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ARTICLE

Relationships between Chinook Salmon Swimming Performance and Water Quality in the San Joaquin River, California

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Abstract

There is currently only a limited understanding of the relationship between water quality and predation on Pacific salmon *Oncorhynchus* spp. smolts. We addressed the hypothesis that poor water quality will decrease a smolt's swimming performance and presumably its predator evasion capabilities. Predation is a major factor affecting salmon smolt survival throughout the San Joaquin River and the Sacramento–San Joaquin Delta of California. Prior studies have quantified predation rates, but the effect of water quality on predator evasion capability has not previously been evaluated. We quantified the swimming performance of juvenile Chinook Salmon *O. tshawytscha* in relation to water quality variables. The maximum swim speeds (U_{max}) of 45 hatchery-reared smolts (7.1–9.9 cm FL) were measured in controlled (laboratory) and field environments by using a mobile swim tunnel respirometer; measurements were obtained before and after the fish received a 2-d exposure to the lower San Joaquin River while being held in flow-through cages. To sample across a diversity of environmental conditions, we conducted trials during a 6-week period that coincided with the peak smolt out-migration. Regression models were constructed to evaluate relationships between swimming performance and four water quality covariates (water temperature, turbidity, dissolved oxygen, and conductivity). We found negative relationships between U_{max} and both temperature and turbidity, and we described these relationships graphically. Our findings suggest that water quality management strategies with the potential to improve salmon smolt survival include managing temperatures and suspended sediment concentrations to optimize the swimming capacity of migrating smolts and possibly improve their ability to evade predators.

In the lower San Joaquin River and the Sacramento–San Joaquin Delta (hereafter, "Delta") of California, predation by nonnative predatory fishes, such as Largemouth Bass *Micropterus salmoides* and Striped Bass *Morone saxatilis*, is a major cause of mortality in emigrating salmon smolts (Grossman et al. 2013; Sabal et al. 2016). Telemetry and predation studies (Demetras et al. 2016) are increasingly focusing on quantifying the rates of predation on juvenile salmon, but thus far, few such studies have been able to pinpoint the mechanisms that influence predation rates. Grossman et al. (2013) proposed that although predation may be the proximate cause of mortality for juvenile salmon, other factors such as poor water quality may increase smolts' vulnerability to predation by reducing their ability to successfully evade predators.

The survival of salmonids during early life stages may be strongly influenced by predation (Mather 1998). Since salmon lack other defensive mechanisms, the ability to swim at burst or sprint speeds greatly influences their susceptibility to predatory attacks (Taylor and McPhail 1985; Reidy et al. 1995; Watkins 1996). Swimming capability is also likely to affect the ability of smolts to forage and successfully perform long-distance migrations (Drucker 1996; Plaut 2001). The swimming performance of fishes is known to depend on environmental conditions (Randall and Brauner 1991). Since negotiating the ecological interactions that are necessary for survival depends on individuals' scope for physical activity, an understanding of water quality effects on swimming performance is crucial for informing effective restoration and management of freshwater habitat for fish populations. The sublethal effects of elevated temperatures and other water quality metrics on fish may be difficult to quantify (Armour 1991), yet they are relevant to predator–prey dynamics (Marine and Cech 2004), foraging ecology (Fraser et al. 1993), and movement (Baker et al. 1995) and can influence population viability.

Extensive research has been performed to understand relationships between water temperature and salmonid growth (Brett et al. 1969), swimming performance (Brett 1967; Brett and Glass 1973), and aerobic scope (Brett 1971; Lee et al. 2003; Clark et al. 2011). Fewer studies have focused on the effects of dissolved oxygen (Davis et al. 1963; Dahlberg et al. 1968) and pollutants (Howard 1975; Waiwood and Beamish 1978) or other water quality characteristics. Field-specific knowledge of the physiological effects of water quality variation on Chinook Salmon *Oncorhynchus tshawytscha* is lacking; although laboratory studies can measure the precise effects of individual treatments on fish, they are less suited to account for the multiple dimensions of varying water quality that a fish may experience in a natural environment.

The San Joaquin River, which contains the southernmost populations of Chinook Salmon, is arguably one of the most degraded rivers on the West Coast of North America (Dubrovsky et al. 1998; Jahagirdar 2006). Water quality attributes such as temperature often exceed experimentally determined viability thresholds for salmon. Results from coded wire tag studies (Brandes and McLain 2000) and acoustic telemetry studies (Buchanan et al. 2013) have clearly demonstrated that juvenile salmon smolts migrating through the lower San Joaquin River and the estuarine Delta experience extremely high mortality compared with salmon from other basins on the West Coast. Telemetry has been successful in quantifying mortality rates but has been less successful in relating environmental variables to survival. These types of studies cannot pinpoint exact causes of mortality, making it difficult to understand whether fish are being preyed upon or are unable to withstand environmental conditions or whether predation and environmental conditions interact to impact mortality rates.

Swim performance testing is a common and repeatable method for assessing the effects of environmental conditions on fish (Hammer 1995). Critical velocity tests that measure maximum sustained swim speed for small fish are relatively simple to conduct by using swim tunnel respirometers. Critical swim speed (U_{crit}) is known to depend on temperature (Brett 1967) and oxygen saturation (Davis et al. 1963). Decreased swimming performance directly relates to a fish's ability to evade predators and to navigate migration pathways. An understanding of the effect of ambient water conditions on swimming performance will help to disentangle the proximate causes of juvenile salmon mortality in the Delta (e.g., predation or entrainment into pumps) from the ultimate causes of juvenile mortality (e.g., acute thermal stress).

We evaluated the effects of water quality on the swimming performance of juvenile Chinook Salmon in the San Joaquin River. We used a constant-acceleration protocol (Reidy et al. 2000; Farrell 2008) to measure the maximum swimming speed (U_{max}) of hatchery-reared juvenile Chinook Salmon in (1) a controlled laboratory setting before a 48-h cage exposure to the San Joaquin River and (2) in the field immediately after the river exposure. A mobile swim tunnel respirometer was used to perform tests at the field site. Using continuously recorded environmental data, we generated models that described relationships between swimming performance and four different water quality metrics: water temperature, turbidity, conductivity, and dissolved oxygen concentration.

METHODS

Study area.—This study focused on the San Joaquin River's lowest reach, where the river enters the Delta (Figure 1). Historically, the Delta comprised 1,770 km^2 (1,100 mi^2) of tidal marsh, but since the turn of the 20th century, it has been levied into 1,126 linear kilometers (700 linear miles) of interconnected waterways surrounded by islands, with the waterways being primarily used for agriculture but also for industrial and urban development. Flow dynamics are strongly influenced by tidal forcing and now are frequently more
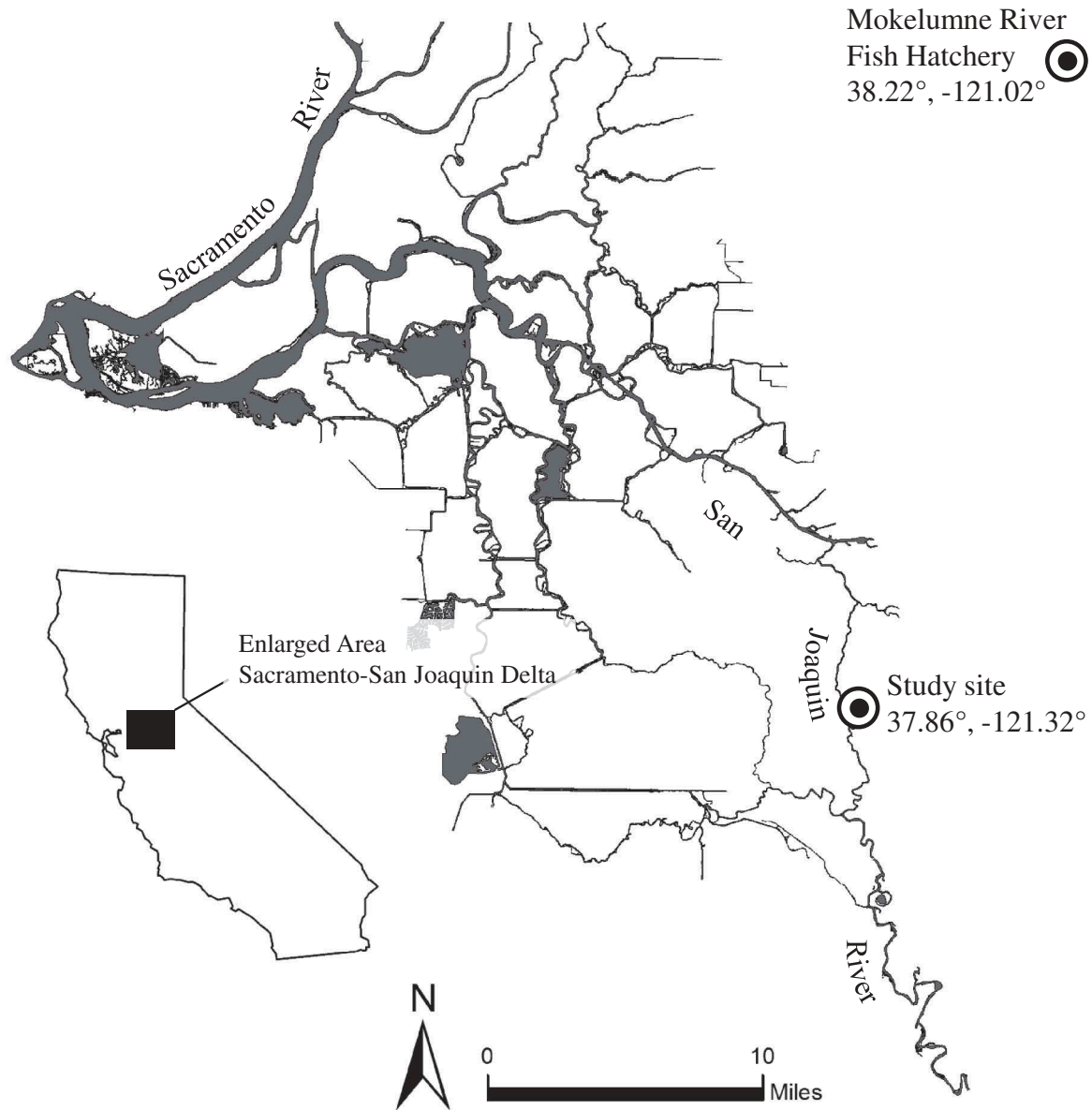
FIGURE 1. Map of the Sacramento–San Joaquin Delta, California, showing the location of the Mokelumne River Hatchery and the cage exposure site on the San Joaquin River.

influenced by dam releases and water diversions than by natural runoff and weather patterns.

As a result of these structural and hydrographic changes, particularly the withholding of spring runoff-associated discharge at upstream dams, the thermal profile of the San Joaquin River is highly altered; in drought years especially, summer temperatures typically exceed lethal levels for salmonids and other native species. Land use practices in the region have resulted in high concentrations of nitrates, agricultural pollutants, and pesticide pollutants (Saiki et al. 1993; Pereira et al. 1996; Kratzer et al. 2004). Many of these changes have been detrimental to native fish species while allowing nonnative species to thrive, leading to alterations in the biological composition of the lower San Joaquin River and Delta (Moyle and Williams 1990; Moyle 2002).

Swimming performance measurements.—Our objective was to measure the U_{max} of individual juvenile Chinook Salmon that were reared and tested under controlled ambient conditions and then to measure their U_{max} after a 2-d period of acclimation to conditions in the San Joaquin River. We measured the pre-exposure performance of each fish to account for interindividual variation in our analysis, and we

subjected each fish to three successive swim tests both at the hatchery (described below) and at the river site in order to account for intra-individual variation. We intended to collect measurements across a spectrum of environmental conditions in order to test the effects of water quality on swimming performance; therefore, we ran tests continuously for 6 weeks during the peak out-migration season.

We selected juvenile Chinook Salmon (7.1–9.9 cm FL) from a raceway at the Mokelumne River Hatchery (California Department of Fish and Wildlife [CDFW], Clements) and placed them in an indoor trough 2 weeks before the experiments began. Water was maintained between 12.2°C and 14.4°C throughout the duration of the experiment. Fish were exposed to a natural photoperiod and were fed an ad libitum ration daily, except during the 48 h prior to testing.

All swimming performance trials were conducted in a 5-L Brett-type swim tunnel manufactured by Loligo Systems (Viborg, Denmark). The section that contained the fish was 30 cm long, with a 7.5-cm cross section. There was a honeycomb material at the front to provide rectilinear flow and a stainless-steel mesh grate at the back. The entire swim tunnel was covered to prevent visual distraction to the fish, and an LED flashlight was placed at the back of the chamber to encourage the fish to swim into the current. Temperature was maintained at ±1°C of ambient throughout each test. We observed the fish's behavior through a small window in the back of the chamber and with a submersible video camera. The propeller motor that controlled water velocity was powered by a computer-operated DC inverter (AutoResp; Loligo Systems), and we quantified water velocity relative to each fish's body length (BL). Water velocity was regularly calibrated against propeller frequency by using a vane wheel flowmeter. We used dye to make sure that flow was constant across the cross section of the chamber and not turbulent. All equipment was cleaned and disinfected between each sampling period.

Immediately before testing, fish were transferred to the swim tunnel via water-to-water transfer techniques; FL was estimated by using a measuring tape at the bottom of the transfer container. Since U_{max} increases with fish length (Jobling 1995), we chose to standardize and express all velocities in BLs/s. The fish acclimated to the chamber at a flow of 1.5 BLs/s. We excluded individuals that did not appear to be comfortable swimming steadily within the chamber after several minutes, although this was rare. The first of the three successive tests began 10–20 min after the chamber was sealed.

Maximum swimming speed protocol.—After the initial acclimation period at 1.5 BLs/s, water velocity was increased in 0.25-BL/s increments every minute. In general, fish swam steadily for the majority of each trial. As they transitioned from steady to burst–glide swimming, we monitored closely for the failure point. Failure was determined when the fish became impinged sideways on the grate for more than a few seconds and could no longer remain upright. The U_{max} was calculated according to Brett (1964).

About a third of the fish attempted to avoid swimming by tail-propping against the grate at the back of the chamber at some point. To discourage this behavior, we would tap a pencil against the chamber wall, which usually resulted in the fish moving back towards the front. Repetitive tail-propping behavior rarely resulted in a premature test failure because at velocities approaching U_{max}, it became too difficult for the fish to prop parallel to the current, and the individual was forced to swim.

Immediately after failure, flow was decreased to 1.5 BLs/s for a 1-min recovery period before the second trial was initiated. Generally, fish would resume swimming immediately after the velocity decrease, but if they remained impinged against the grate, the flow was stopped altogether until the fish oriented itself parallel to flow. An identical 1-min recovery period was given before the third trial.

Transportation and caging.—After the initial swimming tests conducted at the hatchery, each fish was transferred to a 3.8-L plastic container into which 6-mm holes had been drilled; the container with the fish was placed in an aerated cooler and was held there until all other fish had been tested. The cooler was then transported by truck to the lower San Joaquin River near Lathrop, California (37.8614°N, −121.3204°W). The cooler water was brought to ambient river temperature at a rate no faster than 2°C per hour. After a temperature equilibrium was reached, we placed fish in cages made from modified crayfish traps that were attached to a private dock and suspended approximately 2 m below the river's surface. Temperature loggers were attached to the cages. Dissolved oxygen, turbidity, conductivity, and pH data were collected continuously with an autonomous water quality data logger (Hydrolab DS5X; Hach Company, Loveland, Colorado), and chlorophyll-*a* concentration data were obtained from local stream gauges.

Post-caging swimming trial.—After a 48-h acclimation period, we removed individual fish from their cages and immediately tested them by using the same protocols as above to obtain three successive U_{max} values. The swim tunnel was set up at the field site and was filled with coarsely filtered river water that we refreshed between tests and maintained within 1°C of ambient temperature. After three trials, each fish was euthanized in a lethal dose of tricaine methanesulfonate, weighed, and remeasured to confirm FL.

Data analysis.—We performed one-way ANOVA to test for differences in U_{max} between groups of fish that were tested under identical conditions and to evaluate whether or not fish tended to perform differently on their first, second, and third trials.

To examine for effects of multiple water quality metrics on fish swimming performance, we used two modeling approaches that offered unique methods of accounting for

physiological variation between individual fish. First, to account for variation in swimming capacity between individuals, we defined the difference between each fish's pre- and postexposure U_{max} values as the response variable ΔU_{max} (i.e., difference in U_{max}: $U_{max,post} - U_{max,pre}$) such that a negative value for ΔU_{max} indicated a decrease in performance after exposure. We then modeled the relationship between ΔU_{max} and multiple water quality metrics. Since we expected a nonlinear relationship between swimming performance and environmental variables, we constructed a generalized additive model using the "mgcv" package in R. In our second approach, since all fish used in this study were reared under identical conditions, we also modeled the relationship between water quality metrics and postexposure swimming performance only. We used a linear mixed-effects (LME) model via the "lme4" package in R; LME modeling extends regression by adding an individual coefficient of variability between groups—in this case, individual fish that were tested multiple times. The second approach offered increased model sensitivity but at the cost of producing nonlinear graphical response curves (i.e., only linear general trends could be modeled rather than asymptotic relationships between swimming performance and water quality metrics).

Prior to model fitting, we compared covariates for collinearity ($|r| < 0.70$). To avoid issues associated with the inclusion of collinear variables in the same model, we selected the single covariate from each pairwise comparison that had the most reasonable interpretation as an explanatory variable (Dormann et al. 2013). Model selection was executed by using Akaike's information criterion (AIC).

We determined the R^2 value for the best-performing models using k-fold cross validation (Hastie et al. 2009). We split the data into equal-sized parts and then iteratively used one subset of the data to fit the model and a different subset to test the model. We repeated each k-fold cross-validation process 500 times and then examined the distribution of R^2 and other model evaluation criteria.

RESULTS

Overall, 239 individual swim trials were performed on 45 individual fish. We tested U_{max} at water temperatures ranging from 12.2°C to 21.5°C. Average river temperatures for the 48-h acclimation periods ranged from 17°C to 22.5°C. Other environmental data collected while fish were held in the river is summarized in Table 1. Every fish successfully performed U_{max} tests after being transported and held in the river, with the exception of three fish that died after being caged when river temperature averaged 22.5°C. The U_{max} did not differ between groups of fish tested in the hatchery setting across sampling intervals (ANOVA: $P = 0.51$), although variation among individual fish from each group varied about twofold (Figure 2). There was no significant trend of decreasing performance over the first, second, and third successive tests for the pre-exposure trials conducted at the hatchery ($P = 0.82$) or the postexposure trials performed in the field ($P = 0.67$).

Modeling the Difference in Maximum Swim Speed: Generalized Additive Model

After collinear covariates were removed from the analysis, average river temperature, minimum river oxygen concentration, conductivity, turbidity, and FL remained as candidate covariates in the selection process for our model to describe variation in swimming speed between the hatchery trials and the postexposure trials. The best model for explaining the difference between an individual's laboratory and field U_{max} values (i.e., ΔU_{max}) included average river temperature only (Akaike weight $w_i = 0.670$, cross-validated $R^2 = 0.51$; Figure 3).

Modeling the Maximum Swim Speed after River Exposure: Linear Mixed-Effects Model

Using the same candidate set of covariates, the most parsimonious of the LME models with equivalent weight ($\Delta AIC < 2$) included temperature and turbidity ($w_i = 0.203$, cross-validated $R^2 = 0.70$; Table 2). The relationship between U_{max} and the average

TABLE 1. Summary of environmental data that were collected during the 48-h holding periods for Chinook Salmon that were used in cage exposure trials in the San Joaquin River (temp = temperature; O_2 = dissolved oxygen concentration; chl a = chlorophyll-a concentration; cond = conductivity; max = maximum; min = minimum). All columns represent average values across each sampling period unless otherwise noted. Negative discharge values indicate periods of very low flow, strong tidal influence, and/or substantial water diversions from upstream pumping facilities.

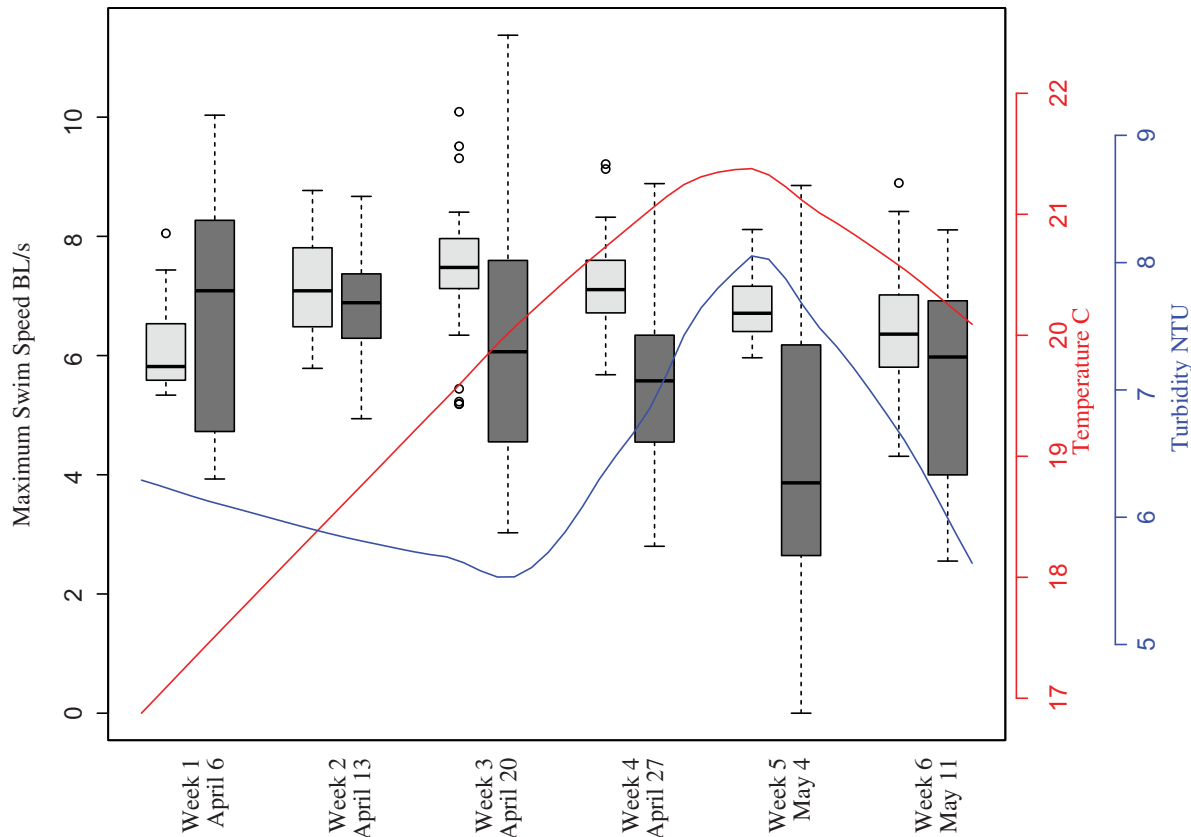| Week	Temp (°C)	Max temp (°C)	O_2 (mg/L)	Min O_2 (mg/L)	pH	Turbidity (NTU)	Chl a (µg/L)	Cond (µS)	Discharge (m^3/s, mean daily)
1	17.0	17.5	8.2	7.5	7.6	6.2	4.1	322.3	8.69
2	18.4	19.4	8.4	7.8	7.6	6.8	2.3	215.7	21.84
3	20.0	20.5	7.9	7.4	7.7	5.4	3.3	201.5	4.49
4	21.2	22.0	9.7	8.3	8.0	6.0	11.3	335.7	–0.07
5	22.0	22.5	9.1	8.1	8.2	9.7	14.9	437.1	–6.25
6	20.0	20.9	8.4	7.2	8.0	5.4	8.2	636.7	–0.88

FIGURE 2. Box plot of maximum swimming speed (body lengths [BL]/s) for Chinook Salmon tested during each week at each location (horizontal line within box = median; ends of rectangle = first and third quartiles; range = ends of whiskers). Values are for pre-exposure trials conducted at the hatchery (light-gray boxes) and for trials with the same group of fish after a 2-d cage exposure to San Joaquin River conditions (dark-gray boxes). Mean daily temperature (°C; red line) and turbidity (NTU; blue line) are also plotted.

river temperature and turbidity was described by $U_{max} = 15.67 - (0.32 \times temperature) - (0.35 \times turbidity) + e$, where e is the residual (Figure 4). The standardized coefficients for the fixed effects of temperature and turbidity were –0.26 and –0.27, respectively.

DISCUSSION

We measured the swimming performance of juvenile Chinook Salmon in a controlled setting and in a field environment across the duration of a spring out-migration season. To our knowledge, this study represents the first field-based assessment of swimming performance in a California population of Chinook Salmon. Although U_{max} varied among individual fish, the low variability among groups taken from the hatchery suggests that there were few ontogenetic or temporal factors affecting the baseline swimming performance of the fish used during this study. Tests for the same individuals varied less than the overall variation among different fish, suggesting that our measurements of U_{max} were repeatable and that the constant-acceleration test did not elicit excessive postexercise oxygen

consumption—at least at all but the warmest temperatures. This agrees with the results of Reidy et al. (2000), who found U_{max} to be repeatable for individual fish. Values for U_{max} and the variability among fish fell within previously reported ranges for Central Valley juvenile Chinook Salmon (Cech and Myrick 1999), allowing us to describe the relationship of U_{max} with temperature and turbidity across the range of conditions that occurred during this study.

Although no control measurement was taken to account for potential handling and transportation effects on U_{max}, several fish outperformed their initial hatchery tests after being held in the San Joaquin River (Figure 2). The response curve of ΔU_{max} in relation to temperature (Figure 3) illustrates that juvenile Chinook Salmon that were acclimated to the river when temperatures were below approximately 18.5°C actually swam faster than they did at cooler temperatures in the hatchery. This is expected, as the U_{crit} of Chinook Salmon has been found to peak at temperatures between 15°C and 17°C (Brett 1967).

Similar to previous laboratory studies (Brett 1967), we saw a decrease in swimming performance at temperatures above
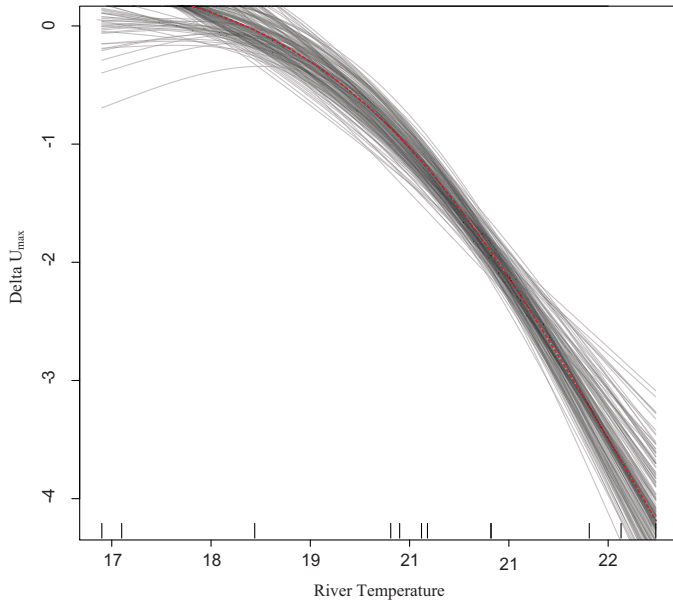
FIGURE 3. Response plot showing the modeled relationship between San Joaquin River temperature (°C) and the difference in maximum swimming speed (U_{max}; body lengths/s) of Chinook Salmon (ΔU_{max}; the difference between a fish's U_{max} when tested at the hatchery and the U_{max} observed after the fish was held in the river for 2 d). The black lines are the output from 100 k-fold model runs; the tick marks along the x-axis (i.e., rug plot) indicate the observed data points.

approximately 19°C (Figure 3). The magnitude of change in U_{max} across temperatures in this field setting was somewhat greater than that observed in prior laboratory studies, suggesting the occurrence of interactive effects between temperature and other variables influencing fish stress. Where individual lines on the response plot converge, there is a stronger relationship between the covariate and the response variable. Our findings indicated that the strongest relationship between temperature and U_{max} was at river temperatures between 19°C and 21.5°C. Where lines on the response plot diverge, temperature may be less influential on U_{max}, and other factors may have larger effects. Water bodies that exhibit temperatures at or above this range have been found to exclude salmonids based on thermal niche modeling (Huff et al. 2005) and

TABLE 2. Results of linear mixed-effects model selection, with maximum swimming speed (U_{max}) of Chinook Salmon as the response variable. The best-performing model among the equivalent top-three models (difference in Akaike's information criterion [ΔAIC] < 2) is shown in bold italics (w_i = Akaike weight).

Model	ΔAIC_c	w_i
Temperature + turbidity |fish	*0.00*	*0.205*
Temperature + conductivity + turbidity |fish	0.48	0.161
Conductivity + turbidity |fish	0.72	0.143

based on reviews by McCullough (1999) and Richter and Kolmes (2005).

The LME analysis was more sensitive and included temperature and turbidity as covariates affecting U_{max} in the top model (Table 2). The response curves (Figure 4) illustrated a negative relationship between U_{max} and temperature or turbidity. The temperature curve showed the same trend exhibited in the ΔU_{max} model.

Turbidity in the San Joaquin River is primarily associated with suspended sediment. Although the lower San Joaquin River regularly exceeds temperatures that are lethal to salmonids, the levels of turbidity measured across this study fall within the range that many salmon commonly experience: between 2 and 15 NTU, which equates to a suspended sediment concentration (SSC) of up to 15 mg/L (Rasmussen and Gray 2010). Suspended sediment concentrations as low as 2 mg/L have been reported to affect salmonid health (Newcombe and Macdonald 1991; Servizi and Martens 1992). However, most studies have focused on acute effects that occur at much higher SSCs. The San Joaquin River is chronically contaminated with agricultural pollutants, such as DDT, and a legacy of heavy metals from California's gold rush (McKee et al. 2006; Schoellhamer et al. 2007). These toxins persist in the sediments that are temporarily suspended in the water column during certain tidal cycles or large flow events (Leatherbarrow et al. 2005). It is possible that when salmon are exposed to higher SSCs in the San Joaquin River, they are concurrently exposed to higher concentrations of a cocktail of toxins that increase physiological stress.

Due to drought conditions and upstream dam operations, discharge of freshwater into the lower San Joaquin River during the present study never exceeded 15 m³/s, which is too low to cause streambed disturbance in the system. However, the instantaneous magnitude and direction of water speed in the Delta are influenced by tidal fluctuations and are responsible for the vertical mixing and suspension of solid particles. When discharge coming from upstream is insufficient, tidal forcing reverses water flow twice per day at our study site, and sediments are temporarily suspended due to the processes described by Allen et al. (1980). Semidiurnal spikes in SSC due to reverse flows were documented in the Sacramento–San Joaquin estuary by Morgan-King and Schoellhamer (2013). This effect was captured during several of the sampling periods in our study and corresponded to poor swimming performance in tested Chinook Salmon.

The temperature plus turbidity model only explained 48% of the deviance in U_{max}. Other environmental factors likely influence the swimming performance of juvenile salmon in the San Joaquin River system; however, we either did not measure them or were unable to disentangle their effects due to collinearity with other candidate covariates. In particular, pH and average dissolved oxygen concentration were correlated with river temperature, thus precluding them from the model selection process and making their effects ambiguous even though
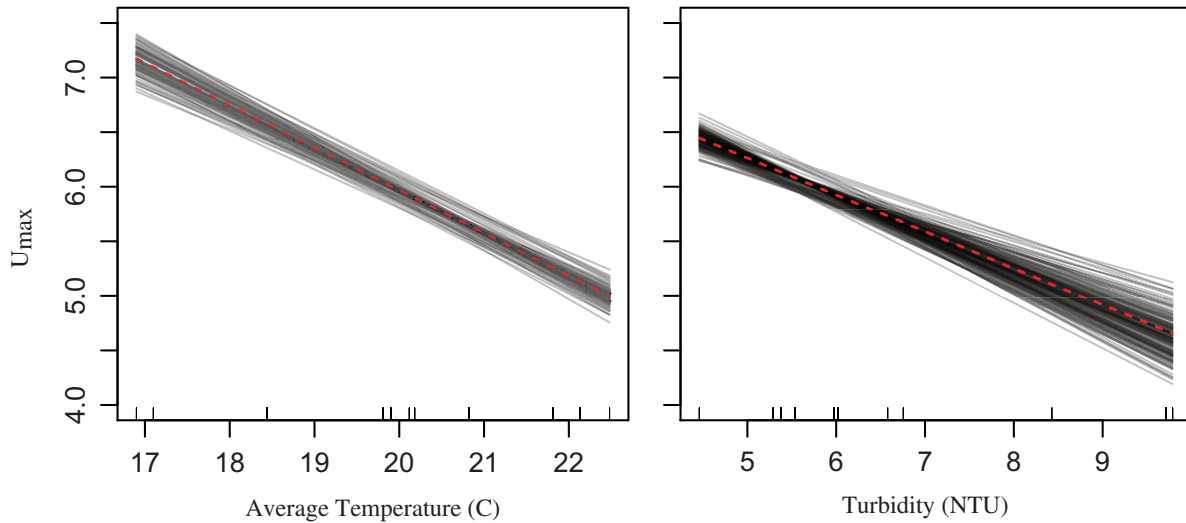
FIGURE 4. Response plots showing the modeled relationships for the maximum swimming speed (U_{max}; body lengths/s) of Chinook Salmon acclimated to the San Joaquin River over a range of temperatures (°C) and turbidity levels (NTU). In these plots, only the variable of interest is changed, whereas all other model variables are held constant at their median values. The dotted red line represents the output from the logistic regression; the black lines are the output from 100 k-fold model runs to provide an indication of model error. The tick marks along the x-axis (i.e., rug plot) indicate the observed data points.

both metrics fluctuated within ranges that are known to independently affect swimming speed in salmonids (Davis et al. 1963; Ye and Randall 1990). We believe that poor water quality in this portion of the San Joaquin River system can be exacerbated by low streamflow and the resulting lower turnover rate of water. Under such conditions, salmon may be subject to a mélange of environmental stressors that decrease swimming performance.

Our findings have management implications for water operations in the Delta and in other highly modified river systems. Although we do not wish to overemphasize the absolute numbers generated in our response curves, the trends are clear. These results indicate that (1) water quality in the Delta cannot be managed for salmon health solely by setting threshold temperatures and (2) other easily measurable metrics may be useful tools for setting environmental thresholds that are relevant for salmon. More rigorous investigation may reveal the relationships between other environmental covariates and swimming performance, which will provide direction for habitat restoration actions. Freshwater turnover may be just as important for salmonid health in this system as temperature. By coordinating dam releases and diversion pump operations so as to maintain freshwater turnover in tidal channels, managers may improve the health of salmonids that are rearing in the Delta or migrating toward the Pacific Ocean.

We used hatchery Chinook Salmon to generate estimates of physiological response to environmental covariates. Each fish began the study in excellent condition, with no signs of pathogen infection, and each individual was only exposed to the river for 2 d. However, wild fish migrating through the system may already be experiencing the effects of infection or poor condition and must spend substantially more time navigating between relatively high-quality upstream habitat and the ocean; therefore, wild individuals may experience some effects described by our models to a greater degree.

We do not know whether U_{max} is the most direct estimate of a Chinook Salmon juvenile's physiological capacity to successfully mitigate predatory interactions. However, it is logistically feasible to measure U_{max} in a field environment, and it is reasonable to assume that U_{max} can provide a relative index for predator escape capacity. There may be an interactive effect between different dimensions of river conditions that negatively affect salmon physiology and predation by several species of nonnative piscivorous fish. We showed that juvenile Chinook Salmon cannot swim as fast at elevated temperatures, particularly above around 19°C. Nonnative Largemouth Bass, which are suspected to consume a large quantity of juvenile salmon in the Delta, become increasingly capable swimmers and consume more food at temperatures between 10°C and 25°C (Beamish 1970; Rice et al. 1983; Lemons and Crawshaw 1985). Environmental conditions may mediate both the quantity and outcome of predator–prey interactions between Chinook Salmon and Largemouth Bass —as well as several other nonnative predatory species—by both increasing predation activity as well as reducing the ability of salmon to effectively avoid being eaten. Determining whether or not this interactive relationship actually occurs in the San Joaquin River system is beyond the scope of our study, but future research on the topic is warranted.

In the San Joaquin River system, where major Chinook Salmon population declines have been observed, increasing the survival probability of migrating fish may be the most effective management tool for restoring populations (Yoshiyama et al. 1998; Michel et al. 2015). Largemouth Bass and other nonnative predators (e.g., Striped Bass and catfishes) have become widespread, and for logistical as well as political reasons they are likely impossible to eradicate from California's largest freshwater system. However, managing the habitat to increase the potential for salmon success when interacting with predators is possible by optimizing dam and pump operations or restoring habitat structure that improves water quality.

ACKNOWLEDGMENTS

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