

Effects of predator and flow manipulation on Chinook salmon (*Oncorhynchus tshawytscha*) survival in an imperiled estuary

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Abstract We evaluated the effects of non-native, piscivorous fish removal and artificial flow manipulation on survival and migration speed of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, emigrating through the eastern Sacramento-San Joaquin Delta of California (Delta) using a Before-After-Control-Impact study design. Acoustically-tagged salmon survival increased significantly after the first predator reduction in the impact reach. However, survival estimates returned to pre-impact levels after the second predator removal. When an upstream control gate opened (increasing flow and decreasing tidal effect) juvenile salmon emigration time decreased and survival increased significantly through the impact reach. Though a short-term, single season experiment, our results demonstrate that predator control and habitat manipulation in the Delta tidal transition zone can

be effective management strategies to enhance salmon survival in this highly altered system.

Keywords Predation · Telemetry · Tidal · Flows · Sacramento—San Joaquin Delta

Introduction

The San Francisco Estuary is the largest of its kind on the west coast of North America and among the most altered ecosystems in the United States (Cohen and Carlton 1998). Diversions from the Sacramento-San Joaquin Delta (Delta), the upper extent of tidal estuary, provide water for 25 million people and support a \$32 billion agricultural industry (CDFA 2006). Juvenile Chinook salmon (*Oncorhynchus tshawytscha*), including two endangered stocks, suffer high mortality rates as they migrate through the industrialized Delta (Perry et al. 2010), and predation by striped bass (*Morone saxatilis*) and other non-native fish is thought to be one of several major contributing factors although to what extent has not been established (Nobriga and Feyrer 2007; NMFS 2009). Flow, turbidity, habitat quality, and predator density are thought to influence predation (Anderson et al. 2005), but no Delta experiments have evaluated the relative influence of these factors (although see Lindley and Mohr 2003 for a paper modeling striped bass predation on winter-run Chinook salmon). As a consequence, the

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efficacy of predator removal as a potential management action is also unclear.

The need to aide in the recovery of salmon populations, identified as endangered or threatened under federal and state regulations (Lindley et al. 2004), while also allowing for continued use of water for societal purposes (e.g. hydropower, flood control, municipal and agricultural diversions) has led to increased interest among resource managers for the potential implementation of predator control measures throughout major salmonid systems of the Pacific United States (Beamesderfer et al. 1996; Zimmerman and Ward 1999). However, there is considerable uncertainty regarding whether such actions might be effective in the Delta. The failures of predator control programs implemented elsewhere have been attributed to a number of factors, including: 1) prey populations were not limited by predation, 2) removal efforts did not impact a sufficiently large fraction of the predatory population, 3) strong evidence was lacking for the benefits of predator removal, 4) poor understanding of non-native predator life history traits, or 5) large removals triggered a compensatory response in the predator populations (Hubbs 1940; Jacobsen 1945; Meachum and Clark 1979; Otis 1988; EIFAC 1991; Goeman and Spencer 1992; Moyle and Marchetti 2006).

Nevertheless, there have been a number of successes in controlling predaceous fishes. Examples include sea lamprey (*Petromyzon marinus*) in the Great Lakes (Smith and Tibbles 1980; Koonce et al. 1993), reduced predation on sockeye salmon (*Oncorhynchus nerka*) following arctic char (*Salvelinus alpinus*) reduction in Alaska's Wood River system (Meachum and Clark 1979), and the increased production of sockeye salmon following an eradication program of northern pikeminnow (*Ptychocheilus oregonensis*) in Cultus Lake, British Columbia (Foerster and Ricker 1941). Beamesderfer et al. (1996) evaluated the effectiveness of northern pikeminnow removal in the Columbia and Snake rivers. Their results indicated that the number of large piscivorous northern pikeminnow could be significantly reduced by exploitation rates of only 10–20 %. Moreover, they concluded that salmonid survival in the Columbia River would benefit greatly from a low rate of northern pikeminnow exploitation as long as it did not stimulate a compensatory response among other predator populations.

Within the highly engineered Delta system, flow manipulation via artificial pulse and control structure

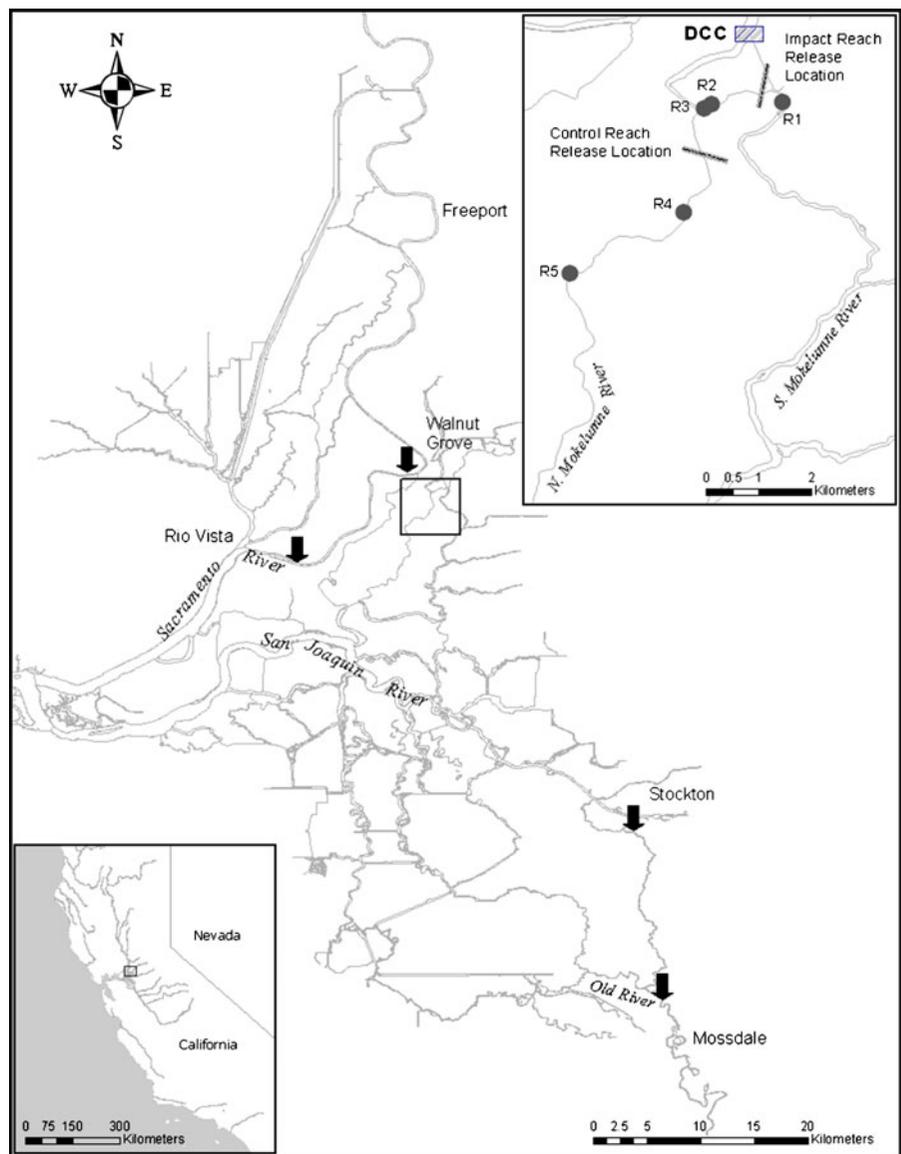
operations has also gained interest in affecting survival of emigrating Chinook salmon (Perry et al. 2010). Analysis of coded-wire tagging releases between 1989 and 2006 in the southern Delta have shown river flows can positively influence juvenile salmon survival, but have also shown considerable variability between and within years. These experiments to-date have been unable to untangle complicated interactions between hydrologic conditions (where river inflow is only one factor) and biological factors such as predation (Hankin et al. 2010).

Though some aspects of Delta salmon ecology are well-studied (Sommer et al. 2001; McLain and Castillo 2009; Perry 2010), no experimental investigations have been conducted to directly estimate short-term, reach-specific changes in salmon survival associated with: 1) intensive predator reduction, and 2) large magnitude flow change (caused by opening of the Delta Cross Channel [DCC]). In this study we examined the relative effects of experimental reductions of potential predators and a flow pulse on the survival of emigrating juvenile Chinook salmon in the Delta.

Material and methods

The study was conducted on the North Fork Mokolumne River between 15 and 30 May 2010, within the migration period of fall-run Chinook salmon and when the DCC operation may change (Fig. 1). The experiment area is approximately 5.6 km of the North Fork Mokolumne River and includes one 1.6 km predator-removal reach (impact) and one 2.0 km control reach. These sites were chosen because they were similar in size, depth and general habitat structure and previous fish sampling in the area demonstrated similar fish species (unpublished data). We utilized a paired Before-After Control-Impact (BACI) design (Stewart-Oaten et al. 1986), where acoustically-tagged fish were released in 8 paired groups (16 subgroups each with 25 to 42 fish; average 32) both before and after predator removal and before and after a change in river flows (DCC opening). Five acoustic receivers were deployed at entrances to all potential study area pathways to detect experimental fish as they emigrated from the study reaches (Fig. 1). Acoustic receivers were retrieved and the final data was downloaded at the study's completion on 29 June 2010.

Fig. 1 Sacramento-San Joaquin Delta. Upper right corner inset shows North Fork Mokelumne River study area including release locations for acoustically tagged fish and acoustic receivers (R1 to R5). Study area was approximately 2.7 km downstream of the Delta Cross Channel (DCC). In the impact reach, survival was estimated from the release point to R2 (1.6 km). In the control reach, survival was estimated from the release point to R4 (2.0 km). Solid arrows bracket the channel length within which riverine conditions (*unidirectional flows*) rapidly change to tidal conditions (*bidirectional flow*). Downstream most arrows indicating transition point at high river flows, upstream most arrows indicating transition point at low river inflows. See Fig. 6 for further information



Our study utilized Juvenile Salmon Acoustic Telemetry System (JSATS) acoustic tags which have been used extensively in rivers of the Pacific Northwest (McMichael et al. 2010), but which are new to the Delta. JSATS acoustic transmitters are small (0.433 g in air; 5.21 mm W×12.00 mm L×3.77 mm H; volume 0.14 ml) and have been designed specifically for use in juvenile salmonids. JSAT tags used in this study were set to a programmable pulse rate (PRI) of 5 s. The ability to tag smaller Chinook salmon is critical because the vast majority of juveniles passing through the Delta are less than 100 mm (Brandes and McLain 2001; McLain and Castillo 2009; Miller et al. 2010).

Tagging procedure

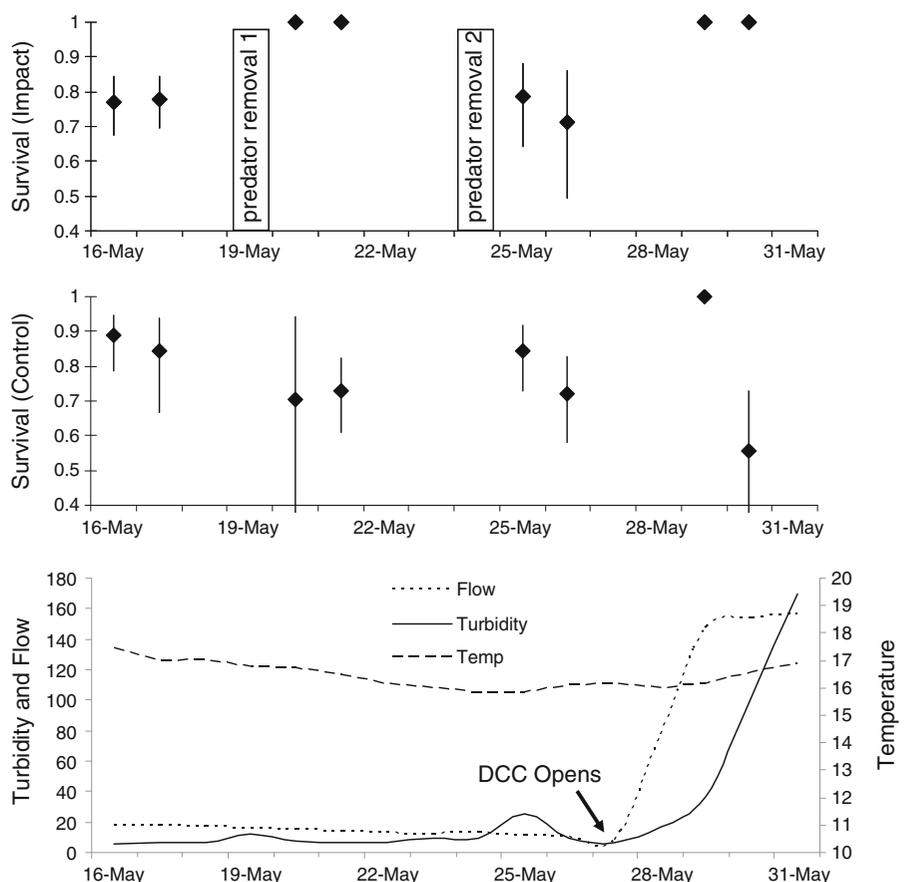
Juvenile fall-run Chinook salmon were obtained from the Mokelumne River Hatchery. Experimental fish averaged 102 mm (86–121±6.9 SD) in fork length (FL), with an average weight of 11.4 g (± 0.8 SD). Only healthy, uninjured, and unstressed fish were used for this study; fish were transferred from the holding area by a dip net with a water sanctuary to an anesthetic tank containing a 100 mg/l buffered tricaine methanesulfonate (MS-222) solution. Once anesthetized, fish were reassessed for health (e.g., infections, abrasions,

hemorrhaging, gill coloration). Fish with obvious injuries, deformations, >20 % scale loss or other health issues were rejected. Fish too small for tag burden (i.e., tag weight >4 % body weight; Zale et al. 2005) or unduly stressed were also rejected. In a surgery cradle, fish were placed ventral-side up and anesthetic solution was pumped into their mouths via a tube attached to a pipette. The anesthetic was flushed over gills in order to keep the fish fully anesthetized throughout the procedure. An incision ~10 mm in length was made parallel to the ventral midline (~3 mm to the side of the ventral midline and 3 mm anterior to the pelvic girdle). A sterilized ultrasonic tag was then inserted into the peritoneal cavity of the fish, placed just under the incision. The incision was then closed with two interrupted sutures (using Suprmid Extra Nylon Cable Sutures). Once finished, fish were placed in live tanks and allowed to recover from surgery and anesthesia for at least 18 h (Moser et al. 1990; Stuehnenberg et al. 1990).

Experimental release

Experimental fish were released at the peak ebb tide available during daylight hours. On days when tagged fish were released, one paired group was released near-simultaneously into both the control and impact reaches. No more than one paired group was released per day. On consecutive days, two paired groups (G_1 and G_2) were released at the beginning of the study (before), 2 paired groups were released on consecutive days after the first predator removal (G_3 and G_4), 2 paired groups were released on consecutive days after the second predator removal (G_5 and G_6) and the final 2 paired groups were released on consecutive days 1 week after the second predator removal (G_7 and G_8). Prior to the release of the last two paired fish groups, the DCC, located upstream, was opened and flow conditions in the experimental area (affecting both the impact and control reaches) changed from tidal influence (9 to 18 m^3 sec^{-1} average daily flow) to river discharge influence (150 m^3 sec^{-1} ; Fig. 2).

Fig. 2 Model averaging-based estimates of mean survival (± 95 % confidence intervals) for salmon in the impact reach (top graph) and control reach (middle graph). Daily average flows (m^3 sec^{-1}), turbidity (NTU), and water temperature ($^{\circ}C$) for the study area (bottom graph)



Predator removal

Boat electrofishing was conducted by a four-person crew using a shallow-draft, 5.3 m aluminum boat (Smith-Root, Electro-fishing model SR-16H; outboard motor with power trim) to perform a three-pass depletion sampling to remove and estimate numbers of potential predators in the impact reach (Raleigh and Short 1981; Meador et al. 1993). A single pass of electrofishing required ~5 s of electrofishing effort per meter of shoreline sampled. The combination of boat design, highly experienced operators, and slow shoreline water velocities allowed fine control of anode position and very thorough coverage of the immediate shoreline area relative to typical boat electrofishing operations. The reach was not blocked by nets because populations within discrete sites can be treated as effectively closed for the 24 h period associated with sampling (Korman et al. 2009). Captured fish were held in a live well with running water until each sampling pass was completed and then transported to holding pens at the bottom of the study site. Individual fish were measured and species was noted. Fish species identified in the literature as potentially predatory (Moyle 2002) were placed in the holding pens until the end of the study and then released to the impact reach (e.g. Fritts and Pearsons 2004; Sanderson et al. 2009). Non-predators were returned to the impact reach after identification and measurement.

Data analysis

We determined predator population density by least squares linear regression of predator catch per effort (CPE; electrofishing pass; y-axis) against cumulative catch (x-axis), lagged for one unit of effort (previous cumulative catch) because each electrofishing removal effort remained constant (Maceina et al. 1995).

We used the Cormack-Jolly-Seber mark-recapture model to estimate survival probabilities for both the control and impact reaches; estimation methods were analogous to those described by LaCroix (2008) and Skalski et al. (2001). For both the impact and control reaches, the full model estimated detection probability and survival for each subgroup. Reduced models for the control reach included modeling survival as constant among subgroups, and modeling

survival as a covariate of flows. In the impact reach, our paired BACI experimental design made it possible to fit a reduced model whereby survival was estimated as a covariate of survival estimates for the control reach, and also as a covariate of predator removal treatments and flows. Specifically our covariate constrained model for estimating survival in the impact reach was:

$$\text{logit}(\Phi_{IGi}) = \beta_0 + \beta_1(\Phi_{CGi}) + \beta_2(I_1) + \beta_3(\text{Flow}) \quad (1)$$

where Φ_{IGi} is the estimated survival in the impact reach for subgroup of paired group i (linked to beta slope parameters by the logit function to constrain parameters to the interval between 0 and 1); Φ_{CGi} is estimated survival in the control reach for subgroup of paired group i ; I_1 is a dummy variable coding for the first predator removal; flow is a dummy variable coding for the change in flow conditions.

We assessed goodness-of-fit (GOF) for the full models using a parametric bootstrapping technique. Reduced candidate models were evaluated for their fit to tag detection data using an information theoretic approach (Burnham and Anderson 2002). Akaike's information criterion adjusted for small sample size (AIC_c) was calculated for each model. Model weights (AIC_{cw}) were then calculated using the difference in AIC_c values between the "best model" and other candidate models. Model weights range from 0–1 and are interpreted as the probability that the model under consideration is the best given the data. Model averaged survival and unconditional confidence intervals were calculated using model weights.

To assess differences in travel times of tagged fish through the study area we used a general linear mixed model with release group as a random effect and tested for effects of flow and fish size. Flows, turbidity and temperatures in the study area were downloaded from CDEC (California Data Exchange Center; <http://cdec.water.ca.gov>) for stations DLC (downstream of DCC) and WBR (Woodbridge Dam on the Mokelumne River). However, flows for our specific study reach are not measured directly, and so we estimated study reach flows using CDEC stations DLC and WBR, and "base" DSM2 HYRDO simulations described by Kimmerer and Nobriga (2008). To assess the influence of river inflows on the location of the tidal transition zone experienced by juvenile salmonids, we calculated percentage of time

with positive flows by river kilometer (rkm), again using DSM2 HYDRO data from Kimmerer and Nobriga (2008).

General trend analyses were performed in using the JMP linear regression model function, which performs an analysis of variance (ANOVA; Sall et al. 2001). AIC, Akaike weights, Bootstrap analyses and mark-recapture estimates were performed in Program MARK (White and Burnham 1999).

Results

Within the study reach, mean daily flows ranged from 18.1 m³ sec⁻¹ (16 May) to 8.6 m³ sec⁻¹ (27 May) before DCC opening to 156.3 m³ sec⁻¹ (31 May) after DCC opening. Mean daily temperatures ranged from 17.4°C (16 May) to 15.9°C (24 May) before DCC opening to 16.9°C after opening. Mean daily turbidity ranged from 5.4 NTU (16 May) to 25.7 (25 May) before DCC opening to 169.5 (31 May) after opening. A total of 641 potential predators, consisting of 15 different introduced taxonomic groups (including hybrids), were removed during the study (Table 1). Each successive electrofishing pass captured fewer predators, indicating predators were being depleted

by removal from the impact reach (Fig. 3). From the depletion relationships depicted in Fig. 3, we estimated 91 % (144 of 158) of predators vulnerable to electrofishing were captured in the first removal (19 May), and 83 % (497 of 601) in the second removal (24 May). The most common predators were *Lepomis* spp. ($n=330$ fish) and *Micropterus* spp. ($n=255$ fish). Ten striped bass were also captured in predator removals.

Goodness-of-fit testing indicated full models for control and impact reaches fit the data well ($P=0.7$ and $P=0.2$, respectively) and \hat{c} was estimated near 1 for both; thus, no evidence of overdispersion in tag detection data. In the control reach, the model estimating survival for each release group (i.e. the full model) provided the best fit with an AIC_c weight > 0.99. For the impact reach, the model including paired survival estimates from the control reach as covariates and which included the first predator removal and flow effects was the “best fit” with an AIC_c weight = 0.72. The next best model was the same as the “best fit”, but also included the second predator removal effect (AIC_c weight = 0.28).

Survival estimates and unconditional 95 % confidence intervals varied considerably among release groups, with mean values ranging from 1 (100 %

Table 1 Potential predatory fish captured in the Impact reach of the North Fork Mokelumne River, 19 and 24 May 2010

| Common name | Scientific name | Removal period | | Fork Lenth (mm) Mean±SD |
|------------------|--------------------------------|----------------|-------------|----------------------------|
| | | 19-May | 24-May | |
| American shad | <i>Alosa sapidissima</i> | 0 | 3 | 365±46.1 |
| Black crappie | <i>Pomoxis nigromaculatus</i> | 0 | 1 | 195 |
| Blackbass hybrid | <i>Micropterus</i> spp. | 8 | 0 | 114±40.7 |
| Bluegill | <i>Lepomis macrochirus</i> | 21 | 91 | 121±27.5 |
| Brown bullhead | <i>Ameiurus nebulosus</i> | 0 | 11 | 110±64.3 |
| Green sunfish | <i>Lepomis cyanellus</i> | 2 | 0 | 126±5.7 |
| Hybrid sunfish | <i>Lepomis</i> spp. | 0 | 21 | 127±25.0 |
| Largemouth bass | <i>Micropterus salmoides</i> | 50 | 81 | 175±79.2 |
| Redear sunfish | <i>Lepomis microlophus</i> | 44 | 171 | 126±28.0 |
| Redeye bass | <i>Micropterus coosae</i> | 0 | 74 | 111±34.0 |
| Smallmouth bass | <i>Micropterus dolomieu</i> | 5 | 0 | 228±99.9 |
| Spotted bass | <i>Micropterus punctulatus</i> | 6 | 39 | 143±64.8 |
| Striped bass | <i>Morone saxatilis</i> | 7 | 3 | 265±62.5 |
| Warmouth | <i>Lepomis gulosus</i> | 0 | 1 | 132 |
| White catfish | <i>Ameiurus catus</i> | 1 | 1 | 270±24.0 |
| | Totals | | 144+497=641 | |

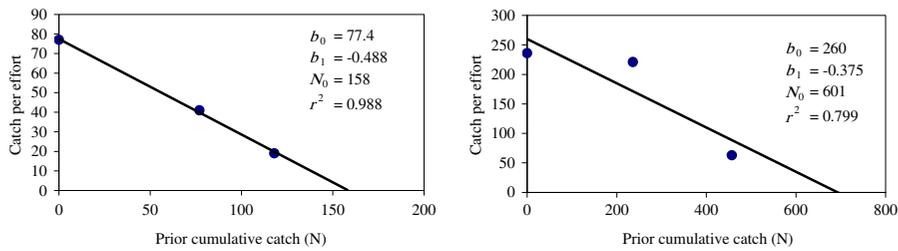


Fig. 3 Plots and regressions for numerical catch per effort versus cumulative catch (N) for the predator removal reach on the North Fork Mokelumne River (see Fig. 1). Three consecutive passes were made in the impact reach on 5/19/2010 (*left*)

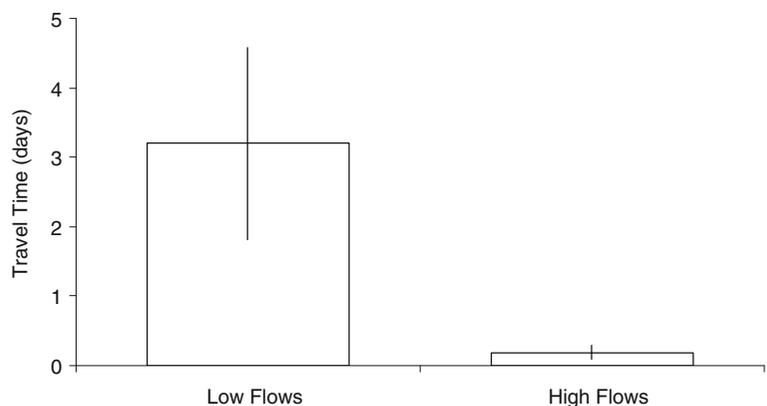
and 5/24/2010 (*right*). Dashed lines indicate least-square regression lines. Regressions intercepts (b_0), regression slopes (b_1), and coefficients of determination (r^2) are given; N_0 represents estimated numbers of predators inhabiting the study reach

survival through the study reach) to 0.55 (Fig. 2). Survival in the control reach varied among the eight release groups, and was not explained by the flow covariate. Impact reach survival also varied among groups, but model selection indicated that a significant proportion of the changes were associated with predator removal and flow effects. Survival improved significantly after the first predator reduction treatment (from <0.80 to >0.99), but estimated survival decreased to pre-impact levels after the second predator reduction treatment (Fig. 2). Flows and turbidity in the study area changed when the DCC gates opened on 27 May 2010. Flow (and turbidity) changes did not clearly influence survival in the control reach; both the highest and lowest survival rates observed occurred on consecutive days in the control reach after DCC gates opened (Fig. 2). However, in the impact reach, estimated salmon survival increased when the DCC gates opened. Opening of the DCC gates was also associated with a significant reduction ($P=0.027$) in travel time through the study area, from an average of 3.19 ± 1.38 days to an

average of 0.19 ± 0.09 days (Fig. 4). In addition to changes in daily average flows (Fig. 3), analysis of 15-minute increment flow data showed opening of the DCC gates stopped tidal reverse flows and caused daily tidal flux to decrease from $250 \text{ m}^3 \text{ sec}^{-1}$ to less than $150 \text{ m}^3 \text{ sec}^{-1}$ (Fig. 5).

The influence of river inflows on the location of tidal transition zones differs among Delta locations. For the Sacramento River, 43 km of riverine habitat (with 100 % positive or unidirectional flow) is added as river flows increase from $292 \text{ m}^3 \text{ sec}^{-1}$ to $837 \text{ m}^3 \text{ sec}^{-1}$ and the tidal transition zone is displaced downstream by approximately 16 rkm (Fig. 6a). With DCC open, the Mokelumne River experienced mostly positive flows, more so with inflows at $18 \text{ m}^3 \text{ sec}^{-1}$ (relative to inflows at $8 \text{ m}^3 \text{ sec}^{-1}$). With DCC closed, the Mokelumne River was entirely tidal and insensitive to the three levels of inflow assessed (Fig. 6b). As San Joaquin River inflows increased from $40 \text{ m}^3 \text{ sec}^{-1}$ to $162 \text{ m}^3 \text{ sec}^{-1}$, the tidal transition zone moved approximately 21 rkm downstream (Fig. 6c).

Fig. 4 Average travel time in days (\pm SE) through the study area for release groups G1 to G6 (*Low Flows*) and for release groups G7 and G8 (*High Flows*). General linear mixed model analysis indicated a significant effect of flow ($P=0.027$), but no significant effect associated with fish size ($P=0.878$)



Discussion

Observational studies using acoustically tagged salmon in the Delta have allowed estimation of survival and migrations rates (e.g. Perry et al. 2010) and are greatly enhancing our understanding of salmon migration behavior. Our telemetric study of juvenile Chinook salmon is novel because it is the first instance of Delta survival and migration rates being estimated for Chinook smolts less than <135 mm, and also because this study marks the first use of acoustic tags as part of an experimental manipulation of predators and flows, two factors thought to influence emigrating salmon in the Delta and elsewhere (Lindley and Mohr 2003). Our results suggest intensive, site-specific predator removals can improve juvenile salmon survival immediately following the first predator removal. However, effectiveness with repeated treatments is unclear. Similar to some previous studies (Goeman and Spencer 1992), we observed an apparent response from the predator removal whereby predator densities increased and salmon survival decreased (to pre-impact levels) following the second predator removal. While mechanisms are unclear, removal of a stable predator community accomplished in the first treatment was apparently undone within one week by an influx of new predators. If site-specific predator removals are to benefit juvenile salmon survival, sustained effort over time (with daily rather than weekly removals) may be necessary. Alternatively, predator removals over a

larger geographic area might be effective in reducing the pool of predatory fish available to re-colonize. On the Snake and Columbia rivers, the apparent success of northern pikeminnow bounty harvest (Beamesderfer et al. 1996) may be attributable to the relatively aggressive and geographically broad scope of predator reductions.

Delta studies have shown increased river flows may be associated with enhanced salmon survival (reviewed by Hankin et al. 2010), but no studies have elucidated the scale at which these benefits may occur. Though the spatial and temporal scope of our study was limited to an intensive investigation over a short time period, juvenile salmon survival changed in apparent response to experimental manipulation of predators and flows. While a significant response to the second predator removal was not apparent, we observed significantly improved survival after the first predator removal in the impact reach and significantly decreased travel times throughout the study area after the DCC gates opened and flow conditions rapidly shifted from tidal (bidirectional) to riverine (unidirectional). Perry et al. (2010) observed slower migration rates and increased mortality for juvenile Chinook salmon entering the tidally-influenced portion of the Sacramento River. Our study is consistent with the analysis by Perry et al. (2010) and supports a mechanism where river flows may affect salmon survival by altering the location of the tidal transition zone. If the tidal transition zone occurs where habitat conditions

Fig. 5 15-min DSM2 HY-DRO simulated flows with DCC closed (top) and DCC open (bottom) and NF Mokelumne River inflows at 8 m³ sec⁻¹ (dashed line), 18 m³ sec⁻¹ (solid line), 47 m³ sec⁻¹ (heavy line). Simulations for DCC open conditions are limited because DCC gates close for flood control when Sacramento River flows exceed approximately 700 m³ sec⁻¹

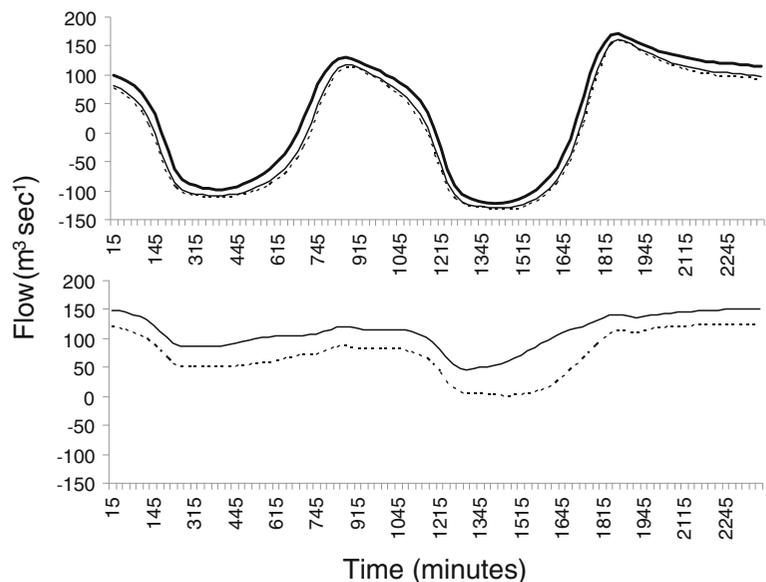
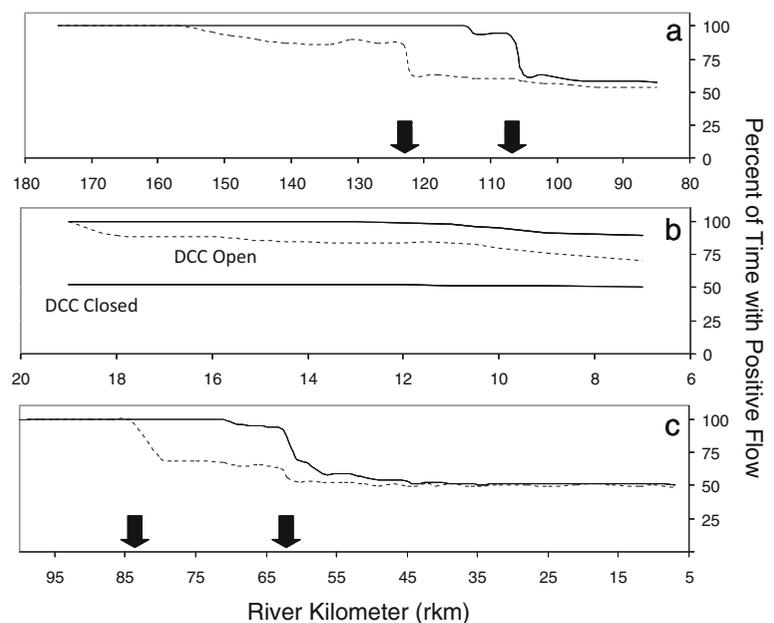


Fig. 6 Transition, by river kilometer, from riverine conditions (*unidirectional flow*) to tidal conditions (*bidirectional flow*). Sacramento River **a** inflow at $837 \text{ m}^3 \text{ sec}^{-1}$ (solid line) and at $292 \text{ m}^3 \text{ sec}^{-1}$ (dashed line). NF Mokelumne River **b** inflow at $18 \text{ m}^3 \text{ sec}^{-1}$ (solid line), and at $8 \text{ m}^3 \text{ sec}^{-1}$ (dashed line) with DCC closed and open. San Joaquin River **c** inflow at $162 \text{ m}^3 \text{ sec}^{-1}$ (solid line) and at $40 \text{ m}^3 \text{ sec}^{-1}$ (dashed line). Moving from upstream to downstream for each inflow level, solid arrows indicate the point of rapid transition from riverine conditions (*unidirectional flow*) to tidal conditions (*bidirectional flow*). Arrows correspond to those depicted in Fig. 1



are poor, or where predator densities are high, juvenile salmon are likely to experience greater predation mortality, and perhaps impaired growth. This should be studied more fully.

Electrofishing depletion data (Table 1) illustrates that the community of potential predators was effectively altered in our experiment. However, we cannot rule out that observed changes in impact reach salmon survival occurred for reasons other than reduced predation pressure. For example, reduced interspecific interactions (e.g. interference competition for shoreline rearing habitat) is also a plausible mechanism for improved salmon survival (Case and Gilpin 1974). Changes in biotic or abiotic conditions unmeasured in our study could have also caused or contributed to observed changes in juvenile salmon survival. Additional replicated experiments and different experimental designs would be necessary to identify and resolve these uncertainties.

Management implications

Resource managers seeking to improve salmon survival might target habitat enhancement actions or predator removals to channel segments where tidal transition typically occurs. Our analysis of flow data identifies these channel segments on the mainstem Sacramento and San Joaquin rivers. As an alternative

to modifying habitat or predator abundance, managers could alter flow regime to increase the linear distance of river habitat with unidirectional flow. These small-scale habitat perturbations could provide a short, temporal expansion of complexity, which has been for the most part eliminated within the central Delta (Moyle et al. 2010). While DCC gate operations provide an outstanding setting for heuristic experimentation, the drastic flow change which occurs when the DCC gates open is not typical or representative for Delta water operations on the Sacramento River. For example, to produce an equivalent event on the adjacent Sacramento River would require flows to increase from 292 to $4,380 \text{ m}^3 \text{ sec}^{-1}$ (a 15x increase); a magnitude of flow change which occurs only during flood events. As illustrated by conditions with DCC gates closed (Fig. 5), Mokelumne River inflows within the range of typical operations (8 to $47 \text{ m}^3 \text{ sec}^{-1}$) cannot appreciably influence or displace the tidal transition zone. While closing the DCC gates may be beneficial to Sacramento River emigrants, our study suggests it is likely detrimental to juvenile salmonids originating from the Mokelumne River.

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