Final Report

Pre-Screen Loss and Fish Facility Efficiency for Delta Smelt at the South Delta's State Water Project, California

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Abstract

Water conveyance operations have long been implicated in the decline of fish populations in the upper San Francisco Estuary, where the State Water Project (SWP) and Federal Central Valley Project (CVP) are located. We conducted the first experimental evaluation of the relation between delta smelt salvage at the John E. Skinner Fish Protective Facility (Skinner Fish Facility or SFF) and underlying entrainment losses at the SWP in the south Delta. We tested the use of cultured delta smelt in mass mark-recapture experiments in February and March 2009 (adults) and June 2009 (juveniles) to estimate: 1) the percent of fish recaptured at SFF of the total released at the entrance of SFF (fish facility efficiency), 2) the percent of fish recaptured at SFF of the total released at the entry point of Clifton Court Forebay (CCF), a reservoir for SWP exports (percent recovery), and 3) the fish losses in CCF (pre-screen loss). All fish released (n) were calcein-marked; adults were also marked using injectable fluorescent paint (photonic marks) and strontium (trans-generational mark). Mean fish facility efficiency estimates declined in successive releases: February (53.2%, n = 400), March (44.0%, n = 200) and June (24%, n = 800). The mean percent recovery of fish released in CCF declined greatly over time: February (3.01%, n = 5,707); March (0.41%, n = 2,849) and June (0.03%, n = 14,413). Correspondingly, mean pre-screen losses increased in successive releases: February (94.3%); March (99.1%) and June (99.9%). Juvenile mark-recapture tests conducted in June 2008 and 2009 showed consistently higher fish losses with increasing release distance from the fish facility. We concluded that: 1) entrainment losses of delta smelt could be much higher at times compared to other species previously studied at the SWP; 2) pre-screen loss was overwhelmingly the largest source of mortality for delta smelt; 3) Distance from the SFF and increased residence time in CCF and decreased exports were strongly associated with decreased percent of recovered fish at the SFF. We hypothesize that these losses were primarily due to increased predation mortality within CCF as concluded in previous studies. Entrainment monitoring in CCF could be readily applied to interpret and validate critical relations between salvage statistics and the magnitude and variability of direct entrainment losses for delta smelt.

Introduction

Although water diversions for urban and agricultural uses have long been a common feature of aquatic ecosystems, the long-term implications of reduced fresh water inflow and increased entrainment losses on aquatic organisms present challenging management trade-offs for ecosystem sustainability and water use reliability (e.g. Lund et al. 2010; Vörösmarty et al. 2010). Due to record low fish population abundance indices for several pelagic species in the 2000's, this challenge has become increasingly critical for the Delta of the upper San Francisco Estuary (hereafter Delta), one of the most intensively water-managed estuarine systems in the world. The water diversions by the State Water Project (SWP) and Central Valley Project (CVP), including water export from the south Delta for agricultural, industrial and urban use have long been considered factors contributing to the decline of fishes in the upper San Francisco Estuary (Erkkila et al. 1950; Stevens and Miller 1983; Moyle et al. 1992; Arthur et al. 1996; Bennett and Moyle 1996; Sommer et al. 2007).

Limiting entrainment losses of fish has been central for the management of species in the Delta, particularly for listed species such as the delta smelt (*Hypomesus transpacificus*), an endemic osmerid and predominantly annual species. It was listed as threatened (federal and state) in the early 1990's, endangered in 2009 (state). Delta smelt was also deemed to warrant federal endangered status in 2010. The SWP and CVP use fish facilities to collect a fraction of the fish that are drawn to the export pumps. Estimated salvage data from the SWP's Skinner Fish Protective Facility (hereafter SFF) has been commonly used as an index of direct entrainment of some fish, including delta smelt, into Clifton Court Forebay, hereafter CCF, a SWP reservoir located in the south Delta (37.8298° N - 121.5574° W, Figure 1). A percentage of the fish entrained into CCF is lost and unable to reach the screens of the SFF. Such loss has been termed pre-screen mortality or pre-screen loss (Tillman 1993; Brown *et al.* 1996). Fish subject to pre-screen loss along with a fraction of the fish that enter the SFF remain unaccounted for in the salvage. Results of 11 studies conducted for juvenile fishes between 1976 and 2007 in CCF (Chinook salmon, striped bass and steelhead) revealed consistently high pre-screen losses ranging from 63% to 99% (Gingras 1997; Clark *et al.* 2009).

The reliance on fish salvage data as index of fish entrainment has been widespread (e.g. Moyle et al. 1992; Brown et al. 1996; Sommer et al. 1997; Bennett 2005; Grimaldo et al. 2009). Efforts aimed at interpreting salvage data in terms of their effectiveness (Brown et al. 1996) or in terms

of population level losses (Kimmerer 2008) have been challenged by the significant uncertainty due to the lack of empirically derived pre-screen loss estimates for delta smelt. The extent and variability of entrainment-related losses, including pre-screen losses at the SWP, remain long-standing critical unknowns for delta smelt (e.g. EWA Review Panel 2001; Hymanson and Brown 2006; IEP Delta Smelt Review 2006; Kimmerer 2008; Independent expert panel review 2009). Thus, the critical need for empirical estimates on the magnitude of the direct export losses resulting from pre-screen loss and fish facility efficiency. Complementary information - such as hydrodynamic particle entrainment models, fish surveys and water quality data have also been used to infer fish entrainment by SWP and CVP (Kimmerer 2008; USFWS 2008). Yet, processoriented methods are needed to validate the hypothesized relations between reported delta smelt salvage and underlying entrainment losses inferred through distribution and particle tracking based methods. The lack of empirical tools to quantify entrainment losses for delta smelt has prevented basic understanding on the magnitude and variability of such losses.

As part of a two year pilot study, we conducted the first mark-recapture experiments to gain knowledge on the entrainment losses of delta smelt at the SWP. This investigation provided the first empirical estimates for two unaccounted sources of entrainment losses of delta smelt at the SWP: fish facility losses (i.e. losses within the fish facility) and pre-screen losses in CCF. Other water project impacts include near- and far-field losses in the south Delta and the entire Delta system, as revealed by long-term declines in the quality of physical habitat for several fishes (e.g. Feyrer *et al.* 2007; Nobriga *et al.* 2008); and shifts in fish assemblage composition away from native and desirable species (Moyle *et al.* 2010). In addition, short-term salvage mortality due to collection, handling, trucking and release (CHTR) has been reported at the SFF (e.g. Miranda *et al.* 2010; Morinaka, In progress, California Department of Fish and Game, Stockton). Our ultimate goal is to empirically quantify entrainment losses of delta smelt at the SWP. Specific objectives of this study were to obtain mark-recapture estimates for:

- 1- Salvage efficiency of juvenile and adult delta smelt at the SFF.
- 2- Percent of juvenile and adult delta smelt recovered at the SFF and released in CCF.
- 3- Pre-screen loss for juvenile and adult delta smelt in CCF.

Study area

The SWP in the south Delta comprises CCF, SFF, the Harvey O. Banks Pumping Plant and seasonally, temporary barriers in several Delta channels. The SFF and CCF are located close to the CVP Tracy Fish Collection Facility (TFF, Figure 1). The CCF is a 38.24 million m³

reservoir (31,000 acre feet) primarily used for off peak pumping storage (i.e., it stores diverted water so that most export pumping can occur at night when electricity is less costly). The original SWP operations in the South Delta began by late 1968 and did not result in prescreen losses due to CCF operations. Fish were initially entrained into the SWP from the Delta through the Italian Slough and arrived directly to the SFF, formerly known as the Delta Plant (Heubach ca. 1973; Kano 1990). When CCF became operational in November of 1969, the end of the Italian Slough intake channel was closed, and the remainder of the channel was connected to the Forebay. The Forebay diverts water from the Delta through an intake structure which connects CCF to the West Canal. The West Canal in turn is connected to Old River. Inflow into CCF is regulated by five radial gates positioned side by side at the southeast corner of the reservoir, with a combined operational limit of 339.8 m³/s (12,000 cfs). Water circulation patterns in CCF are largely driven by the interaction of wind and the operation of the radial gates which allow inflow to CFF and the operation of the Banks Pumping Plant exports water from CCF (Kano 1990; MacWilliams and Gross in progress). For a fish entrained into the SWP to be salvaged, it must first pass through CCF, avoid predation and other potential mortality sources. and then directed into holding facilities at the SFF. The minimum distance from the radial gates to the primary louvers of the SFF is 4.0 km (Figure 1). The SFF is a system of primary louvers, secondary louvers, perforated plates and connecting pipes that can direct some of the entrained fish into holding tanks where they are counted and subsequently transported by trucks to two locations in the west Delta where these salvaged fish are released with the purpose of reducing entrainment losses. The TFF and the SFF were originally designed to salvage juvenile Chinook salmon (Oncorhynchus tshawytscha)

Methods

Culture and Marking

All delta smelt used for this study were produced at the U.C. Davis Fish Conservation and Culture Lab (FCCL), located adjacent to the SFF and a short distance to other release locations used throughout this study (Figure 1). We used cultured delta smelt because the

and striped bass (Morone saxatilis), (Brown et al. 1996). Delta smelt were not the focus of the

process at these fish facilities (Kimmerer 2008), including the SFF (J. Morinaka, in progress.

California Department of Fish and Game, Stockton, CA).

design criteria. Juvenile delta smelt < 30 mm FL seem particularly undersampled in the salvage

number of delta smelt needed to conduct mark-recapture experiments far exceeded the number of wild fish we would have been able to obtain due their limited abundance and take restrictions. Delta smelt were spawned during 2008 to provide ca. 4,000 juveniles for the June 2008 experiments, 16,200 juveniles for the June 2009 experiments and 11,200 adults for the February-March 2009 experiments. Production of delta smelt was based on rearing methods developed at the FCCL (Lindberg *et al.*1999; Baskerville et al 2004).

Fish marking was conducted at the FCCL and involved three types of marks: 1) calcium (Sutphin and Morinaka 2010; Castillo *et al.* In progress, U.S. Fish and Wildlife Service, Stockton, CA). SE-MARK[™] Calcein was the primary mark used for all juvenile and adult delta smelt, 2) photonic marks used in all adult delta smelt to differentiate days and/or location of fish releases (Sutphin 2008) and 3) trans-generational marking (Hobbs *et al.* in progress, UC Davis, CA).

An SE MARKTM detector (Western Chemical) was used to distinguish calcein marked and unmarked fish. Calcein marking during the 2009 mass mark-recapture experiments was based on calcein marking protocols developed as part of this project under the Investigational New Animal Drugs Program (INAD): 1) a 3 minute bath (full immersion) in a 1% salt solution and 40 mg/l ms-222 (pre-treatment) and 2) a 5 minute bath in calcein - 5.0 g/l (adults) and 2.5 g/l (juveniles) - (treatment). Extensive tests revealed 100% mark retention for at least 3 months, that is, far beyond the entire period in which fish were recaptured (up to 20 days), (Castillo *et al.* In progress, U.S. Fish and Wildlife Service, Stockton, CA).

Photonic marking was conducted using pressurized CO₂ guns (model BMX2000 POW'R-Ject System, New West Technologies) and BMX2000 Photonic Marking Solutions (Cobalt Green, Cobalt Blue and Titanium White). Photonic marking was only used for adult delta smelt as preliminary tests showed increased mortality for juveniles. Most photonic marks were readily visible by direct observation of fish in a petri dish. We also used the SE MARK[™] detector or a stereomicroscope when photonic marking required further verification. We observed 100% retention of photonic marks in all recovered calcein-marked adults released in February and March 2009.

All recaptured delta smelt were independently examined for calcein and photonic marks by at least two persons. All unmarked delta smelt were considered wild fish. Although it was

considered very unlikely, it was deemed possible that marked adults could successfully reproduce in CCF and bias the juvenile salvage that follows the adult salvage period. Thus, all adults were trans-generationally marked with strontium chloride hexahydrate to provide a means to distinguish between wild and culture-origin offspring salvaged at the SFF. The effectiveness of trans-generational marking in distinguishing marked and unmarked fish was tested in the lab and results showed no overlap in Sr isotopic ratios between the otoliths of offspring from marked and unmarked fish. Hence, the method is considered valid (Hobbs *et al.* In progress, UC Davis, CA). Trans-generational marking resolved the California Department of Water Resources (DWR) concerns that the offspring of earlier released cultured adult delta smelt into CCF would count against their ESA-mandated take limits.

Fish releases

We released juvenile and adult fish during actual export conditions to assess fish facility efficiency and pre-screen loss. Marked fish were released downstream of the trash rack in front of SFF primary louvers to assess fish facility efficiency (location 1 in Figure 1), (Figure 2). In response to seasonal temperature increases, juvenile fish were acclimated to ambient temperatures for ca. a week prior to their release at the SFF and CCF in June 2008-09. Five-gallon black buckets secured with a rope in the handle and another rope attached to the bottom of the bucket were used to empty the bucket just above the water surface. Juvenile delta smelt were released midday at two CCF locations in June 2008 to obtain initial estimates of loss in CCF: near intake channel (location 2) and near the center of CCF (location 3), (Figure 1). A total of 500 marked juveniles were transported by boat (ca. 250 fish / 20-gallon carboy) to the west side of Clifton Court Forebay and released on June 12, 2008. A total of 2,647 marked juveniles were transported by boat in 20-gallon carboys (ca. 500 fish per carboy) to the middle of CCF and released on June 26, 2008 (Figure 1). In 2009, adult and juvenile fish were released in CCF from the boat ramp adjacent to the radial gates to assess percent recovery at the SFF and to estimate pre-screen losses (location 4, Figure 1). Fish were released in CCF in early afternoon hours in February, March and June, coinciding with a period of day-today export operations.

Release controls

Control groups of marked fish were held in tanks at ambient water temperature to evaluate post release survival of marked fish. Water originally diverted into CCF was pumped to the control tanks from the export channel immediately downstream of the primary louvers of the SFF.

Control fish were fed daily and held in predator-free 235-gallon circular tanks (122 cm diameter x 76 cm height) at the FCCL. Tanks were covered with shade cloth to protect fish from avian predators. Controls were terminated after no fish were recaptured at the SFF for at least a week.

Fish recapture

Fish were recaptured from routine Department of Water Resources (DWR) fish counts after their arrival to the SFF (Figure 2). Whenever possible we inspected all the salvaged fish collected in the fish holding tanks and from the routine DWR fish counts (total census). The total census of the holding tanks was completed just prior to loading of transport truck and release in the Delta. Due to constraints on the authorized take of other listed species, routine DWR counts were only used to estimate the number of marked fish recovered from the March 2009 experiment. The number of marked fish recovered was calculated by multiplying the number of marked fish observed in each routine count by the time period of fish collection divided by actual duration of the counts (usually a fraction of the collection time). This formula is the same procedure used to estimate fish salvage. A few of the marked fish were also obtained alive from the SFF's secondary louver channels as part of DWR's routine weekly predator removal operations in the secondary bypass. No attempt was made to examine stomach contents of potential delta smelt predators.

Data analyses

Fish facility efficiency (*FFE*) was computed as:

$$FFE = 100 \frac{TRrec}{TRrel}$$
;

where *TRrec* is the total number of marked fish that were released at the trash rack and recaptured in the regular counts, total census and in the weekly predator removal operations. *TRrel* is the number marked fish released at the trash rack.

Percent recovery (PR) was computed as:

$$PR = 100 \frac{CCFrec}{CCFrel};$$

where *CCFrec* is the number of marked fish recaptured at the SFF that were released at a particular location in CCF and *CCFrel* is number of marked fish released at the corresponding

location in CCF. In the case of fish released at the radial gates, we further define percent of entrainment loss as 100 - PR (e.g. total entrainment losses of non-salvaged fish).

Percent pre-screen loss in CCF (PSL) was computed as:

$$PSL = 100 \left[1 - \left\{ \left(\frac{RGrec}{RGrel} \right) \left(\frac{1}{0.01FFE} \right) \right\} \right];$$

where *RGrec* is the number of marked fish recaptured at the SFF that were released in the radial gate area and *RGrel* is number of marked fish released at the radial gate area and *FFE* is as defined earlier.

Bypass velocity ratio (BR) for primary or secondary louvers at SFF is defined as:

$$BR = \frac{Vb}{Vc}$$
;

where *Vb* is the water velocity entering the primary or secondary bypass openings and *Vc* is the average channel velocity upstream of the louvers (Bates *et al.* 1960). Bypass velocity ratios above 1.0 provide a "capture velocity" for fish near the bypass entrance (Bowen *et al.* 2004). More detailed formulas used to compute *BR* and water velocities are included in the appendix.

The daily residence time for entrained water in CCF over each recapture period (*T*) was computed as:

$$T = \frac{V}{O}$$
;

where *V* is the estimated volume of CCF at 12:00 a.m. and *Q* is the daily average outflow (export). Because changes in outflow and residence time of CCF often exceeded 100% over the course of a mark-recapture experiment, average *T* was computed over different periods to evaluate hydrodynamic patterns during mark-recapture experiments. Daily exports were obtained from the Day-flow database (http://www.water.ca.gov/dayflow/). Daily water volume of CCF was provided by Tracy Hinojosa (DWR, Sacramento, CA). Michael MacWilliams (River Modeling) further provided hourly volumes used to estimate volume of CCF at 12:00 a.m.

Results

Fish Facility Efficiency, Percent Recovery and Pre-Screen Loss

Juvenile Experiments (June 2008-2009)

Only 24% to 30% of the juvenile fish released upstream of the primary louvers at the SFF in June 2008-2009 were recaptured at the SFF, indicating low fish facility efficiency (mean = 27.0%, SE= 3.0, Table 1). The recovery of all juvenile delta smelt released in CCF -west side (intake channel area), center and east side (radial gate area) - took place within 4 days in 2009 and 7 days in 2008. Increasing distance between the release location and SFF did not result in consistent increase of recovery time (Table 2). Juvenile experiments in June 2008 and 2009 occurred during a period of lower water exports and higher residence time in CCF when compared to adult experiments (Table 2). Moreover the daily peak in percent recovery of juveniles occurred just one day after the releases, both in the west side and center of CCF (Figure 3A) and in the east side of CCF (Figure 3B). The juvenile delta smelt group released in June 2009 showed extremely low percent recovery (0.03%) and extremely high pre-screen loss (99.88%).

Daily survival of juvenile delta smelt controls remained consistently high at ambient temperatures below 27 °C for 5 days following the last fish recovery. In contrast, survival declined strongly when maximum water temperatures reached a threshold (c.a. 27.5-28.0 °C). Subsequent decrease in water temperatures below that threshold did not prevent further decline in juvenile survival (Figures 4A, 4B).

Adult Experiments (February-March 2009)

Photonically-marked fish groups released at the SFF in February and March 2009 had recapture rates ranging from 36% to 89 (Table 1). The average fish facility efficiency was slightly higher in February (53.2%, SE= 12.2) than in March (44.0%, SE= 1.0). Hence, overall fish facility efficiency was only about 50% for adult delta smelt.

The percent recovery for adult delta smelt released at the radial gate area over four consecutive days from February 24 to 27, 2009 was very low (mean= 3.01%, SE=0.78). The peak recovery per group occurred 2 or 3 days after the release and except for one fish, all fish were recovered within 10 days (Table 2, Figure 5A). The pre-screen loss for the February 2009 release group was very high (mean= 94.3%, SE=1.5). On the other hand, the survival rate (S) of control marked fish held at the lab remained very high until the control was terminated on March 16, 2009 (S = 99.3%, n = 400). Thus, the very low recovery can not be attributed to experimentally induced post-release mortality (i.e., the handling and marking).

Compared to February experiments, the recaptures from radial gate area releases conducted on March 26 and 27, 2009 occurred over a shorter period and only within five days from the releases. March experiments coincided with a period of lower exports and higher residence time in CCF (Figure 5B). Although take restrictions on winter-run Chinook salmon prevented total censusing during the March 2009 experiments, regular fish counts sub-sampled approximately 25% of the fish salvaged at the SFF. Despite expanding the number of mark-recaptured fish in DWR counts, the percent recovery for both fish groups released in March was extremely low (mean= 0.41%, SE=0.41, Table 2). Hence, the estimated pre-screen loss for the March 2009 release group was extremely high (mean= 99.1%, SE=0.9). Similar to the February 2009 experiment, the survival rate of the control fish held in the lab in March 2009 was still very high on March 31 (S=100%, n=100); the last day marked fish were recovered, Survival was still 98% when the control experiment was terminated on April 20, 2009.

Size Composition of Delta Smelt

The size composition of recaptured delta smelt overlapped with that of unmarked wild delta smelt when the later were also reported at the SFF (Figure 6). No obvious differences were observed between the size of fish released and those recaptured for adult delta smelt released either in February or March 2009 (Figure 6). However, recovered juvenile delta smelt released in the center of CCF in June 2008 and in the radial gate area in June 2009 seemed larger relative to the size composition of released fish (P < 0.001 Mann-Whitney U test); (Figure 6).

Factors Influencing Percent Recovery

The percent of recovered delta smelt at the SFF declined significantly with increasing distance from the release site, both for juvenile releases (Figure 7A) and combined adult and juvenile releases (Figure 7B). Despite the higher fish facility efficiency for adults, the percent recovery for the six groups of adults released at the radial gates between February and March 2009 was consistent with the very low percent recovery of juveniles released in the center of CCF and in the radial gate area.

To evaluate the short-term influence of residence time and export flow on the percent recapture, three day averages were considered for these parameters as all mark-recapture experiments showed a peak in recapture within 3 d from the time of release (except for one of the releases conducted in March 2010 where no fish were recaptured over the entire salvage season). The percent recovery of delta smelt also declined exponentially with increasing residence time in CCF for seven groups of fish released at the radial gate area between February and June 2009 (Figure 8A). Predictably, increased exports were associated with higher percent recovery (Figure 8B). Relative to the number of fish released at the radial gate area, the number of adult delta smelt recovered showed nearly a ten-fold decrease from February to March 2009. A similar ten-fold decrease was observed for juvenile recoveries in June relative to adults in March 2009 (Figures 8A and 8B).

Discussion

Our results revealed significant spatio-temporal variability in fish recapture. Residence time in CCF and the attendant export levels seem to control the extent of entrained delta smelt accounted for at the SWP. Thus, depending on residence time and export levels, similar levels of fish recoveries in the salvage at the SWP could represent substantially different levels of underlying entrainment losses. Only a negligible number of juvenile and adult delta smelt released into CCF were subsequently recovered at the SFF. The substantially lower recoveries for fish released in CCF relative to SFF are ascribed to extremely high pre-screen losses in CCF. The percent recovery of delta smelt showed a consistent decline from February (adults) to March (adults) and then to June (juveniles). Such decreased recovery is primarily attributed to

increased residence time in CCF which increases exposure time to predators and other potential mortality sources to be discussed further. Mean daily water exports from CCF decreased moderately from February to March 2009. However, water exports and CCF storage volume in June were significantly lower. The extremely high loss of juvenile delta smelt in June 2009 was likely due to predation in CCF, which may have been enhanced by unusually low water levels in CCF (coinciding with low exports and high residence time) and extensive aquatic vegetation coverage and increasing temperature in CCF relative to previous adult mark-recapture experiments in 2009. The lower percent recovery juvenile delta smelt in the June 2009 experiment is secondarily attributed to decreased SFF efficiencies through time, as expected, as the size of the test fish decreased.

All past studies to estimate pre-screen loss at the SWP also made use of cultured fishes and a combination of fluorescent dye; coded-wire tags; fin clips (Gingras 1997) and PIT tags (Clark et al. 2009). In addition, release and recapture locations were not constant among all studies. Importantly, all past studies also relied on fish releases at the SFF to derive pre-screen loss estimates. Despite methodological differences among studies, our reported pre-screen losses in CCF are consistent with the high pre-screen losses reported in all previous studies. However, juvenile fish used in previous studies generally had larger mean sizes and experienced lower average pre-screen losses (*PSL*) than those reported in our study: 86.7% *PSL* for 88.1 mm FL Chinook salmon; 82% *PSL* for 53.5 mm FL striped bass (Gingras 1997) and 80% *PSL* for 217 mm FL steelhead (average *PSL* of two estimates by Clark *et al.* 2009).

Relative to fish facility efficiencies for juvenile Chinook salmon (Brown *et al.* 1996), our estimated fish facility efficiencies were generally low for adult delta smelt and substantially lower for juvenile delta smelt. On the other hand, our SFF efficiency estimates for adult delta smelt was nearly 2 times higher when compared to the estimated fish facility efficiency for adult delta smelt at the TFF (22.5 % *FFE*, Bowen and Svoboda, in review). On the other hand, the prescreen accumulation of debris and aquatic vegetation along with the attendant headloss at the TFF trashrack (SDFFF 2003a) could contribute to unaccounted direct losses. This unaccounted direct loss combined with the significantly lower fish facility efficiency at the TFF may contribute to offset CCF losses at the SWP. Thus, possibly explaining the similar long-term median densities between CVP and SWP reported for salvaged delta smelt (Kimmerer 2008). Nevertheless, unaccounted direct entrainment losses between the SWP and CVP may not be assumed similar in the short- or long-term. Besides the absence of a reservoir at the CVP, an

equivalent practical definition of pre-screen loss at the CVP would require an explicit consideration of the significant operational differences between projects.

Prior to the construction of CCF, the original SWP water diversion through the Italian Slough may have greatly reduced unaccounted entrainment losses by salvaging more entrained fish at the SFF. Interestingly, when the SFF facility was disconnected from the Italian Slough and became connected to CCF, Heubach (ca. 1973) reported both a significant decline in the salvage of salmon and a significant increase in the salvage of striped bass at the SFF relative to the TFF. However, since delta smelt reporting started at the SWP in 1968 but not until 1979 at the CVP, a comparison of the salvage of delta smelt between facilities is not possible for the corresponding period.

Reservoirs can delay fish migration, increase the role of predation and fish disease and favor exotic fishes to the detriment of native fishes (Gray and Rondorf 1986; Li *et al.* 1987). Our finding of decreased percent recovery of delta smelt with increasing residence time of CCF or decreased exports (Figures 8A and 8B) is consistent with the inverse relations between survival of outmigrating salmonids in impoundments and their residence time (e.g.Trefethen 1968; Mullan 1980) and with the overall pattern of lower water exports from CCF resulting in higher prescreen losses (Gingras 1997). Residence time and exports act as key forcing factors on prescreen loss. The estimated magnitude and variability of the pre-screen loss strongly suggests that using salvage alone as an entrainment estimate results in significant, and inconsistent, underestimates of delta smelt entrainment into CCF.

Potential Mortality Sources and Study Biases

Several potential mortality sources and experimental biases could individually or in combination account for the pre-screen losses and facility efficiencies reported in our study: 1) predation; 2) starvation; 3) unfavorable physical-hydrodynamic conditions; 4) emigration through CCF intakes; 5) post-mark release induced mortality; 6) use of cultured fish; and 7) calculation biases. These factors are discussed below:

1) Predation mortality: pre-screen loss has been largely explained in terms of predation in CCF (e.g. Kano 1990; Brown *et al.* 1996; Clark *et al.* 2009). The highest population estimates of predators reported by Kano (1990) were white catfish (*Ictalurus catus*, range: 67,000 - 246,000) and striped bass (*Morone saxatilis*, range: 35,000 - 118,000). However, predation by striped

bass may account for much of the pre-screen loss (Kano 1990; Brown et al. 1996) while white catfish feed opportunistically on a broad food base, including invertebrates (Turner 1966). Yet, the number of predator-sized striped bass in CCF may have been greatly higher than Kano's estimate (Marty Gingras, California Department of Fish and Game personal communication). Five other species of potential piscivores reported in Kano's (1990) study were: channel catfish (I. punctatus), black crappie (Pomoxis nigromaculatus), largemouth bass (Micropterus salmoides), brown bullhead (I. nebulosus), and Sacramento pikeminnow (Ptychocheilus grandis). In addition, the potential for avian predation in CCF has also been recognized (Mayfield 2008, unpublished data, California Department of Fish and Game, Stockton, CA; Clark et al. 2009). The extremely low recovery of juvenile delta smelt released at the radial gate area in June 2009 took place only within four days from the release. Despite the extended residence time and reduced exports, such short recovery time seems surprising for a release of nearly 14,000 fish. Examination of fish present in the regular DWR secondary bypass flushing to remove predators in June 2009 revealed over 2,000 juvenile striped bass. However, virtually all of them were less than 50 mm FL. The mean size of striped bass in DWR counts was 33.3 mm FL (SE= 1.37) over the juvenile delta smelt mark-recapture period (June 22-26, 2009). Although age-0 striped bass may rely on invertebrates and fish as prey (Stevens 1966), no larval fish were reported among the prey items of age-0 striped bass during the summer (Bryant and Arnold 2007), striped bass may not become piscivore until 70-100 mm FL (Robert Fujimura, California Department of Fish and Game, personal observation). On the other hand, over an annual period, Kano (1990) reported that the lowest sizes of striped bass in CCF occurred in July (Mean= 341 mm FL, SE= 3). Thus, the possibility that striped bass may have preyed upon marked juvenile delta smelt in the SFF is far less likely when compared to predation in CCF.

2) Starvation: Based on the regular influx of water containing plankton and pelagic organisms from the Delta into CCF and the high export/outflow ratio for phytoplankton carbon in the Delta (Jassby *et al.* 2002), and the very short period of fish recapture following the releases in CCF, evidence on starvation induced mortality to account for the observed very high pre-screen losses is lacking. For the smallest corresponding size of delta smelt released in CCF (20 mm FL), cod juveniles (*Gadus morhua*) are able to survive at least a week of food deprivation (Folkvord 1991). On the other hand, cultured larva and juvenile delta smelt up to 120 days post hatch are able to switch prey within 2 hours of exposure to zooplankton (Lindsay Sullivan, In progress, Romberg Tiburon Center, San Francisco State University). Thus, marked delta smelt in CCF are not likely to have experienced starvation mortality within days from their release.

3) Unfavorable physical-hydrodynamic conditions within CCF: although CCF cannot be considered a physically favorable area for delta smelt, the very high pre-screen loss experienced by adult delta smelt in March 2009 (Figure 5B, Table 2) a period of low temperatures, rule out temperature as the cause of high pre-screen loss. For juvenile delta smelt acclimated at 17 °C, Swanson et al. (1998) reported 25.4 °C as the critical thermal maxima (loss of equilibrium endpoint). Based on our temperature controls for juvenile delta smelt initially acclimated to temperatures ca. 20-22 °C (Figures 4A and 4B), cumulative exposure to peak daily ambient water temperatures above 27 °C could have significantly reduced juvenile survival. However, all recaptured juvenile fish released at the radial gate area in 2009 were recovered between June 23 and 25, in spite of the fact that most control juvenile fish were still alive by June 30 (Figures 3B, 4B). Temperature gradients in different areas of CFF, if large enough, could have potentially resulted in survival differences for delta smelt, irrespective of their origin (wild or cultured). Yet, we observed entrained wild juvenile delta smelt being salvaged at the SFF for several days after our last recaptures of marked fish in 2008 and 2009. On the other hand, increased temperatures in CCF could have interacted synergistically with predation (e.g. by increasing prey vulnerability and/ or predator activity).

The hydrodynamic characteristics of CCF can also reduce the likelihood that entrained delta smelt will be salvaged, particularly during low export when residence times are longer. Based on simulated 3D water circulation patterns for CCF during June 2007 (MacWilliams and Gross, In progress), and drifter trajectory during our June 2008 experiments (Cathy Ruhl, USGS, unpublished data) a basin wide counter-clockwise circulation in CCF seemed a persistent hydrodynamic feature. Conceivably, such wind-driven circulation pattern in combination with low exports could enhance dispersion and residence time of entrained fish within CCF, increasing the likelihood of pre-screen loss. On the other hand, during high export and low wind conditions, residence times in CCF are much shorter. Under such conditions most particles are transported roughly in a straight line trajectory from the radial gates to the Banks Pumping Plant (MacWilliams and Gross, in progress).

The observed low reservoir level and excessive aquatic vegetation in June 2009 could have contributed to increased mortality through lack of pelagic habitat and by reducing access to the salvage facility. Other potentially lethal conditions such as contaminants or reduced dissolved

oxygen, if present, should have been also reflected in lower than observed juvenile control survival, making such mechanisms unlikely.

The apparent unfavorable habitat in CCF is consistent with the lack of detection of any transgenerationally marked juvenile delta smelt in salvage operations at SFF following the release of mature adults. Thus, supporting the conclusion that the likelihood of spawning, successful reproduction and rearing to the juvenile stage in CCF is very remote (Castillo 2009; Hobbs *et al.* In progress). Considering that estimates of development time from hatching to a 20 mm delta smelt larvae range from ca. 40 days (Bennett 2005) to 60 days (Mager *et al.* 2004), a newly hatched delta smelt in CCF would most likely be exported from CCF to the pumps rather than being detected in salvage at SFF.

4) Emigration though CCF intakes: Emigration from CCF has been documented for radio-tagged striped bass (Gingras and McGee 1997) and steelhead (Clark *et al.* 2009), two strong swimming species. Clark *et al.* 2009 further accounted for steelhead emigration from CCF through the radial gates and estimated a pre-screen loss of 78%, relative to 82% without emigration. However, they suggested that this lower estimate could underestimate pre-screen loss given the uncertainty of the radio telemetry data used in such calculation.

Water velocity through the radial gates often exceeds 300 cm/s (Kano 1990) and approaches 400 cm/s at maximum CCF/Old River stage differential (Gingras 1997). In contrast, the critical swimming speed juvenile-adult delta smelt (40-60 mm SL) has been estimated to be ca. 25-29 cm/s (Swanson *et al.* 1998, 2000). Hence, potential emigration of delta smelt through the CCF intakes seems unlikely, except toward the end of the water intake period when water velocities become significantly reduced.

5) Potential marking induced mortality: based on the extremely high survival of control adult fish and the very high survival of juvenile marked fish at temperatures below 27°C, this scenario seems unlikely. Further, we conducted laboratory tests designed to evaluate striped bass predation on marked and unmarked delta smelt. These revealed no significant differences between marked (calcein and photonic marking) and unmarked delta smelt. Moreover, these tests suggested no significant differences on predation among the photonic mark colors used in our field experiments (Castillo *et al.* in preparation).

6) Use of cultured fish: the extent to which potential differences between cultured and wild delta smelt may have affected our results is unknown. Predator avoidance in other species seems more developed in fish habituated to predators (e.g. Patten 1977; Healey and Reinhardt 1995; Berejikian 1995; Alvarez and Nicieza 2003). Nevertheless, a mark-recapture test of 383 field collected juvenile Chinook salmon released in CCF in May 1996 resulted in only 0.32% of the fish being recovered at the SFF (Jerry Morinaka, California Department of Fish and Game, Stockton, unpublished data). Assuming 75% fish facility efficiency (e.g. the mid-range value estimated by Brown et al. (1996), such recovery would correspond to a 99.6% pre-screen loss for Chinook salmon habituated to predators. Thus, results from other species and environments may not be safely extrapolated to our study, particularly if the habituated fish have not been recently exposed to predators in the wild.

Comparison of secondary louver efficiency at three different speeds between cultured and wild delta smelt revealed no significant differences (Bowen 2005). These results lend support to use of cultured delta smelt to approximate the behavior of wild fish to louver systems. On the other hand, the CHTR experiments revealed that wild delta smelt experienced higher levels of cortisol response and took longer to recover than cultured delta smelt (Afentoulis and Rockriver, In progress, California Department of Fish and Game, Stockton, CA). Therefore, cultured and wild delta smelt may differ in their physiological responses to human-induced stress. Despite the lack of enough wild delta smelt for research purposes at the time of our study, further field experiments to address this potential bias could be considered.

7) Calculation Biases: pre-screen losses were inferred from the number of recovered fish released at the radial gate area and from facility efficiencies. Facility efficiencies were estimated a few days before fish released in CCF were recovered at the SFF. Therefore, short-term changes in fish facility efficiency could have affected actual pre-screen loss. Yet, such estimation biases are negligible when considering the relatively smaller contribution of facility losses relative to the pre-screen losses in CCF (Tables 1 and 2). Our estimated fish facility efficiencies also accounted for potential predation losses. Nevertheless, our results should reflect the prevailing facility efficiencies under normal operation conditions. Over the course of our experiments, DWR continued conducting routine weekly removal of predators from the secondary bypasses. Continued search for marked delta smelt was conducted by DWR operators in regular counts through the end of the salvage season. Based on our results and all previous pre-screen loss studies conducted at the SWP, we further found no statistical evidence

that the number of fish released at the radial gate area of CCF affects pre-screen loss or percent recovery estimates (F test, P > 0.16).

Because we only considered fish recovered from the regular counts, total census and weekly secondary bypass flush, subsequent salvage related losses due to the hauling, transport, and release fish in the Delta are not accounted for in our fish facility efficiency estimates. Additional losses could be inferred from DFG CHTR Acute Mortality and Injury Study (Morinaka, In Press).

Management Implications

The record low abundance of delta smelt since the early 2000s and the high level of prescreen losses reported for delta smelt in this study, and for other species in previous studies, point out the critical need to reexamine current management practices. Such assessment could accelerate the development of new management options to better account for delta smelt entrainment losses and reduce or eliminate pre-screen losses. Importantly, given the significant decline of delta smelt in salvage since the mid 2000s, the likelihood of detecting entrained delta smelt in salvage could be substantially lower relative to pre-decline years. Thus, management actions to eliminate or greatly reduce pre-screen losses could result in enhanced detection of entrained delta smelt and other species at the SFF. This in turn, could facilitate active adaptive management through improved evaluations on the effectiveness flow management to control fish entrainment (e.g. Old and Middle river flows).

We found that the number of entrained fish per salvaged fish in different periods could potentially vary 10-100 fold. Thus, salvage seems a highly inconsistent predictor of delta smelt entrainment. This is evidence that the continued use of salvage as an index of delta smelt entrainment could compromise the intended management purpose of the salvage process and derived delta smelt take estimates. Despite the very low estimated detection of entrained fish in the salvage at the SWP, one initial option would be to consider using correction factors for unaccounted pre-screen losses and fish facility efficiencies similar to those developed for Chinook salmon.

The implications of our study are relevant to some long-standing management issues in CCF involving residence of delta smelt in CCF. For instance, in response to elevated salvage for juvenile delta smelt in May 2007, SWP exports were discontinued from May 31 to June 9, 2007.

However, upon resumption of exports, delta smelt salvage continued until early July. Whether the seasonal salvage reported from June 10 onwards resulted from potential delta smelt residing in CCF prior to May 31, or due to newly entrained delta smelt, or a combination of both, is unknown. Retrospective assessment of this salvage event suggests that adaptive management and regulatory flexibility, if had been in place, could have been considered to resolve this uncertainty. For instance, rather than stopping pumping on May 31, continued pumping from CCF while keeping the radial gates closed, to some extent, would have reduced residence time in CCF and enhanced potential detection of entrained delta smelt in the salvage during the period in which the radial gates were closed.

Evaluation of management efforts to effectively limit fish entrainment through flow restrictions in the south Delta could be improved by considering complementary management options, namely, reducing pre-screen losses and promoting enhanced detection of entrained fish at the salvage facilities. Suggested options to reduce prescreen losses in CCF have included: 1) removing predators from CCF (Tillman 1995); 2) export operational criteria to minimize exposure of entrained fish to predators within CCF (Gingras 1997) and 3) alternative configuration of the fish facility and intake channel (SDFFF 2003b). These management options are discussed below:

Predator removal: this option was suggested as a measure to reduce SWP impacts on winterrun Chinook salmon and delta smelt (Tillman 1995). However, a general review of 250 fish
control projects indicated that most were unsuccessful (Meronek *et al.* 1996). In the case of
CCF, predator removal to limit pre-screen losses was deemed unfeasible by Gingras (1997)
based on the rationale provided by Gingras and McGee (1997), namely: i) CCF is an open
system. Thus, any reduction in predators at CCF would have no effect on striped bass
recruitment as predator removal would be offset by movement of predator-sized striped bass
into the forebay; ii) Methods for abundance estimation at that time were not valid when CCF is
operated normally and iii) The success of predator control efforts would be ambiguous as
changes in pre-screen survival attributable to predator removal efforts could not be easily
quantified. In addition, the lack of consensus on criteria to quantify success of predator control
efforts has been a major reason why such efforts have not been implemented in CCF (Gingras
and McGee 1997). Using delta smelt pre-screen loss estimates as a success criteria in predator
control may be confounded by high variability of pre-screen loss as suggested in our delta smelt
experiments. Moreover, Gingras and McGee (1997) suggested that the level of exploitation to

substantially reduce predation at CCF would need to be very high. Such predator control scenario could be counterproductive if it results in concurrent take of listed species in CCF.

- 2) Export operational criteria: this option was based on a review of eight studies in which Chinook salmon were released in CCF to evaluate pre-screen loss (Gingras 1997). This review indicated that export level is inversely related to pre-screen loss. Gingras (1997) further concluded that operational criteria are warranted to minimize the time entrained juvenile salmon are exposed to predation in CCF. Yet, to prevent additional entrainment, such criteria would require increasing exports while keeping the radial gates temporarily closed. Our results are also consistent with the potential development of operational criteria aimed at reducing delta smelt entrainment and residence time in CCF. However, because Hill's (1998) radial gate equations do not describe well the current radial gate operations, MacWilliams and Gross (in progress) recommended updating the implementation of CCF operations in the DSM2 model.
- 3) Alternative configuration of the fish facility and intake channel: This is the best short-term option to greatly reduce or eliminate pre-screen loss in CCF while potentially providing greatly enhanced monitoring of entrained fish. Our results support Kano's (1990) conclusion that a reservoir preceding a fish screen system such as CCF and SFF increases the opportunity for fish predation and should be avoided. A number of alternative designs to the SWP have been proposed to significantly reduce pre-screen losses in CCF (SDFFF 2003b, 2003c). Potential options include: i) completely bypassing CCF by diverting Delta water through the Italian Slough, as the SWP was originally operated; ii) remove CCF by creating a narrow intake channel along the west side of CCF leading to the existing SFF, and iii) constructing a state-of-the-art salvage facility with positive barrier fish screens at the intake of CCF (Gingras and McGee 1997). Any of the previous alternative configurations would reduce residence time of fish at the SWP and hence, reduce pre-screen losses due to stressors.

Future Entrainment Monitoring and Evaluations

Our results support the need for a comprehensive entrainment monitoring and the continued evaluation of experimental methods to better interpret and validate critical relations between salvage statistics and the magnitude and variability of direct delta smelt losses in CCF. We recommend further studies to evaluate month-to-month pre-screen losses and fish facility

efficiencies over the seasonal salvage periods for juvenile and adult delta smelt. Such studies would be useful to further quantify the extent to which additional entrained fish into CCF could be salvaged by manipulating CCF residence time, exports and SFF operations. However, initial analyses could be readily performed by integrating our results and those of MacWilliams and Gross (in progress) with previous studies (Gingras 1997, Clark *et al.* 2009). Because our average monthly adult delta smelt entrainment estimates at the SWP ranged from values similar to those assumed for SWP-CVP by Kimmerer's (2008) to losses ca.10 times higher, we further recommend modeling population-level effects of entrainment based on separate empirically derived entrainment estimates for the SWP and CVP, coupled with further estimates of near-field and far-field water project related losses and population size. Additional studies are critically needed to enhance the larval fish sampling and to quantify larval loss at the SWP and CVP. Moreover, the survival of salvaged delta smelt following their release in the Delta remains an important question.

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Figure 1. Location of Clifton Court Forebay, the John E. Skinner Delta fish Protective Facility (SFF) in the south Delta of the upper San Francisco Estuary. Locations denoted by numbers are release locations: (1) trash rack upstream of primary louvers; (2) west side of Clifton Court Forebay; (3) center of Clifton Court Forebay and (4) radial gate area. Light color in the upper San Francisco Estuary denotes the distribution of delta smelt (adapted from DFG-IEP).

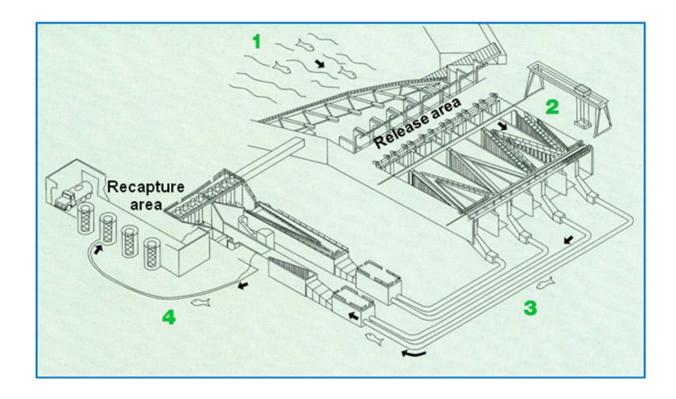


Figure 2. Schematic of Skinner Fish Protective Facility (SFF) and passageway for salvaged fish in the facility. Indicated are release and recapture areas for marked delta smelt. 1: intake channel from Clifton Court Forebay; 2: primary louvers; 3: bypass pipes toward the secondary louvers/screens; 4: holding tanks where fish are collected. Recapture area only shows holding tanks for the old building. The old and/or new buildings were operated by DWR during the present study (adapted from DWR).

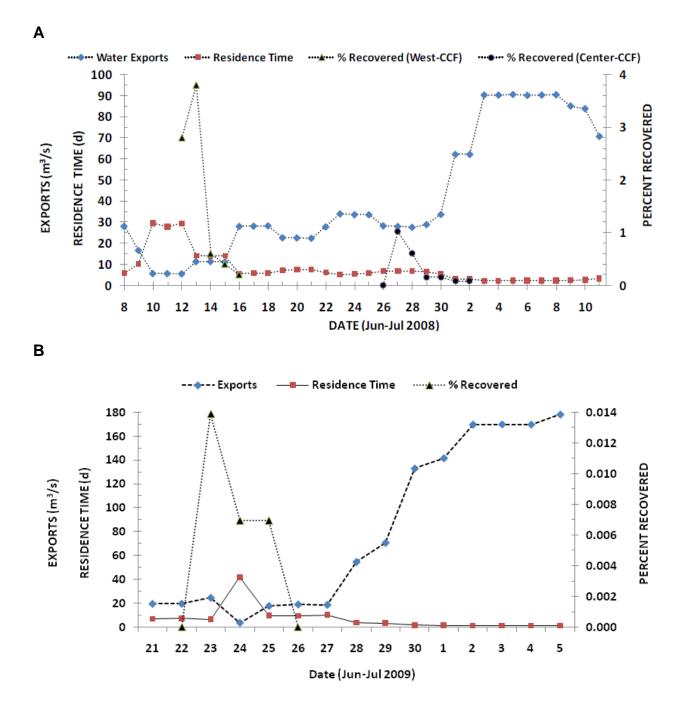
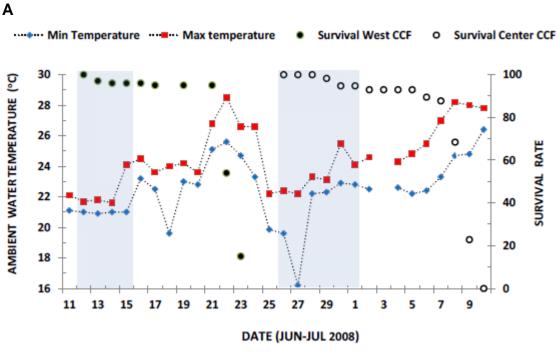


Figure 3. Daily water exports and residence time in Clifton Court Forebay in relation to the percent of calcein-marked juvenile delta smelt recovered at the Skinner Fish Facility: (**A**) Two groups of fish released in the west (n = 500 fish, June 12, 2008) and the center of Clifton Court Forebay (n = 2,647 fish, June 26, 2008). (**B**) One group of fish released in the radial gate area of Clifton Court Forebay (n = 14,413, June 22, 2009).



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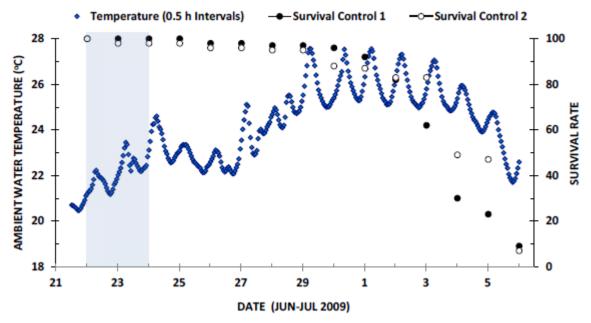
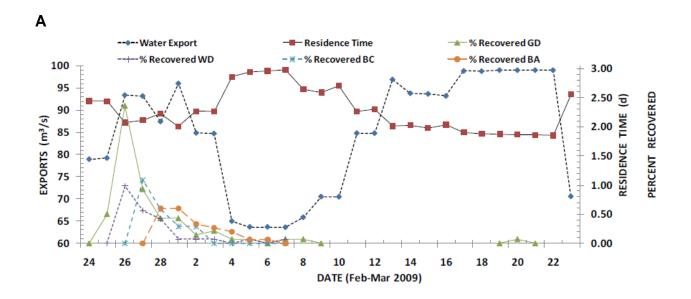


Figure 4. Daily survival of calcein marked juvenile delta smelt controls exposed to ambient water temperature: (A) Controls for releases conducted in the west and center of Clifton Court Forebay on June12 and 26, 2008. (B) Controls for the releases conducted in the east side of Clifton Court Forebay (radial gate area) on June 22, 2009. Bars denote the period between each field release and the last recapture. Initial number of fish per control was 100 at the time of releases in CCF.



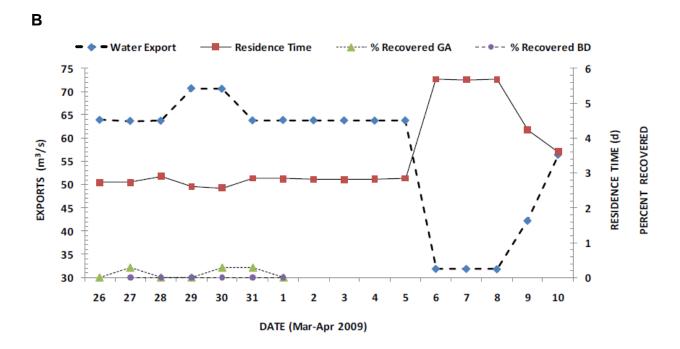


Figure 5. Daily water exports and residence time in Clifton Court Forebay in relation to the percent of recovered calcein- and photonically-marked adult delta smelt released in the radial gate area of Clifton Court Forebay: (A) Four fish groups released on February 24-27, 2009. (B) Two fish groups released on March, 26-27, 2009. Photonic mark codes are shown in Table 2.

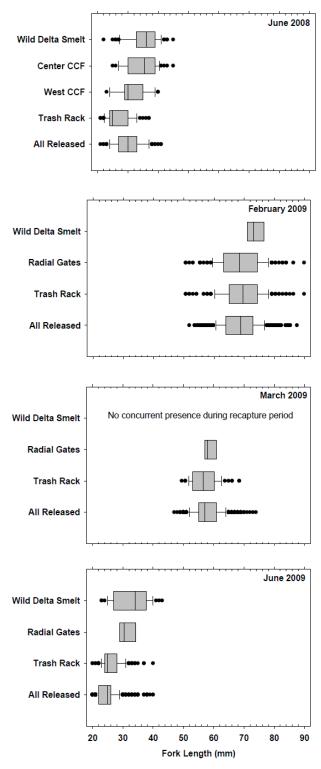


Figure 6. Size composition of marked (cultured) and unmarked (wild) delta smelt concurrently collected at the Skinner Fish Facility during mark-recapture experiments in June 2008 and 2009 (juveniles) and in February and March 2009 (adults). Size composition prior to releases is denoted as all released.

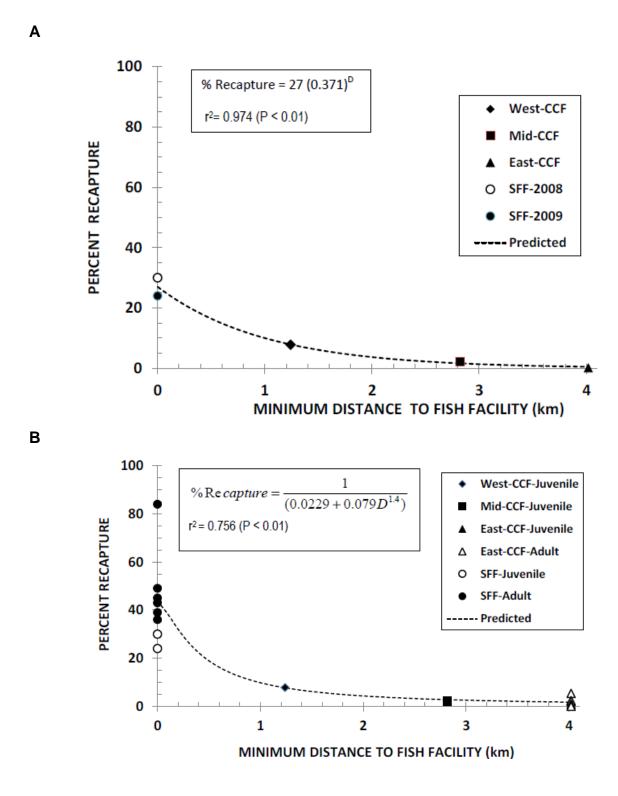


Figure 7. Percent of recaptured delta smelt at the Skinner Fish Facility as a function of the minimum distance (D) from each release site to the Skinner Fish Facility: (A) Juvenile delta smelt. (B) Combined juvenile and adult delta smelt.

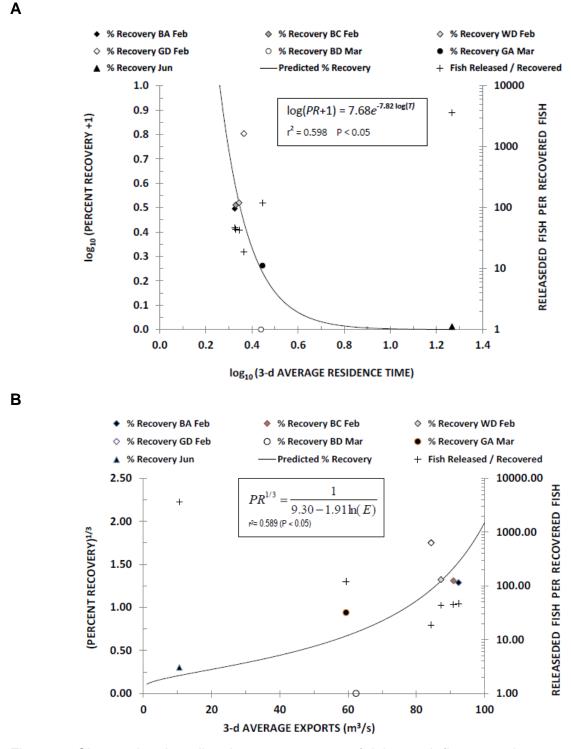


Figure 8. Observed and predicted percent recovery of delta smelt (log_{10} or cube-root transformed) as a function of: (**A**) residence time and (**B**) exports for releases conducted from February to June 2009. The total number of released fish per recaptured fish is indicated in the right axis (excluding the BD group released in March in which no fish were recovered).

Table 1. Delta smelt released and recaptured at the Skinner Fish Facility, south Delta, in February (adults), March (adults) and June 2008-2009 (juveniles) and concurrent mark-recapture results and hydrodynamic conditions.

						Secondary Bypass Ratio				
Experiment	Mark ¹	Release Date	Mean daily Export (cfs)	Channel Velocity ² (ft/s)	Primary Bypass Ratio	Old Bldg	New Bldg	No. Fish Released	No. Fish Recaptured ³	Facility Efficiency
SFF1	GA/D	2/23/09	2896	3.27	1.22	1.24	0.61	100	39	39
SFF1	W-A/D	2/23/09	2896	3.27	1.22	1.24	0.61	100	36	36
SFF1	B-C/D	2/23/09	2896	3.27	1.22	1.24	0.61	100	89	89
SFF1	B-A/D	2/23/09	2896	3.27	1.22	1.24	0.61	100	49	49
SFF2	G-A	3/23/09	2498	3.10	1.19	1.21	N/A	100	43	43
SFF2	B-D	3/23/09	2498	3.00	1.22	1.21	N/A	100	45	45
	-	•								•
SFF0	Calcein	6/04/08	2260	1.70	1.19	1.21	N/A	200	60	30
SFF3	Calcein	6/19/09	532	1.30	1.22	N/A	1.18	800	193	24

¹ First letter denote photonic mark colors: B, G, W (blue, green, white). Second and third letters denote marked fins per fish: A, C, D (anal, caudal, dorsal). All juvenile and adults were calcein marked.

² Average channel velocities upstream of louvers at the time of fish releases.

³ Total time from release to the last recaptured fish < 24 hr.

Table 2. Delta smelt released in Clifton Court Forebay and recovered at the Skinner Fish Facility, south Delta in February (adults), March (adults) and June 2008-2009 (juveniles) and concurrent recapture results and hydrodynamic conditions.

Experiment	Mark ¹	Date of Release	Total Days ²	Mean Daily Export (cfs) ³	Residence Time (days) ³	Fish Released n	Fish Recaptured n	Percent Recovery	Pre-Screen Loss
RG1	G-D	2/24/09	24	2945	2.36	1398	75	5.36	89.9
RG1	W-D	2/25/09	10	2880	2.42	1426	33	2.31	95.6
RG1	B-C	2/26/09	4	2822	2.47	1382	31	2.24	95.8
RG1	B-A	2/27/09	7	2778	2.53	1501	32	2.13	96.0
RG2	G-A	3/26/09	5	2233	2.77	1447	12	0.83	98.1
RG2	B-D	3/27/09	none	2226	2.78	1402	0	0.00	100.0
West-CCF	Calcein	6/12/08	5	674	8.63	500	39	7.80	-
Mid-CCF	Calcein	6/26/08	7	1914	3.89	2647	55	2.08	-
RG3	Calcein	6/22/09	3	957	9.54	14413	4	0.03	99.9

¹ First letter denote photonic mark colors: B, G, W (blue, green, white). Second letter denote marked fins per fish: A, C, D, C (anal, caudal, dorsal). All juvenile and adults were calcein marked.

² Total days: days from release to last recapture.

³ Daily mean over 10 days post-release.

Appendix.

Calculation of primary and secondary bypass ratios

Primary Bypass Ratio Calculations

Primary flow per bay =
$$\frac{\text{Primary channel flow}}{\text{No. of bays in use}}$$

Secondary Bypass Ratio Calculations

Secondary bypass ratio =

(Secondary channel approach velocity)