Jassby et al. 1995; Kimmerer 2002a; Dege and Brown 2004; Feyrer et al. 2007).

There is considerable concern about the number of fish entrained at the export facilities. Unlike the X_2 -fish relationships, there is no direct evidence that entrainment affects population-level responses of fish. However, reductions in entrainment are obviously desirable given the status of pelagic fishes in the estuary; better information is needed about the factors that influence the timing, duration, and magnitude of entrainment losses. Because there are excellent long-term data sets on fish abundance, water quality, and hydrology in the Delta, we reasoned that it should be possible to identify the factors that have a strong influence on fish losses. In this paper, we compare long-term trends of hydrology, biological variables, and water quality with trends in the collection of several kinds of fishes counted at large fish facility louvers situated in front of the large export pumps. To develop a broader understanding of the effects of water diversions, we examined fishes from several representative groups: (1) pelagic fishes (delta smelt, longfin smelt Spirinchus thaleichthys, and striped bass Morone saxatilis); (2) littoral fishes (largemouth bass Micropterus salmoides and Mississippi silverside Menidia audens); and (3) demersal fishes (prickly sculpin Cottus asper and white catfish Ameiurus catus). These species are particularly important for protection (e.g., delta smelt and longfin smelt), for supporting recreational fisheries (e.g., largemouth bass and striped bass), or because they are numerically dominant species in their communities (e.g., prickly sculpin and Mississippi silverside). Our questions were (1) what are the long-term patterns in entrainment at the SWP and CVP; and (2) what factors influence entrainment of these fishes from the estuary on interannual and intra-annual scales? We hypothesized that pelagic fishes would show strong patterns in entrainment related to water project operations, while patterns in littoral and demersal fishes would be less evident. Our intent was to develop information that would provide insight into potential management actions that can be implemented at the SWP and CVP and perhaps at water diversions in other regions.

Study Area and Background

The Sacramento and San Joaquin rivers drain into the San Francisco Bay through the Delta (Figure 1). The Delta has been transformed over the last century from a large, contiguous marsh ecosystem into a channelized, armored-levee network of dredged sloughs (Conomos et al. 1985) that is unstable in structure and subject to dramatic change (Moyle 2008).



FIGURE 1.—Map of the San Francisco Estuary and the Sacramento–San Joaquin Delta, California. The State Water Project (SWP) and Central Valley Project (CVP) export and fish facilities are located in the southern Delta. The SWP and CVP water exports are best measured by combined daily tidal net flow of the Old River (blue line) and the Middle River (red line). Continuous monitoring stations for water temperature and specific conductance (A), Old River flow (B), Middle River flow (C), and turbidity (D) are indicated.

Upstream dams and diversions have substantially altered the hydrograph. Spring flows are approximately one-tenth of what they would be without the operation of upstream reservoirs (Knowles 2002). In contrast, late-summer and fall flows are now higher than what they were historically (Knowles 2002) because reservoir releases are made to fulfill export demands and to maximize storage capacity in upstream reservoirs for flood control. Releases are also made to produce suitable habitat for Chinook salmon *Oncorhynchus tshawytscha* below the reservoirs (National Marine Fisheries Service 2004).

The SWP Harvey O. Banks Pumping Plant is

operated by the California Department of Water Resources (CDWR), and the CVP Jones Pumping Plant is operated by the U.S. Bureau of Reclamation. The CVP and SWP both divert water from Old River, a tidal slough that intersects the lower San Joaquin River. Even at minimal exports, SWP and CVP operations can cause the tidally averaged flow in the Old River, Middle River, and other adjacent channels in the southern Delta to reverse and flow landward towards the diversions (Arthur et al. 1996; Monsen et al. 2007). The SWP can export water from the Delta at a rate of up to 292 m³/s, and the CVP can export water at up to 130 m³/s. At the entrance of the SWP are five gates $(6.1 \times 6.1 \text{ m})$ that are opened and closed on a tidal basis (Le 2004). Behind the gates is Clifton Court Forebay, a relatively shallow (average depth ~ 2 m), 9.2-km² staging reservoir for SWP exports and the California Aqueduct (Kano 1990).

In front of the CVP and SWP pumps are fish salvage facilities designed to capture entrained fishes (Arthur et al. 1996; Brown et al. 1996; Bowen et al. 1998). The Tracy Fish Collection Facility on the CVP and the Skinner Fish Facility on the SWP use large behavioral louvers to steer fish into bypass structures, where the fish are counted and identified (Brown et al. 1996; Bowen et al. 1998). Daily salvage counts for each species at each facility are calculated by the following:

$$N_{di} = \sum_{p=1}^{N} \frac{N_{dpi} M_{dpi}}{m_{dpi}},\tag{1}$$

where N_{di} is the total daily salvage at facility *i* (SWP or CVP), P_{di} is the number of time periods sampled during day d at facility i, N_{dni} is the number of fish counted at facility *i* during time period p (min) on day d, M_{dni} is the duration (min) of a fish salvage period p on day d for facility i, and m_{dpi} is the duration (min) of the subsampling interval during a fish salvage period p on day d for facility i. Typically, there are 12 sample periods/d. From each species, 20 individuals greater than 20 mm fork length (FL) are measured. Captured or "salvaged" fish are put into aerated tanks on trucks and then released back into the Delta downstream of the facilities. The term "salvage" is used by convention because the targeted Chinook salmon and striped bass are assumed to be saved from entrainment and released unharmed downstream (Brown et al. 1996). Other fish, particularly delta smelt, are likely to have low survival rates in the handling process (Swanson et al. 1996); therefore, under the federal ESA such fish are considered to be lost from the population upon collection (U.S. Fish and Wildlife Service 2005).

In this paper, we use salvage as an index of entrainment. Actual entrainment losses at the SWP and CVP are unknown because fish are not sampled continuously and because the louvers are less than 100% effective (Brown et al. 1996; Puckett et al. 1996; Bowen et al. 1998). Louver efficiency varies by species, life stage, and probably facility (Bowen et al. 1998, 2004), but for the purposes of this paper we assume that louver efficiencies are constant within and among years. The SWP salvage data also do not include additional fish losses in the Clifton Court Forebay as a result of predation before reaching the louvers (Gingras 1997) or within the holding tanks themselves (Liston et al. 1994). We assume that relative predation losses in the forebay have remained constant among years in the absence of monitoring of predator numbers. Finally, prior to 1993, identification of fishes by technicians was focused on striped bass and Chinook salmon, with little consistency in the identification and counting of other fishes (Brown et al. 1996). In 1993, the California Department of Fish and Game (CDFG) emphasized accurate identification of all species. We only analyzed data collected since 1993.

Life History Traits of the Fishes Examined

The delta smelt is a near-annual species that resides in brackish waters around the western Delta and Suisun Bay region of the estuary (Moyle 2002). In the winter (December to April), prespawning delta smelt migrate to tidal freshwater habitats for spawning, and larvae rear in these areas before emigrating down to brackish water (Bennett 2005). Adult longfin smelt may also migrate into the Delta during the winter for spawning, generally moving up from San Francisco Bay or the Pacific Ocean (Rosenfield and Baxter 2007). Longfin smelt are native to the Pacific coast and generally spawn in brackish and freshwater of the estuary when 2 years old (Rosenfield and Baxter 2007), although some will live for up to 3 years (Moyle 2002). Longfin smelt were recently proposed for listing under CESA and the federal ESA (Bay Institute et al. 2007).

Striped bass, introduced to the San Francisco Estuary in 1879, generally migrate during the spring from saltwater (ocean or bay waters) to freshwater for spawning. Some age-1 and adult striped bass will return upstream during the fall (Stevens 1979). Age-0 striped bass generally rear in the Delta and Suisun Bay during the late spring and summer, and most then migrate to the San Francisco Bay or Pacific Ocean during the fall (Stevens 1979).

Resident fishes selected for analyses included the most abundant littoral and demersal fish species in the Delta (Feyrer and Healey 2003; Grimaldo et al. 2004; Nobriga et al. 2005; Brown and Michniuk 2007). The littoral species we chose were largemouth bass (introduced to California in 1891), which are strongly associated with submerged aquatic vegetation (Grimaldo et al. 2004; Nobriga et al. 2005), and Mississippi silversides (introduced to California in 1967), which are most often found in open-shoal areas. The demersal species analyzed were prickly sculpin (native), the larvae of which commonly occur in the water column (Grimaldo et al. 2004), and white catfish (introduced to California in 1874), the most abundant demersal species recorded in the salvage during the last two decades (Brown et al. 1996).

TABLE 1.—Summary of model inputs used to examine salvage of pelagic, demersal, and littoral species at the State Water Project and Central Valley Project fish facilities in the Sacramento–San Joaquin Delta, California. Life stage was determined from the length files in the salvage database. Mean fork lengths (FL; with SD) of life stages are also provided. Analyses were performed at interannual (inter) and intra-annual (intra) time scales depending on available monitoring data (na = no available data).Variables are combined Old and Middle River flows (OMR; m³/s) water temperature (WT; °C), turbidity (T; nephelometric turbidity units), zooplankton abundance (ZA), position of the 2-psu (practical salinity units) isohaline (X_2), and California Department of Fish and Game survey indices (FMWT = fall midwater trawl; TNS = tow-net survey; 20 mm = survey for juvenile fish ≥ 20 mm FL).

Species	Life stage	FL (mm)	Inter	Intra	Period	Years	Variables
Delta smelt	Age 0	29 (5)	Yes	Yes	May–Jun	1995-2005	OMR, WT, T, ZA, 20 mm
	Adult	67 (7)	Yes	Yes	Dec-Mar	1993-2005	OMR, WT, T , ZA, X_2 , FMWT
Longfin smelt	Age 0	30 (6)	Yes	Yes	Apr–May	1995-2005	OMR, WT, T, ZA, X_2 , 20 mm
U U	Adult	89 (24)	Yes	Yes	Dec-Feb	1993-2005	OMR, WT, T, ZA, X_2 , FMWT
Striped bass	Age 0	43 (35)	Yes	Yes	Jun–Aug	1995-2005	OMR, WT, T, ZA, X_2^2 , TNS
-	Age 1	114 (47)	Yes	na	Jan–Mar	1993-2005	OMR, WT, T, ZA, X_{2} , TNS
Prickly sculpin	Age 0	31 (8)	Yes	Yes	May-Jul	1995-2005	OMR, WT, T, ZA, X_2 , 20 mm
• •	Adult	80 (20)	Yes	na	Jan–Mar	1995-2005	OMR, WT, T, ZA, X_2
White catfish	Age 0	47 (17)	Yes	Yes	Jun–Aug	1995-2005	OMR, WT, T, ZA, X_2^2 , 20 mm
	Age 1, adult	136 (69)	Yes	na	Jan–Mar	1993-2005	OMR, WT, T, ZA, X_2^2
Mississippi silverside	Age 0	34 (11)	Yes	Yes	Jun-Aug	1995-2005	OMR, WT, T, ZA, X_2^2 , 20 mm
	Adult	69 (17)	Yes	na	Jan–Mar	1993-2005	OMR, WT, T, ZA, X_2
Largemouth bass	Age 0	36 (21)	Yes	Yes	Jun-Aug	1995-2005	OMR, WT, T, ZA, X_2^2 , 20 mm
C C	Age 1, adult	116 (79)	Yes	na	Jan–Mar	1993-2005	OMR, WT, T, ZA, X_2^2

Methods

Data Sources

For each species, adult and age-0 life stages were estimated from length measurements that were made between December 1992 and 2005 and that were reported in the salvage database. Because not all of the fish counted on each day were measured, we estimated the total number of age-0 fish and age-1 and older fish in the daily counts by extrapolating the proportion of each life stage in the fish measured to the expanded counts for each day. We omitted one data point for longfin smelt from April 7, 1998, when 616 longfin smelt were recorded during the salvage count at 0400 hours (California Fish and Game 2007). We doubt the accuracy of this record because it occurred during a high-flow period (e.g., San Joaquin River, >594 m³/s; Old and Middle rivers, $>288 \text{ m}^3/\text{s}$), when salvage is generally low and when fish dispersion should be high, resulting in a catch that is spread out over a few days or hours. The highest upstream observation of larval longfin smelt in the CDFG 20-mm survey (sampling of young fish between March and July) that year was in San Pablo Bay (Dege and Brown 2004), corroborating our logic that longfin smelt salvage should have been very low.

The daily salvage data for each species (SWP and CVP combined) were plotted to show general recruitment patterns. Inspection of these plots allowed us to identify the primary months when each species was salvaged (Table 1). For example, the historical data showed that more than 90% of the total adult delta smelt collections occurred between December and March (>99% in 8 of 13 years) and that over 90% of the longfin smelt collections occurred from December to February, so we used these winter months to define the peak adult entrainment period for these species.

Factors that May Affect Entrainment

To determine factors that influence salvage of fishes at the CVP and SWP, we compiled data on hydrodynamics, water quality, and biological factors (Table 1). The data sources that we used for pelagic fishes were somewhat more extensive than for other species because these fish are of special management significance in the estuary (Service 2007; Sommer et al. 2007). These data sets are described below.

Hydrodynamic and water quality variables.-Combined Old and Middle River daily net flows (nontidally averaged) were used instead of actual SWP and CVP water diversions to determine entrainment effects because these daily net flows reasonably measure the hydrodynamic "pull" of the exports (Arthur et al. 1996; Monsen et al. 2007) when used at the time scale applied in our analyses. Old and Middle River flow integrates a complex set of factors, including flows from the large and small tributaries, daily and neapspring tidal variation, local agricultural diversions, and wind. Old and Middle River flows are measured daily using acoustical velocity meters (installed by the U.S. Geological Survey) located near Bacon Island (Figure 1; Arthur et al. 1996). Total inflow (m^3/s) is the sum of the Sacramento River, San Joaquin River, and Yolo Bypass inflows and several smaller tributary inflows that enter the Delta (Interagency Ecological Program 2007).

Continuous water temperature and specific conductance data were compiled from a gaging station located on the lower San Joaquin River near Antioch (State Water Resources Control Board 1978). Turbidity data were obtained from a continuous monitoring sensor located in the Old River at the entrance to the SWP.

Abundance and distribution.-Abundance of fish in the vicinity of the diversions can have a major effect on entrainment (Sommer et al. 1997). Hence, we included estimates of abundance near the diversions in our analyses of factors that may affect salvage rates. The data differed depending on life stage and number of years of survey data. For age-0 fishes, we used mean annual abundances from the Delta locations in the CDFG 20-mm survey during concurrent salvage periods for all species except striped bass. The CDFG 20-mm survey, which began in 1995, typically samples young fish during each neap tide between March and July (Dege and Brown 2004). For age-0 striped bass, we evaluated the number of young fish near the diversions using the Delta index from the CDFG townet survey (TNS), which is used to quantify abundance of age-0 striped bass (38 mm FL; Turner and Chadwick 1972; Kimmerer et al. 2001). For striped bass, our data set included all years between 1993 and 2005 except for 1995 and 2002, when indices were not calculated for this species.

We used X_2 to test whether the distribution of adult delta smelt, longfin smelt, and striped bass during the month prior to their salvage period influenced annual salvage or intra-annual salvage numbers. X_2 is an effective measure of pelagic fish distribution in the estuary (Jassby et al. 1995; Kimmerer 2002b; Dege and Brown 2004; Feyrer et al. 2007). The effect of yearclass strength was examined using the CDFG fall midwater trawl survey index (Moyle et al. 1992; Kimmerer et al. 2001) for the pelagic fishes. Similar analyses were not conducted on adult demersal and littoral species because there is currently no reliable monitoring program for these fishes in the estuary.

Prey abundance.—Zooplankton abundance from the CDFG 20-mm survey (Delta stations only) was assumed to reflect favorable habitat conditions that either promoted greater residence times or survival of age-0 fishes in the Delta, thereby resulting in greater entrainment risk and salvage. This assumption is probably valid for delta smelt, whose summer–fall survival is linked to zooplankton abundance between July and October (Kimmerer 2008). Only calanoid copepodids and copepods were used from the zooplankton data since these are the dominant prey consumed by delta smelt (Nobriga 2002). For the other fishes, we used total zooplankton abundance

(Delta stations only) because they are known to have more diverse diets (Feyrer et al. 2003).

Data Analysis

Relationships between water quality and hydrodynamic variables were identified using locally weighted scatterplot smoothers (i.e., LOWESS; Venables and Ripley 2002) and visual inspection of bivariate plots. A reduced set of environmental parameters was then selected to compare with salvage data. To remove the effect of autocorrelation within each variable and the large number of zeros in the salvage database, analyses were focused on intra-annual and interannual trends by averaging independent and dependent variables into bimonthly or monthly and annual time periods. Intraannual models were limited to life stages and species for which data were available (Table 1).

We used ordinary least-squares regression to test whether intra-annual and interannual salvage patterns were influenced by physical and biological factors. Statistically significant models were identified using best-subset procedures. Combined Old and Middle River flows constituted the export effect in each model because this variable has been shown to be a good index of diversion flow when examined at the time scales (i.e., intra- and interannual) explored here (Monsen et al. 2007). If inclusion of this variable did not contribute significantly to the model, it was omitted and the remaining variables were examined using the best-subset procedure. The best subsets were determined using Akaike's information criterion (AIC) values; AIC penalizes for increasing the number of free parameters but rewards goodness of model fit (Venables and Ripley 2002). Where the data failed to meet assumptions of normality (Anderson-Darling test: P < 0.05), the data were log transformed. Nonlinear least-squares regression was used for cases in which a linear relationship was deemed unsuitable based on visual inspection of the regression plots (i.e., curvilinear fits) and AIC values.

For adult delta smelt and longfin smelt, the intraannual salvage data were partitioned into monthly averages to determine which factors might influence the timing of salvage. The interaction of Old and Middle River flows and X_2 position in the month prior was examined for adult smelt to see whether their salvage was influenced by their proximity (i.e., distribution) to the SWP and CVP before they migrated upstream. We expected that X_2 would have little or no effect on adult smelt salvage during periods when Old and Middle River flows were strongly seaward. Turbidity was used in the model to test whether salvage followed large precipitation in the basin, otherwise known as "first flush" events. Turbidity



FIGURE 2.—Physical variables used to examine State Water Project (SWP) and Central Valley Project (CVP) fish salvage dynamics in the Sacramento–San Joaquin Delta, California, by season and year (blue triangles = winter, January–March; red squares = spring, April–June; green diamonds = summer, July–September; black circles = fall, October–December; ntu = nephelometric turbidity units). Mean monthly position of the 2-psu (practical salinity units) isohaline (X_2 ; km from the Golden Gate Bridge; Jassby et al. 1995) by year is also shown (gray diamonds = November; black squares = December; white triangles = January; × symbols = February).

was used in lieu of total river inflow since these variables were significantly correlated with each other at the monthly level (averaged daily data) during our study period (r = 0.32, df = 142, slope = 0.003, P < 0.001; excluding 9 months of missing turbidity data). For age-0 fishes, the intra-annual analyses were conducted on data divided into bi-monthly periods coincident with the CDFG 20-mm survey to test the factors influencing when age-0 fish (\geq 20 mm FL) show up in the salvage.

Results

Environmental Factors and Salvage Data

Combined Old and Middle River flows were negative or "reverse" during 47 of the 52 seasons examined (Figure 2). The most notable trend was a decrease in Old and Middle River flows during winter months corresponding to increased exports during the same period. Temperatures were generally consistent among years. Overall, the indices of adult pelagic fish abundance from CDFG monitoring surveys declined during the study period, but indices for age-0 fishes and zooplankton abundances were variable, with no obvious trend (Figure 3). Between December 1992 and July 2005, the SWP and CVP salvaged 590,310 delta smelt, 122,747 longfin smelt, and over 32 million striped bass (Figure 4). Large numbers of littoral and demersal fishes were salvaged: 1,385,880 prickly sculpin, 3,214,687 Mississippi silversides, 596,827 largemouth bass, and 5,060,035 white catfish. Beginning in 1999, salvage of adult delta smelt and longfin smelt increased, with their highest salvage years being 2003 and 2002, respectively. Adult Mississippi silverside and largemouth bass numbers increased between 1999 and 2005, but these numbers are generally lower than numbers recorded in the early 1990s.

Salvage of age-0 native fishes (delta smelt, longfin smelt, and prickly sculpin) was highest during the spring, whereas salvage numbers of introduced species were higher in summer months (Figure 5). First salvage of adult delta smelt occurred within days of "first flush" events marked by sudden increases in river inflows and turbidity (Figure 6).

Statistical Approach

Old and Middle River flows, turbidity, and water temperature were selected as the predicator variables in the salvage, following no obvious trends between them in the bivariate plots except for turbidity and combined Old and Middle River flows. Monthly averaged turbidity and combined Old and Middle River flows were moderately correlated during the study period (r =0.33, df = 142, slope = 0.018, P < 0.001) but this relationship is driven during periods when Old and Middle River flows are extremely positive, which only occurred in a handful of months during periods of extreme high inflow. Therefore, turbidity was left in the models because it is a good indicator of pelagic habitat (Feyrer et al. 2007) and of seasonal river inflow. Specific conductance was significantly correlated with the combined Old and Middle River flows (r = 0.32, df = 146, slope = -3.84, P < 0.001) and therefore was eliminated from regression analyses to avoid confounding interpretations deriving from multicollinearity.

Factors Affecting Age-0 Salvage

The only model that explained interannual age-0 delta smelt salvage was that incorporating zooplankton (calanoid adults and copepodids) abundance from the CDFG 20-mm survey (Figure 7). For age-0 longfin smelt, the Old and Middle River flow variable was the only parameter that explained interannual salvage abundance. Year-class strength was the only predicator of age-0 striped bass salvage. Prickly sculpin salvage was positively correlated with water temperature, and white catfish salvage was positively correlated with seaward Old and Middle River flows (Figure 7), but otherwise there were no significant predictors of salvage for age-0 resident fish. At the intra-annual scale, the best model that explained age-0 delta smelt salvage included Old and Middle River flows, turbidity, and CDFG 20-mm survey abundance (Table 2). For longfin smelt, Old and Middle River flows and 20-mm survey abundance were important predictors.



FIGURE 3.—Biological variables used to examine salvage dynamics in the State Water Project and Central Valley Project, California, by year: (**A**) annual delta smelt (black bars) and longfin smelt (gray bars) index values from the California Department of Fish and Game (CDFG) fall midwater trawl (FMWT) survey, 1992–2004; (**B**) mean abundance of calanoid copepods (open circles) and all zooplankton (stars) in the CDFG 20-mm survey; and (**C**) annual abundances (geometric mean of catch per unit effort, CPUE) of delta smelt (black circles), longfin smelt (× symbols), prickly sculpin (open triangles), largemouth bass (stars), Mississippi silversides (open diamonds), and white catfish (gray squares) from the CDFG 20-mm survey (primary *y*-axis) and Delta index for striped bass (SB) from the CDFG tow-net survey (TNS; plus symbols; secondary *y*-axis).

TABLE 2.—Regression coefficients and statistics for models that best explained intra-annual salvage (\log_{10} transformed) of age-0 delta smelt and longfin smelt at the State Water Project and Central Valley Project, California, between 1993 and 2005. See Table 1 for averaging periods and summary of all factors examined (OMR = combined Old and Middle River flows, m³/s; *T* = turbidity, nephelometric turbidity units; 20-mm survey = index from the California Department of Fish and Game survey of young fishes). The best models, as determined by the lowest value of Akaike's information criterion (AIC), are highlighted in bold. Not all significant models are shown.

Species	OMR	Т	20-mm survey	Intercept	df	r^2	AIC	Р
Delta smelt	-0.008	_	_	2.47	42	$\begin{tabular}{ c c c c c c c c c c c c c c c c c c c$		
	-0.007	_	0.02	1.91	41	0.47	139	< 0.001
	-0.006	0.07	_	1.30	41	0.50	137	< 0.001
	-0.005	0.07	0.02	0.88	40	0.62	128	<0.001
Longfin smelt	-0.005	_	_	1.02	42	0.31	110	< 0.001
	_	_	0.03	0.79	41	0.32	107	< 0.001
	-0.003	—	0.02	0.82	40	0.42	101	<0.001



FIGURE 4.—Annual State Water Project and Central Valley Project (California) salvage numbers (\log_{10} transformed) by fish life stage (age 0, age 1 and older). See text for averaging periods.

Factors Affecting Age-1 and Adult Salvage

For the pelagic fishes, the best models of interannual salvage were based on Old and Middle River flows (Figure 8). We found no significant models for age-1 and older demersal and littoral fishes. At the intraannual time scale, the interaction between the previous month's X_2 and the combined Old and Middle River flows was significant for explaining delta smelt salvage (Table 3). We found no significant model for longfin smelt at the intra-

Discussion

Understanding factors that influence the entrainment of fishes in the estuary is essential for developing management alternatives to protect fishes of concern. Few studies have examined patterns and mechanisms explaining fish losses at the CVP and SWP over the years (Stevens and Miller 1983; Stevens et al. 1985; Brown et al. 1996; Sommer et al. 1997; Bennett 2005; Kimmerer 2008), despite the fact that they are two of the largest continuous fish sampling devices in the world. There have also been relatively few studies of the direct effects of water diversions from riverine and tidal ecosystems (Nobriga et al. 2004; Moyle and Israel 2005). Valuable information has been obtained about power plant entrainment impacts (Kelso and Millburn 1979; Boreman and Goodyear 1981, 1988; Hadderingh et al. 1983; Henderson et al. 1984); in some cases, power plant studies have revealed broader patterns of fish community dynamics (Love et al. 1998; Maes et al. 1998). Here, we show that fish losses are influenced by both biological and physical factors and provide insights into the seasonal behavior of fish in the Delta.

Life Stage

The most obvious trend in the salvage data is that far more age-0 fishes are entrained than age-1 and older fishes. This result was expected since there are simply more age-0 fishes than older age-classes and because smaller fishes are often more vulnerable to entrainment flows (Hadderingh et al. 1983; Henderson et al. 1984;

FIGURE 5.—Mean (\pm SE) annual fish salvage (\log_{10} transformed) in the State Water Project and Central Valley Project, California, by month. Monthly data were averaged across years. Age-classes were identified from length data. Only a small percentage of salvaged striped bass (\sim 4%) and largemouth bass (\sim 13%) were greater than 200 mm fork length.

Maes et al. 1998). However, in the San Francisco Estuary, the biology of the fishes examined here must be considered to understand the salvage patterns of these species (Sommer et al. 1997). For example, adult delta smelt and longfin smelt migrate into freshwater to spawn; thus, they increase their vulnerability to entrainment simply because they move closer to the SWP and CVP. In contrast, age-0 smelt rear in the Delta and eventually move seaward (i.e., away from entrainment risk) during periods of high outflows (Dege and Brown 2004) or unfavorable temperatures or water quality (Kimmerer 2008; Nobriga et al. 2008). Thus, in the case of the native smelts, the notion of protecting fish via traditional screening criteria must not be limited to size and swimming speed of the young. Factors that influence adult entrainment must be understood and mitigated in other ways (discussed in detail under Management Implications).

Fish Species

There were clear differences in the responses of pelagic, demersal, and littoral fishes to water diver-

TABLE 3.—Regression coefficients and statistics for models that best explained intra-annual salvage of adult delta smelt and longfin smelt at the State Water Project and Central Valley Project, California, between December 1992 and March 2005. See Table 1 for averaging periods and summary of all factors examined (OMR = combined Old and Middle River flows, m³/s; T = turbidity, nephelometric turbidity units; X_2 = position of the 2-psu [practical salinity units] isohaline, km from Golden Gate Bridge; OMR × X_2 = interaction of OMR and X_2). The best models, as determined by the lowest value of Akaike's information criterion, are highlighted in bold. Not all significant models are shown.

Species	OMR	Т	X_2	$OMR \times X_2$	Intercept	df	r^2	AIC	Р
Delta smelt	-3.33	_	_	_	1,014	50	0.10	939	< 0.05
	-23.32	119	-6.77	_	374	48	0.29	927	< 0.001
	-5.94	115	_	_	-1,144	49	0.30	926	< 0.001
	_	113	_	-0.09	-1,262	49	0.31	925	<0.001
Longfin smelt									NS

FIGURE 6.—Eight-day running averages of adult delta smelt salvage, total outflow (m³/s), and turbidity (nephelometric turbidity units, ntu) for the eight most abundant delta smelt salvage years between December 1992 and April 2005 at the State Water Project and Central Valley Project, California. Total outflow and turbidity were standardized to a mean of zero.

sions. Though nearshore and demersal fishes can account for a large percentage of the numbers and biomass entrained in water diversions (Nobriga et al. 2004) or cooling water withdrawals (Hadderingh et al. 1983; Boreman and Goodyear 1988; Love et al. 1998), vulnerability is often highest during pelagic life stages or during periods of increased activity (e.g., feeding). Each group showed strong seasonality in entrainment (salvage), but there were major differences in the apparent effect of environmental conditions, including water exports. Specifically, exports as indexed by Old and Middle River flows play a major role in the salvage of pelagic fishes, but no similar pattern was observed in the littoral and demersal fishes. This is consistent with our hypothesis that the usual behaviors (i.e., strong habitat fidelity) of these fish limit their susceptibility to export flow effects. This result was somewhat surprising given that millions of age-0 littoral and demersal fishes are salvaged each year. Better sampling in these habitats may reveal mechanisms underlying entrainment of these fishes or mechanisms that show

why the abundance of these species has increased in recent years (Brown and Michniuk 2007) despite large removal by the water diversions.

Seasonal Patterns

Seasonal variation in entrainment is a common pattern observed at water diversions, often reflecting adult migrations (Jensen et al. 1982), age-0 recruitment (Love et al. 1998) or shifts in habitat use in relation to diversion intakes (Turnpenny 1988; Maes et al. 1998). Our investigation reveals that native fishes (delta smelt, longfin smelt, and prickly sculpin) are more vulnerable to exports during winter and spring months, whereas introduced fishes (striped bass, Mississippi silverside, largemouth bass, and white catfish) are more often salvaged during late spring and summer. The seasonal entrainment patterns observed here are consistent with patterns in the Delta; native species mostly spawn and recruit earlier in the year when temperatures are cooler (~8-16°C), whereas introduced species typically recruit during the summer when temperatures are warmer

FIGURE 7.—Relationships between (A) age-0 delta smelt annual salvage in the State Water Project and Central Valley Project, California, and zooplankton abundance; (B) longfin smelt salvage and combined flow of the Old and Middle rivers; (C) striped bass salvage and the California Department of Fish and Game (DFG) tow-net survey index; (D) prickly sculpin salvage and water temperature; and (E) white catfish salvage and Old and Middle River flow. No other parameters explained the salvage of these species. See Table 1 for averaging periods.

(>15°C; Moyle 2002; Feyrer and Healey 2003; Feyrer 2004; Grimaldo et al. 2004; Bennett 2005). For the smelts, the salvage data indicate that few fish were entrained between July and November (Figure 5), mostly because the smelts' distribution shifts seaward during this period (Dege and Brown 2004; Nobriga et al. 2008), whereas for resident species the seasonality in entrainment is more likely explained by habitat use.

Prey Availability

Prey availability may play a role in losses of fish at the export facilities. Annual salvage of age-0 delta smelt was best predicted by zooplankton (calanoid copepod) abundance. Kimmerer (2008) showed that survival of delta smelt between summer and fall was explained by zooplankton biomass. High zooplankton abundance may increase the survival and residence

FIGURE 8.—Relationships between annual salvage of age-1 and older fishes in the State Water Project and Central Valley Project, California, and the combined flow of the Old and Middle rivers. For pelagic fishes (delta smelt, longfin smelt, and striped bass), Old and Middle River flow was the only variable that explained salvage. Regression models were not significant (NS, P > 0.05) for littoral (Mississippi silverside and largemouth bass) or demersal (white catfish and prickly sculpin) species.

time of age-0 delta smelt in the Delta, thereby increasing their entrainment risk in the southern portion of the Delta. Our study does not address whether entrainment represents a large source of mortality for delta smelt, but Kimmerer (2008) showed that high entrainment during dry years can result in large population losses for delta smelt.

Year-Class Strength

Similar to Sommer et al. (1997), our salvage analyses suggest that entrainment patterns may be affected by year-class strength. Specifically, we found that the number of age-0 striped bass salvaged was well predicted (r = 0.81) by their numbers in the TNS (Delta stations only) conducted by CDFG. Because Old and Middle River flows were not found to be a significant predictor of age-0 striped bass, we believe the relationship between striped bass salvage and yearclass strength highlights the importance of localized effects (Stevens et al. 1985). In the case of age-0 striped bass, fish losses are probably episodic when large aggregations become entrained over short intervals. The longer averaging period used in our study may obscure these sorts of short-term relationships with environmental conditions responsible for movements of schools or changes in behavior. For example, in recent years, water exports have been managed at low levels in April and May to protect delta smelt and emigrating Chinook salmon, but the exports quickly increase in June (Figure 2; see Old and Middle River flow panel) when these species move downstream. The transition in exports between May and June could be the reason why age-0 striped bass salvage increases substantially in June (Figure 5). Our study was not designed to capture such intermonthly variability, but we recognize its importance for understanding salvage patterns at daily to weekly time scales.

Age-0 delta smelt salvage at the intra-annual scale was related to the abundance of these fish in the Delta, but Old and Middle River flows and turbidity were also strong predictors. Thus, for delta smelt, the mechanisms influencing entrainment within a year is probably a measure of the degree to which their physical habitat overlaps with the hydrodynamic "footprint" of the Old and Middle River flows. A similar result was found for age-0 longfin smelt, where Old and Middle River flows and year-class strength (from the CDFG 20-mm survey) were found to be significant predicators (Table 2) of salvage. Although spring represents a low-export period during which Old and Middle River flows are typically slightly negative (Figure 2), entrainment risk for age-0 smelts is likely to be high when they often spawn and rear in the Delta, which happens frequently for delta smelt (Nobriga et al. 2008). For adult delta smelt and longfin smelt, yearclass strength did not predict salvage at the interannual level, but X_2 (used as an index of their distribution) was a predictor for delta smelt salvage at the intra-annual scale when Old and Middle River flows were negative. This result suggests that the role of population size in determining the number of adult smelt salvaged is very small when Old and Middle River flows are seaward but is probably much more important when flows are in the reverse direction, as was noted by Kimmerer (2008) for delta smelt.

Hydrodynamics

A common question in studies of riverine ecosystems is whether fish move with flow. This is a difficult question to address without direct field observations using approaches such as telemetry, a relatively impractical approach for rare and fragile species like the delta smelt (Swanson et al. 1996; Bennett 2005). Moreover, flow is especially complex in estuaries, where short- and long-term variation in tidal flow dominates. Nonetheless, the relatively strong relationships between Old and Middle River flows and the annual adult delta smelt, longfin smelt, and age-1 striped bass entrainment (salvage) indicate that fish are at least partially moving with reverse net flow towards the export facilities. In contrast, juvenile white catfish exhibited a positive relationship between salvage and seaward Old and Middle River flow, suggesting that their salvage is driven by upstream recruits that become vulnerable to entrainment when advected towards the export facilities.

Management Implications

The recent sharp decline of pelagic fish populations in the estuary has increased scrutiny of water diversion impacts in the estuary (Service 2007; Sommer et al. 2007). Though many factors have been identified as candidates for the recent decline (e.g., low food web productivity, contaminants, and water quality), CVP and SWP diversions represent one of the most directly observable sources of mortality. Our study was not designed to address the most important management issue: whether these water diversions have populationlevel effects. Population-level consequences have been best studied for striped bass. Striped bass larval production was historically explained by river flows and southern Delta exports (Stevens et al. 1985). However, Kimmerer et al. (2001) found that export effects were small and sporadic, primarily occurring during the first several months of life. Moreover, striped bass population dynamics is best explained by density dependence between age-1 and age-2 yearclasses, a bottleneck that dampens variation from effects early in life (Kimmerer et al. 2000). However, our analyses indicate that if there are years when density dependence is relaxed, then age-0 striped bass losses could be reduced by managing export flows during periods when these fish are abundant in the Delta.

The degree to which water exports have populationlevel effects on delta smelt is poorly understood. However, losses of delta smelt are perhaps greatest during winter, which represents the main period of adult delta smelt migration and spawning. We observed that recent increases in winter salvage of delta smelt (Figure 4) were associated with higher exports and reverse Old and Middle River flows (Figure 2). These changes were coincident with the low numbers of pelagic fishes in 2000 (Sommer et al. 2007), so it is possible that export losses of adults and their offspring contributed to the recent decline of delta smelt. Bennett (2005) and Kimmerer (2008) provide evidence that losses of larvae produced from these spawners can be substantial; however, the extent to which entrainment losses affect delta smelt population dynamics is unclear. Modeling studies by Bennett (2005) indicate that effects of exports on delta smelt growth and survival are very difficult to detect, so this issue remains unresolved.

Even if the population-level effects of fish entrainment are not well understood, the rapid decline of pelagic fish populations in the San Francisco Estuary has resulted in a substantial interest in finding ways to reduce losses. Traditionally, water diversion impacts are mitigated with placement of diversion screens (Moyle and Israel 2005). The SWP and CVP have fish louvers for this purpose, although they were designed primarily for Chinook salmon (Brown et al. 1996) and other species and life stages have not been adequately addressed. Hence, improvements in fish louver or screen design (e.g., positive barrier screens) could reduce losses of some of the species that we studied (Moyle and Israel 2005). Approach velocity criteria are already implemented for striped bass at 0.30 m/s, but this only provides protection for fish in the vicinity of the water diversions (State Water Resources Control

Board 1978). The present study suggests that water diversion impacts can be mitigated on a larger scale by altering the timing of exports based on the biology of fishes and changes in key physical and biological variables. Such a strategy has been used on the Hudson River, New York, where export reductions at three power plants successfully reduced the number of striped bass entrained during the winter months (Barnthouse et al. 1988). Combined with other efforts to reduce mortality, this seems to have permitted a dramatic restoration of the striped bass population on the Hudson River (Daniels et al. 2005).

The present study also suggests that fish losses can be managed through careful consideration of hydrodynamics and water quality. For example, minimizing reverse flows during periods when delta smelt and longfin smelt are migrating into the Delta could substantially reduce mortality of the critical adult life stage. The relationship between salvage of adult delta smelt and combined Old and Middle River flows (Figure 8) indicates that entrainment can be managed through manipulation of exports. Because the Old and Middle River flow variable improved the models for longfin smelt and striped bass salvage, this variable has reasonably broad applications. In addition, the significant effect of turbidity on adult delta smelt salvage (Table 2) suggests that reducing exports during periods of high outflows could reduce losses of this imperiled fish. One possibility is the implementation of an export reduction during the period immediately after the first flush, when turbidities in the Delta increase to over 10 nephelometric turbidity units (Figure 6).

Similarly, monitoring of the salinity in the estuary gives a good indication of fish distribution (Kimmerer 2002a; Dege and Brown 2004; Feyrer et al. 2007) and hence the potential for fish to be affected by water diversions. As a consequence, exports during higher outflow conditions or when X_2 is downstream would be expected to result in lower pelagic fish losses, an effect noted by Sommer et al. (1997). Temperature monitoring could also assist in the management of some species. For example, if prickly sculpin losses were a concern, exports could be adjusted according to water temperature, the only variable that significantly predicted age-0 prickly sculpin salvage (Figure 7). Overall, the native fishes examined here, and presumably other early spawning native fishes in the Delta, should benefit from a reduction in water exports between December and June. However, if such an export reduction is mitigated by increased exports in fall, then delta smelt habitat could be affected (Feyrer et al. 2007). In contrast, this study illustrates how ineffective it would be to manage the exports to reduce entrainment of largemouth bass or other littoral species because these fish occupy habitat that probably buffers them from entrainment.

In summary, long-term monitoring data from of two of the world's largest water diversions show that patterns of entrainment vary substantially with life history and season and that entrainment interacts in complex ways with hydrodynamics, water quality, and biological variables. Our findings demonstrate that integrated approaches to reduce entrainment are needed as part of a broader effort to restore imperiled fishes in the San Francisco Estuary, especially in light of rapid estuarine change (Moyle 2008). Some of these observations have already been incorporated into management of the San Francisco Estuary (Kimmerer 2002b; U.S. Fish and Wildlife Service 2005). While our findings are in many respects unique to the complex hydrodynamics and exceptionally large water diversions of the San Francisco Estuary, our demonstration of the importance of factors such as seasonality, species differences, fish year-class strength, food availability, and water quality should have application to fish entrainment in other geographical areas.

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