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Experimental Quantification of Piscivore Density and Habitat Effects on Survival of Juvenile Chinook Salmon in a Tidal Freshwater Estuary

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Abstract

Introduction of non-native piscivores has been implicated in the decline of native Chinook Salmon *Oncorhynchus tshawytscha* via predation during juvenile life stages. However, isolating effects of predation on Chinook Salmon survival is complicated by changes in physical habitat that are often concomitant with non-native piscivore establishment. We performed two field experiments with enclosures deployed in tidal freshwater habitat to quantify effects of non-native Largemouth Bass *Micropterus salmoides* density and habitat type on the survival and movement behavior of juvenile Chinook Salmon. In experiment one, bass densities were doubled and quadrupled across treatment levels with a baseline value of field-observed densities. In experiment two, three habitat types (dock, submerged aquatic vegetation (SAV), and open water) were tested while bass density was held at the medium (doubled) value. Juvenile Chinook Salmon implanted with passive integrated transponders were released into the enclosures to assess their survival and movement through the treatments over multiple trials. Mark-recapture models indicated that the survival of juvenile Chinook Salmon was reduced in the medium bass density, but not the high-density treatment, when compared to the lowest density value suggesting relationships may be non-linear. The SAV treatment had a well-supported negative effect on juvenile Chinook Salmon survival relative to a dock or open water. Residence time was positively related to bass density. Relationships with a habitat were not consistently different. These results suggest that restoration strategies targeting non-native SAV control could reduce predation on juvenile Chinook Salmon by Largemouth Bass. However, piscivore density manipulation may only be effective over a narrow range of densities.

Keywords Predation · Mark-recapture · Predator control · California · Enclosures · Telemetry

Introduction

Estuaries provide critical habitat for anadromous salmonids as they migrate between riverine and marine environments. These ecotones can provide feeding and rearing opportunities for juvenile salmonids (Cunjak 1992; Hayes et al. 2008) and support diversity in migration strategies within populations (Koski 2009; Phillis et al. 2018). Despite these potential benefits, estuaries may also host a greater number and variety of potential predators, with several studies reporting lower or more variable survival rates relative to upstream riverine environments (Mather 1998; Thorstad et al. 2012). Predation is one of the fundamental interactions structuring aquatic communities and relative abundance and behavior of species have been observed to change as a result of cyclical or serial responses and dynamics among predator and prey communities

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(Paine 1969; Rodriguez and Lewis 1997; Layman and Winemiller 2004; Tang et al. 2017). For juvenile salmonids, predation has been found to be an important interaction across a range of species, habitats, and spatial scales (Mather 1998). However, there remains a considerable uncertainty regarding predation on juvenile salmonids in estuaries because they have received less attention from researchers relative to natal tributaries (Brodeur et al. 2000). A better understanding of the survival and behavior of juvenile salmonids in estuaries is needed to formulate effective management actions that may increase survival rates during migration.

The San Francisco Estuary (SFE), California, is the largest on the west coast of North America and functions as a migration corridor for four runs of Chinook Salmon *Oncorhynchus tshawytscha*, two of which are listed under Federal and State Endangered Species Acts. Declines in abundance of these Chinook Salmon populations have been attributed to a range of biotic and abiotic drivers both within the estuary and in natal tributaries (NMFS 2014). Low survival rates of juvenile Chinook Salmon in the Sacramento-San Joaquin Delta (hereafter "Delta"), the tidal freshwater portion of the estuary, have been implicated as a potential impediment to the productivity and recovery of these populations (NMFS 2014; Michel et al. 2015; Buchanan et al. 2018). Predation has been hypothesized as the primary source of mortality for juvenile Chinook Salmon in the Delta (Cavallo et al. 2013; Grossman 2016; Michel et al. 2018). However, methods used to estimate survival are not able to identify the specific source or context of mortality, complicating attempts to formulate mitigation strategies. Although Chinook Salmon in the Delta have co-evolved with aquatic piscivores, extensive habitat modifications and species introductions have the potential to influence predator-prey dynamics (Grossman 2016; Merz et al. 2016).

Multiple intentional and unintentional species introductions have occurred in the Delta since the late 1800s, resulting in the establishment of non-native piscivores including Striped Bass *Morone saxatalis*, multiple species of black bass *Micropterus* spp., and catfish *Ictalurus* spp. and *Ameiurus* spp. (Dill and Cordone 1997). Salmonids have been shown to react more strongly to chemical cues from native rather than non-native predators (Kuehne and Olden 2012). Thus, juvenile Chinook Salmon rearing in and migrating through the Delta may be more susceptible to consumption by non-native piscivores (Sih et al. 2009).

Extensive modification of Delta habitat has occurred since the late nineteenth century to facilitate navigation, wetland reclamation, water diversion, and flood control (Robinson et al. 2014). The net result has been general simplification of channels and proliferation of artificial structures such as docks and piers (Lehman et al. 2019). In the last several decades, non-native floating and submerged aquatic vegetation has become prolific (Toft et al. 2003, Brown and Michniuk 2007) and species such as Brazilian Waterweed *Egeria densa* now form dense stands in shallow water habitats and may restrict access to these areas by juvenile salmonids, while providing profitable habitat for invasive piscivorous centrarchids (Conrad et al. 2016; Young et al. 2018). Indeed, the abundance of Largemouth Bass in the Delta has increased concomitant with the proliferation of non-native SAV (Brown and Michniuk 2007; Mahardja et al. 2017). Non-native SAV and artificial structures such as docks are among the main anthropogenic contact points between prey and predators that are hypothesized to be of importance in the Delta (Lehman et al. 2019).

Here, we report results from two experiments within the Delta to separately quantify the effect of Largemouth Bass *Micropterus salmoides* density and habitat type on juvenile Chinook Salmon survival and movement behavior. Our experimental approach was designed to bridge the gap between fully contained mesocosm studies that have maximum control but minimum realism, and observational studies with maximum realism but little or no information on the context of mortality. The goal was to provide data that could reduce uncertainty around potential management strategies to increase survival of migrating juvenile Chinook Salmon in the Delta including tidal habitat restoration and manipulation of piscivore populations. Habitat restoration is hypothesized to reduce predation by removing features that provide contact points between Chinook Salmon and predators such as SAV and artificial structures (Lehman et al. 2019). Piscivore population reduction is hypothesized to increase survival of juvenile salmonids by reducing the frequency of predator-prey encounters either at specific locations (Sabal et al. 2016) or in the Delta generally (Michel et al. 2020). For the density experiment, Largemouth Bass numbers were doubled and quadrupled across three treatment levels (low, medium, and high). The null hypothesis tested was no effect of bass density on Chinook Salmon survival. For the habitat experiment, we tested the effect of a simulated dock, simulated SAV, and open water on survival while bass density was held at the medium level. The null hypothesis tested was no effect of habitat type on Chinook Salmon survival. The results presented here provide insight into predicting the feasibility, benefits, and effectiveness of potential piscivore control activities and habitat restoration strategies in estuaries.

Methods

Study Site

The Delta is the tidal freshwater portion of the San Francisco Estuary located in California, USA. The Delta covers an area of ~2800 km^2 with land use dominated by agriculture. Primary freshwater inputs to the Delta are the Sacramento and San Joaquin Rivers. Inflows are strongly seasonal with

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greater volume in winter and spring and lower volume in summer and fall. However, operation of multiple dams on upstream tributaries has a large influence on the total volume of freshwater flow reaching the Delta (Brown and Bauer 2010). The complex network of channels that comprise the Delta have been intensively modified by levee construction and channelization to support land reclamation, navigation, and water extraction for agricultural and urban use (Whipple et al. 2012). In the southern Delta, two large pumping facilities divert water from the Delta for distribution to areas south of the Delta. All natural-origin juvenile Chinook Salmon produced in upstream tributaries must migrate through the Delta on their way to the Pacific Ocean. Some Chinook Salmon enter the Delta as fry and rear for weeks to months before transitioning into smolts and migrating to the ocean whereas fry that rear in upstream tributaries first enter the Delta as smolts (Brandes and McClain 2001). Actively migrating juvenile Chinook Salmon were the focus of this study and their abundance in the Delta is greatest between April and June (Brandes and McClain 2001). We began the experiment in early April because this is a period when natural-origin fish are abundant, temperatures are favorable, there is sufficient time for multiple trials before temperatures become stressful, and juvenile Chinook Salmon first become large enough to tag.

The experiment took place in the central Delta on the South Fork Mokelumne River approximately 1 km upstream of the confluence with the North Fork Mokelumne (Fig. 1). The Mokelumne River supports a population of fall run Chinook Salmon and fish from the Sacramento River can enter the forks of the Mokelumne River via a natural channel (Georgiana Slough) or an operable gate (Delta Cross Channel). Thus, Chinook Salmon are expected to occur naturally at the study site. Land use in this region is dominated by agriculture with riprapped levees and simplified channel structure. Riparian vegetation is sparse although patches of tule (*Schoenoplectus acutus*) occurred near the banks and on mid-channel islands. Submerged aquatic vegetation (SAV) in the vicinity was abundant with Brazilian Waterweed as the dominant SAV species. Docks, piers, and other artificial structures were common. Water depths at the site ranged from approximately 1 to 1.8 m at low tide, with a total channel width of ~175 m. Water movement was strongly influenced by tides with a semi-diurnal pattern. Maximum tidal range during the study was 1.2 m and the direction of water movement changed with each tide phase.

Experimental Enclosures

Enclosures were designed to balance control over the context of predator-prey interactions while allowing Largemouth Bass and Chinook Salmon to interact in a more realistic way than allowed by small mesocosms where the prey cannot escape the experimental arena. In this experimental set up, Chinook Salmon juveniles were able to exit one treatment enclosure and enter another whereas predators were contained within specific enclosures. Three linearly arranged 15.6- × 6.1- × 1.2 m enclosures were constructed for the experiment with all three connected by netting to form a single experimental array capable of containing both predators and prey (Fig. 2). Each of the three enclosures within the array contained a unique treatment level (predator density/habitat type). Electronic tags implanted in Chinook Salmon and antennas deployed between treatment enclosures (described in detail below) allowed for determining when a fish had left one treatment and entered another. Thus, a single Chinook Salmon could experience more than one treatment during a trial. We assumed that the fate of Chinook Salmon in each treatment was independent of their experience in previous treatments and performed statistical modeling (described below) to inform this assumption. This design attempted to mimic how these species would interact in natural habitat, with Largemouth Bass having a sit-and-wait predation style and small home range (Lewis and Flickinger 1967; Sammons et al. 2003) and Chinook Salmon rapidly migrating through those home ranges on their way to the ocean (Smith et al. 2002; Michel et al. 2015). Tag detections were used to assess the survival rates of fish in individual treatment enclosures and movement rates between enclosures.

The structure was constructed of 5 cm PVC pipe with the upper pipe sections filled with polyurethane foam for flotation (Fig. 2). The bottom and sides of the entire array (containing three consecutive enclosures) was enclosed with a continuous length of netting with 6.4 mm delta mesh (Fig. 2). A five-centimeter polyurethane mesh fencing was placed perpendicular to the long axis inside the array to create the three separate enclosures. The five-centimeter mesh was chosen because it was small enough to retain Largemouth Bass within each enclosure but large enough that juvenile Chinook Salmon could easily move between the three enclosures. A total of six 1.2 m × 6.1 m passive integrated transponder (PIT) antennas, each with a single half-duplex (HDX) reader box (Oregon RFID, Portland OR, USA), were deployed within the array to delineate the three enclosures and detect Chinook Salmon entering and leaving each enclosure. Reader boxes connected to the PIT antennas were synchronized during the experiment to prevent interference. At the terminal ends of the array, two PIT tag antennas were deployed. The first antenna was placed 3 m from the end of the enclosure to ensure PIT tags in predator stomachs could not be detected and mistaken for fish exiting the enclosure. The second antenna was deployed 3 m from the first to create an independent location for detection and to facilitate calculation of detection probabilities for any juvenile Chinook Salmon leaving the enclosure array. The mesh bottom and sides of the arrays extended to these two antennas so juvenile Chinook Salmon had to swim through

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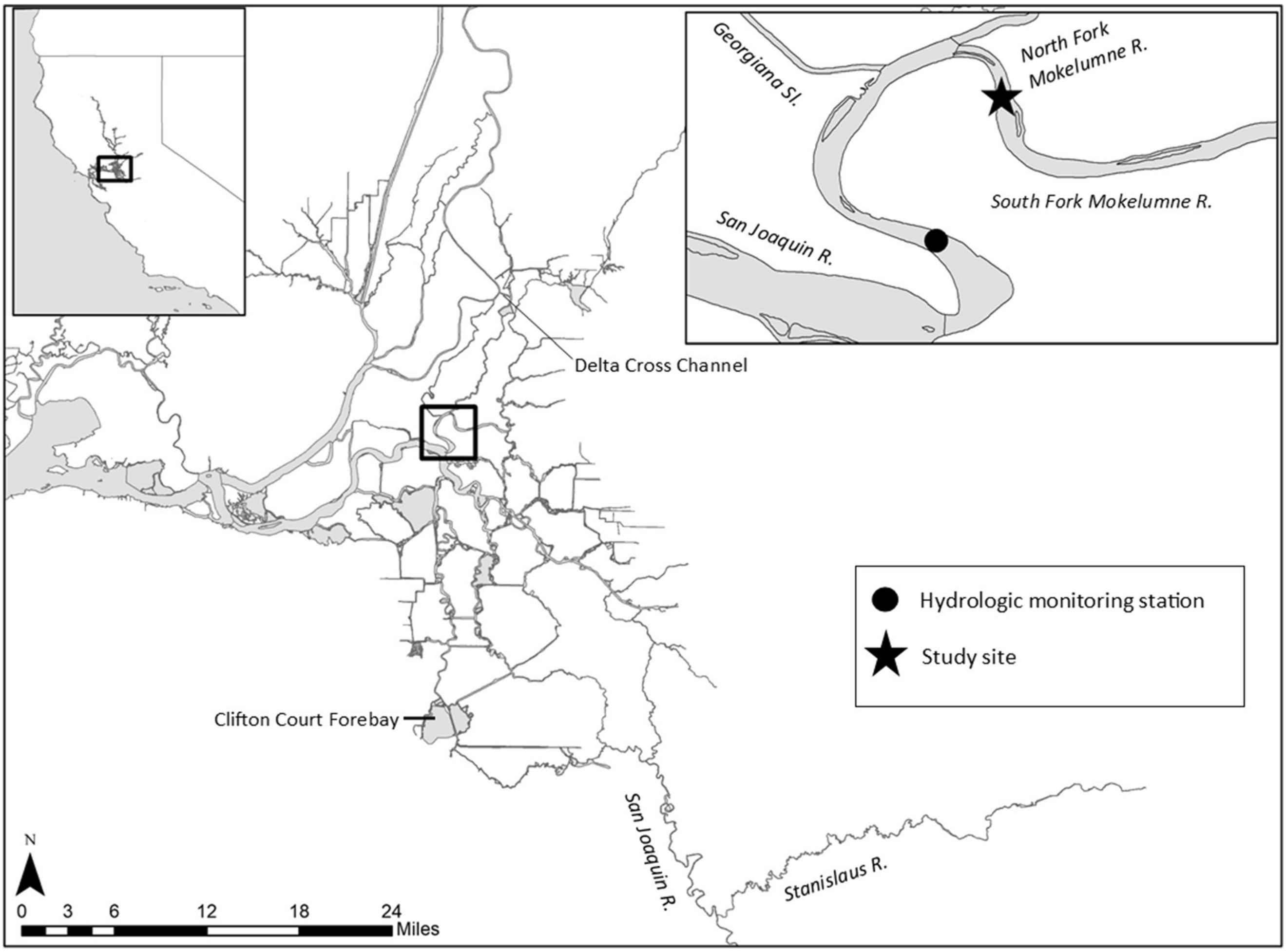

Fig. 1 Map depicting the location of the Sacramento-San Joaquin Delta in California and the location of the study site within the Delta. Stage data at flow stations within the study site inset were used to estimate tidal range during each experiment

the antennas to exit the study area (Fig. 2). A single antenna was deployed between the center enclosure and the two enclosures on either end of the array to detect fish moving between enclosures. These antennas were separated from the ends of each enclosure by ~3 m (Fig. 2). Raptor netting (2.5 cm mesh) was placed across the top of each enclosure to prevent avian predation and prevent Largemouth Bass and juvenile Chinook Salmon from jumping out of the enclosure.

Experimental Fish and Habitats

Largemouth Bass were obtained from California Department of Water Resources electrofishing efforts in Clifton Court Forebay, a water diversion regulating reservoir that has a direct connection to the Delta. Bass were held in circular tanks within a facility adjacent to the forebay for short periods (12–24 h) until being transported to the study sites. Some fish were also collected by hook and line near the study site for the early density trials when electrofishing did not yield enough fish. Largemouth Bass used for the experiment were restricted to between 250- and 550-mm fork length (FL). The three treatment levels included low, medium, and high densities which corresponded to 3, 6, and 12 bass, respectively. The value for the low-density treatment (0.03 bass·m^2) was the density of piscivores observed during multiple pass electrofishing to remove predators of juvenile Chinook Salmon in the Mokelumne River near our study location (Brad Cavallo, Cramer Fish Sciences, Personal communication). The medium-density treatment doubled the low-density treatment, and the high-density treatment quadrupled the low-density treatment.

Juvenile fall run Chinook Salmon were obtained from the Nimbus Fish Hatchery on the American River, Rancho Cordova, California. Fish of the size used in the experiment (≥ 65 mm) may display both rearing and migration behaviors. Our experimental set up assumed fish would primarily be exhibiting migration behaviors and although rearing behavior may have been expressed by some individuals, acoustic tagging studies using Chinook Salmon from Central Valley hatcheries and released during this time period (April and

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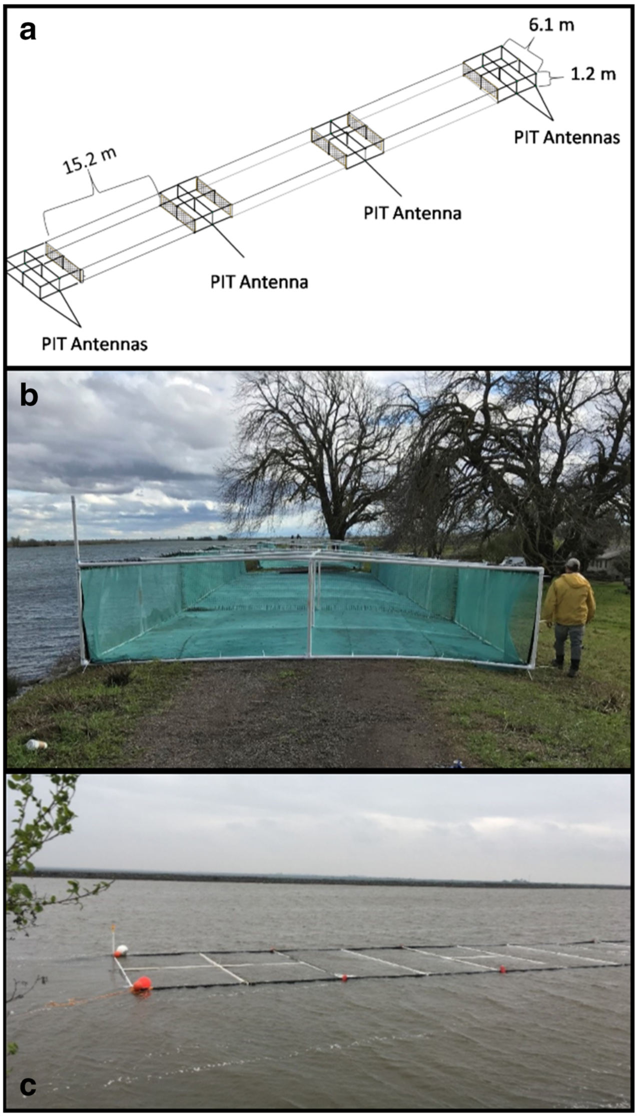

Fig. 2 Diagram of the experimental enclosure with size measurements (top panel), and pictures of the enclosure under construction (middle panel) and deployed during the experiment (bottom panel)

May) indicate that fish initiate migration rapidly following release (Singer et al. 2020, Zeug et al. 2020).

For the SAV treatments, plastic garland was chosen rather than natural SAV so the treatment could be standardized among replicate trials to the greatest extent possible (Savino and Stein 1982; Winfield 1986; James and Heck 1994; Sirota and Hovel 2006). Submerged aquatic vegetation (SAV) treatments were constructed using 1.2-m lengths of plastic garland affixed to a metal matrix that measured 1.2 m × 1.2 m. The SAV treatment received a total of four matrices which accounted for 6.1% of the total surface area of the enclosure. Foam floats were attached to approximately half of all stems to ensure the garland remained upright in the water column. The density of SAV (100 stems·m^2) was similar to the low-density value of stems reported by Ferrari et al. (2014). A dock was replicated using two sheets of plywood measuring 1.2 m by 2.4 m floated above the surface with an inner tube. Vertical pilings were replicated with four lengths of 25 cm diameter PVC pipe that extended through the plywood to the bottom of the enclosure. The dock structure occupied 6.1% of the total surface area of the enclosure in order to match the surface area occupied by the SAV treatment. For both the SAV and dock treatments, the structures were centered horizontally within the enclosure and then attached to the north edge to prevent the structure from moving with tidal action. The open water treatment was an enclosure with no habitat structure.

Experimental Procedures

Juvenile Chinook Salmon were implanted with PIT tags at the hatchery before being transported to the study site prior to each trial. Individual fish were anesthetized with AQUI-S and a small incision was made with a 3-mm stab knife on the ventral side of the fish just off the midline and anterior to the pelvic girdle. A 12-mm HDX PIT tag (Oregon RFID, Portland, Oregon, USA) was inserted into the peritoneal cavity, and fish were transferred to an aerated recovery tank and monitored until they regained full equilibrium. Only fish > 65 mm FL were used to avoid excessive tag burdens. Once tagged fish regained equilibrium and appeared to be swimming normally, they were transported to the study site in an oxygen-aerated tank and transferred to a holding pen, where they were allowed to acclimate to conditions at the study site for ~24 h. No mortalities of transported Chinook Salmon were observed during the study.

Largemouth Bass were transported to the study site in a 680-L holding tank with oxygen aeration. Upon arrival, a PIT tag was injected into the musculature below the dorsal fin. Bass were tagged to facilitate detection in case of escape from the enclosure. The bass were transferred from the holding tank to net pens adjacent to the experimental enclosure and were allowed to acclimate for ~24 h. Bass were then distributed among the three enclosures and allowed to acclimate to the enclosures for ~24 h before the start of each experimental trial. No mortalities of transported bass were observed during the study.

Prior to each trial, the six PIT tag antennas were tested using a PIT tag mounted to a length of PVC pipe to ensure detection was possible in all areas of each antenna (Fig. 3). Antennas were tuned if detection issues were observed. Experimental juvenile Chinook Salmon were transferred from the net pens into buckets and tag codes were recorded. Fish were allowed to acclimate briefly (10–20 min) before release into the enclosure. Thirty-four juvenile Chinook Salmon were released into each of the three enclosures (total of 102 in the array) in each trial. This number was estimated as the minimum necessary to ensure sufficient precision in survival estimates that a 10% difference among treatments could be elucidated. Simulations to obtain these estimates were performed

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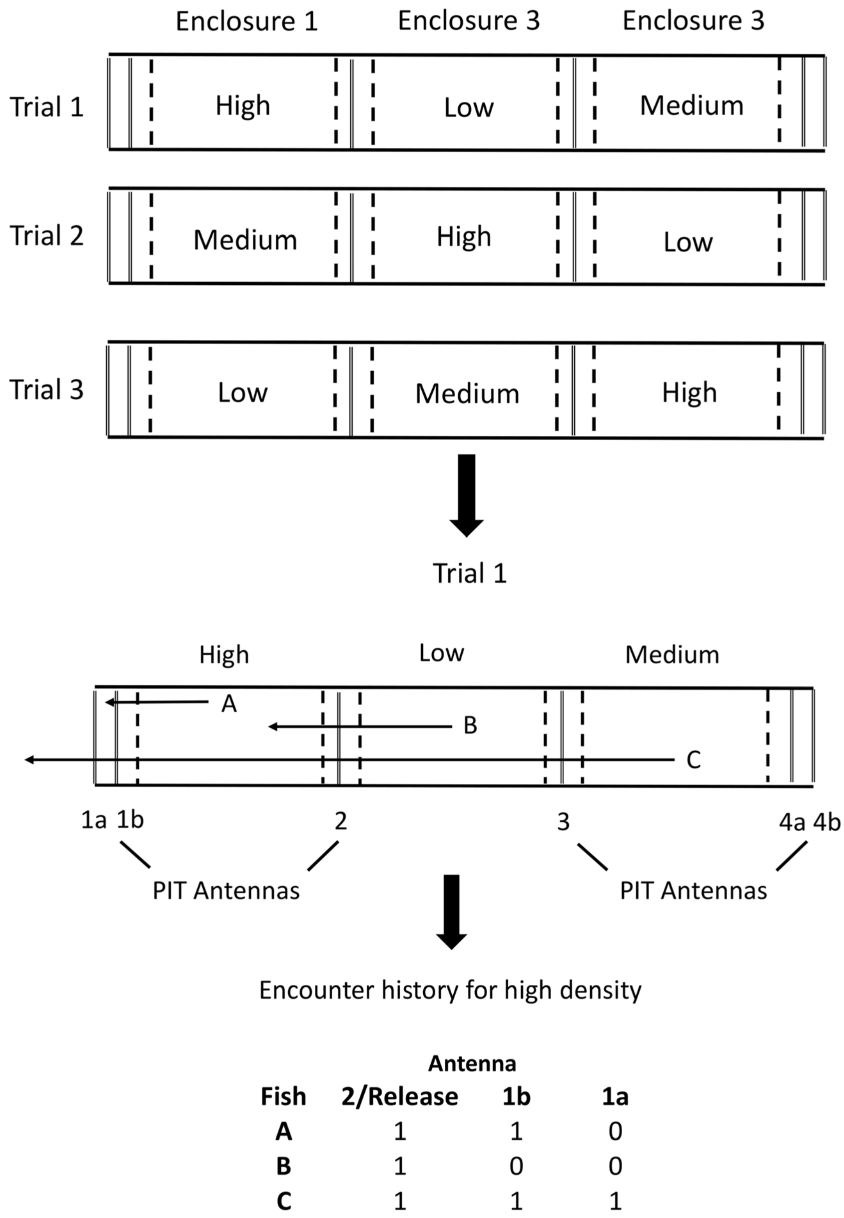

	Antenna		
Fish	**2/Release**	**1b**	**1a**
A	1	1	0
B	1	0	0
C	1	1	1

Fig. 3 Diagram describing the rotation of treatments in each trial during the experiment and an example of how encounter histories used in Cormack Jolly-Seber models were constructed for each enclosure with tagged Chinook Salmon stocked into that enclosure (fish "A"), and those that moved in from and adjacent enclosure (Fish "B" and "C"). The high density treatment in Trial 1 is used as the example enclosure. Dashed vertical lines define each enclosure and independent PIT tag antennas are labeled. Fish received a 1 if they were stocked into the enclosure (Fish A) or were detected on PIT antenna 2 (Fish B and C). Antennas 1a and 1b were used to separately estimate survival and detection probability. Fish A and C were detected leaving the enclosure, but Fish A was only detected on one antenna whereas Fish C was detected on both. The double antennas facilitated the separate estimation of survival and detection probabilities for fish in the enclosure

with the program SampleSize (version 3.1.1, University of Washington).

All releases occurred during a slack tide to ensure relatively similar water velocities were experienced by fish among trials. All trials for the density and habitat experiments began just prior to the beginning of an ebb tide and lasted through one semi-diurnal cycle. Thus, the time of day when fish were released progressed through the experiments. Only the first no-piscivore release occurred on a slack tide just prior to a flood tide. However, that trial also lasted through one semi-diurnal cycle.

Trials ran for ~24 h, based on a pilot effort that indicated most fish left the enclosure within a day. At the conclusion of each trial, a crowder was used to concentrate bass into a small area within each enclosure where they could be captured with a dip net. Bass were sacrificed with an overdose of MS-222, individually bagged, and immediately put on ice before being returned to the lab where they were frozen for later examination of stomach contents. A total of three density trials and three habitat trials were run with specific predator density and habitat treatments rotated among the three enclosures for each trial to ensure each enclosure received each treatment. This eliminated the potential for bias from the treatments' position in the enclosures.

In addition to the three density and three habitat trials, two trials without Largemouth Bass present were performed to obtain an estimate of survival without predation. The first no-piscivore trial took place prior to the first density trial (April 3, 2018) and utilized empty enclosures. The second no-piscivore trial took place after the final habitat trial

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(May 3, 2018) and contained the experimental habitats in the enclosures but no bass.

Environmental Data

Hobo Pendant temperature loggers (Onset™, Bourne, MA) were attached to a dock 95 m away from the enclosure to prevent possible interference with the antennas. Temperature was recorded at 15-min intervals for the duration of the experiments. Turbidity and dissolved oxygen were measured at the beginning of each trial from the dock or at the array site, generally upon arrival at the site on the day of juvenile Chinook Salmon release. Turbidity was measured with a Hach 2100q portable turbidity meter. Dissolved oxygen was measured with a YSI 85 handheld meter. Total freshwater inflow rate to the Delta during each trial was obtained from the California Department of Water Resources Dayflow accounting tool https://data.ca.gov/dataset/dayflow. Water velocities near the study site were characterized using data from a station located in the main stem Mokelumne River just above the confluence with the San Joaquin River approximately 4.5 km from the study site (Fig. 1). This was the closest station to the study site that recorded water velocity and the channels had similar dimensions. Our experimental enclosure was located near the edge of the channel and the mesh material would have slowed velocities inside; however, these velocities should approximate the conditions under which the experiment took place.

Stomach Contents

To confirm the consumption of experimental juvenile Chinook Salmon and to determine if alternate prey were consumed, stomach contents of Largemouth Bass used in the trials were examined. In the laboratory, stomachs were extracted from thawed bass and stored in 95% ethanol. Stomach contents were removed, scanned for PIT tags, and identified to the lowest feasible taxonomic unit.

Predator-Prey Body Size

To confirm that juvenile Chinook Salmon were within the size range of prey selected by the Largemouth Bass, we used the Shiny app developed by Gaeta et al. (2018). This application uses field data on prey sizes found in the stomachs of various predator species to model frequency distributions of expected prey lengths for predators of a given size. The application was run using Largemouth Bass as the predator and the fusiform prey option to represent the body shape of juvenile Chinook Salmon. Distributions were plotted for the maximum, minimum, and mean sizes of bass used in this experiment. Plots were inspected visually to confirm that experimental Chinook Salmon were in the size range frequently consumed by bass of the size of the experimental subjects.

Survival Analysis

Cormack Jolly-Seber (CJS) models were implemented in program MARK (Version 6.1, White and Burnham 1999) to estimate the effect of treatment level on survival of juvenile Chinook Salmon during each experiment (bass density and habitat) and simultaneously estimate tag detection probabilities. For each trial within both experiments, encounter histories were constructed for individual enclosures within the array using Chinook Salmon released directly into each enclosure as well as for fish that moved in from adjacent enclosures (Fig. 3). We assumed that the fate of a Chinook Salmon entering from an adjacent enclosure was independent of their experience in any previous enclosure. To inform this assumption, we constructed a CJS model with a dummy variable to indicate the experience of individual Chinook Salmon in both the density and habitat experiments. Tagged Chinook Salmon were assigned a 1 if they were stocked directly into an enclosure and had no previous exposure to predators (naive). They were assigned a zero if they had moved in from an adjacent enclosure (experienced). A similar variable was included in the residence time model. The covariate estimates and confidence intervals were interpreted as the effect of naiveté on survival or residence time within enclosures for each experiment.

For the CJS model of treatment effects, individual enclosures were the experimental unit for which survival was estimated, and the estimated Chinook Salmon survival·enclosure^{-1} was the observational unit. A grouping variable was assigned to specific trials within each experiment and a dummy variable was assigned to each treatment level. To assess the fit of models including covariates, an intercept-only model was constructed and compared to the covariate model with Akaike's Information Criterion corrected for small sample size (AIC_c). If the AIC_c value for the covariate model was ≥ 7 points lower than the intercept-only model, it was considered a better fit to the data (Burnham and Anderson 2002). Treatment effects on survival were interpreted using their beta coefficients and 95% confidence intervals. If the confidence interval for a beta coefficient did not include zero, it was determined to have a good support for an effect on survival. One treatment level was assigned as the baseline for comparison (β_0) and coefficients β_1 were estimated relative to that treatment level. To facilitate comparisons among all treatments, the level designated as the intercept was rearranged once for each model.

Movement Analysis

Residence time of juvenile Chinook Salmon was analyzed in relation to experimental treatment levels. Residence time was

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defined as the time between first arrival at a new antenna following a departure from an adjacent antenna (including initial release). This definition was applied under the assumption that a fish entering the detection radius of an antenna for the first time must have been moving up to that point in time. While the same logic might be applied to the final departure time at a previous antenna, only first arrivals were counted, since the first arrival at a new receiver is presumably part of the same movement as the last departure at the previous receiver. Calculated residence times of individual fish in each enclosure (measured in minutes, and represented as count data) were analyzed as a negative binomial-distributed function of multilevel effects using the *rstanarm* package (Goodrich et al. 2020; Version 2.19.3) for the R programming environment (R Core Team, 2019). For each experiment (Largemouth Bass density level and habitat type), the model estimated fixed effects of treatment and varying effects of trial, naiveté, and individual fish on modeled residence time.

Results

The field study took place between April 3, 2018 and May 3, 2018. Trials began with the first no-piscivore release on April 3. The three density experiment trials began on April 5, April 10, and April 12. The three habitat experiment trials began on April 19, April 24, and April 27. The final no-piscivore release occurred on May 3, which concluded the field study. Water temperature remained within tolerance limits for juvenile Chinook Salmon throughout the experimental period, but maximum daily temperature approached stressful levels (21 °C; Myrick and Cech 2004) during the final no-piscivore release on May 3. In general, water temperatures declined between the first no-piscivore release on April 3 and the third density trial on April 12. Temperatures began to rise during the first habitat trial on April 19 with an increase of > 2 °C between the second and third habitat trials and the second no-piscivore trial (Table 1).

Flow into the Delta increased between the first no-piscivore trial on April 3 and the second density trial on April 10 and then declined through the rest of the study period (Table 1). However, fluctuation in inflow did not appear to have a large effect on the tidal range near the study site (Table 1). The 2018 water year was classified as “Below Normal” by the California Department of Water Resources. The mean daily maximum upstream velocity during the study period was 0.23 $m \cdot s^{-1}$ (SD, 0.14) and the mean daily maximum downstream velocity was 0.50 $m \cdot s^{-1}$ (SD, 0.06). The maximum velocity recorded during the study was 0.64 $m \cdot s^{-1}$ and occurred in the downstream direction. Turbidity increased from 6.62 NTU on April 5 to >20 NTU during the second and third density trials (April 10 and 12, respectively). This rise in turbidity coincided with a large flow pulse in the Sacramento River. Turbidity was relatively low during the habitat experiment and similar among trials (Table 1) Dissolved oxygen was measured at the beginning and end of each trial, and all values did not fall below levels reported to be stressful for juvenile Chinook Salmon (6.0 $mg \cdot L^{-1}$; Carter 2005).

The size of juvenile Chinook Salmon used in in the experiment ranged from 65 to 96 mm FL. In general, fish sizes were similar among trials (Table 1). An exception occurred with the second no-piscivore release on May 3 when the average size of Chinook Salmon was > 7 mm larger than any other trial. Largemouth Bass used in trials ranged between 250 and 515 mm FL with a mean of 350 mm. An error in data recording resulted in a loss of bass length information for the first density trial. For all other trials, the mean size of bass was similar (Table 1). The size range of juvenile Chinook Salmon used in all trials was well within the distribution of prey sizes predicted to be consumed by Largemouth Bass of the mean, minimum, and maximum sizes used in all trials (Table 2).

In certain trials, one experimental bass was not recovered from an enclosure. During the second density trial, one bass was not recovered from the medium density treatment (six bass stocked and only five recovered). In the first habitat trial, one bass was not collected from the open water treatments. During the second habitat trial, one bass was not collected from the dock treatment. The PIT tags belonging to these bass were not detected on any antennas and their final disposition was unknown. During the third habitat trial, the structure began to submerge in some areas as the flotation foam had become waterlogged. Only six of the 18 experimental bass were recovered across all three enclosures. The numbers of bass recovered from the density trials and first two habitat trials indicated that those data were sufficient for survival analysis whereas data from the third habitat trial were considered suspect and not included in CJS models or the movement analysis. In the third density trial, a small striped bass was collected from the high-density treatment. This individual was retained for analysis of stomach contents and no study fish or tags were observed in its gut.

A total of nine PIT tags from experimental juvenile Chinook Salmon were recovered from bass stomachs, which confirmed that predation was occurring within the enclosures. Most of these tags were found alone in the gut or with partial fish remains attached. This suggested that food items, and potentially tags, were being consumed and excreted during the trial. This result, combined with the potential for regurgitation during crowding and collection of bass, indicated that estimation of predation based only on gut contents would not be reliable (Bowen 1996). Other prey items encountered in gut samples included six crayfish and small quantities of fish parts.

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Table 1 Mean freshwater inflow to the Delta and tidal range at the study site during each trial. Means and standard deviations of Chinook Salmon and Largemouth Bass in each trial, and point measurements of turbidity and dissolved oxygen at the study site prior to the start of each trial. NP1: first no-piscivore trial; D1: density trial 1; D2: density trial 2; D3: density trial 3; H1: habitat trial 1; H2: habitat trial 2; H3: habitat trial 3; NP2: second no-piscivore trial

Trial/Date	Delta inflow ($m^3 \cdot s^{-1}$)	Tidal range (m)	Turbidity (NTU)	Dissolved oxygen ($mg \cdot L^{-1}$)	Temperature (°C, SD)	Chinook Salmon fork length (mm), Mean, SD	Largemouth Bass fork length (mm), Mean, SD
NP1, April 3	1242	0.93	7.28	10.55	16.5 (0.5)	73.0 (4.4)	NA
D1, April 5	1814	0.93	6.62	8.12	15.5 (0.4)	71.7 (4.6)	NA
D2, April 10	2684	0.73	20.15	8.59	14.6 (0.6)	69.2 (3.6)	335 (46)
D3, April 12	2040	0.84	20.95	7.41	14.3 (0.6)	72.4 (5.0)	362 (55)
H1, April 19	944	1.04	6.25	9.93	14.7 (0.7)	74.7 (6.4)	374 (80)
H2, April 24	668	0.91	5.12	10.54	17.5 (0.5)	74.1 (4.7)	343 (53)
H3, April 27	605	0.88	5.26	10.19	18.1 (0.5)	71.4 (4.3)	338 (54)
NP2, May 3	569	1.02	2.87	9.23	18.5 (0.6)	82.1 (5.2)	NA

Effect of Chinook Salmon Experience

There was little evidence to suggest the experience of Chinook Salmon in one enclosure affected their survival in subsequent enclosures For the density experiment, the coefficient for naiveté was positive but had a 95% confidence interval that included zero (0.475, CI −0.048, 0.997). For the habitat experiment, the coefficient was negative, and the 95% confidence interval included zero (−3.101, CI -6.793, 0.593). The lack of consistency in the direction of the effect between experiments and the inclusion of zero in both 95% confidence intervals indicated experience did not have a strong effect. Thus, experience was not considered in the models of treatment effects on survival. In the residence time models, the effect of naiveté was well supported in the density experiment with a positive coefficient and 95% credible interval that did not include zero (0.7, CI 0.4, 1.1). In the habitat experiment, the effect of naiveté did not have good support with a 95% credible interval that included zero (−0.3, 0.8). Given these results, the effect of naiveté was only interpreted in the model of residence time for the bass density experiment.

Table 2 Distribution of predicted fusiform prey sizes from the model by Gaeta et al. (2018) for Largemouth Bass of the minimum, mean, and maximum sizes used in the experiment

	Prey size (mm)		
Largemouth Bass length (mm)	Median	1st percentile	99th percentile
Minimum (250)	49.6	16.5	111.9
Mean (350)	57.2	20.0	145.3
Maximum (515)	67.4	24.9	195.9

No-Piscivore Trials

The first no-piscivore release (Largemouth Bass absent) was performed on April 3, 2018, and the second no-piscivore release (habitats present but Largemouth Bass absent) was performed on May 3, 2018. During the first release, 97 of the 102 juvenile Chinook Salmon released among the three enclosures (34 fish per enclosure) were detected on one or more of the PIT tag antennas. The CJS model produced a survival estimate of 96.0%$\cdot$enclosure^{-1} (95% confidence interval (CI), 90.9–98.3%). Median residence time of juvenile Chinook Salmon in individual enclosures during the first no-piscivore trial was 3.9 h. During the second release, 72 of the 103 fish released (34 fish in two enclosures and 35 in the third enclosure) were detected on one or more antennas. The survival estimate for this release was 83.5%$\cdot$enclosure^{-1} (CI, 70.8–91.4%). However, during this second no-piscivore release, the floatation foam within the experimental structure had become waterlogged and portions were observed to be below the water surface. This could have allowed juvenile Chinook Salmon to escape out of the top of some enclosures so survival results were not interpreted for the second no-piscivore trial.

Density Experiment

Survival$\cdot$enclosure^{-1} estimates for juvenile Chinook Salmon in individual enclosures ranged from 72.8% during trial 2 to 92.5% during trial 3 and all values were lower than the no-piscivore trial survival estimate (Fig. 4a). Tag detection probabilities ranged between 79.6% and 94.3% among the three trials. A model that included covariates for treatment level was a better fit than an intercept-only model ($\Delta AIC_c = 27$):

$$\text{logit}(\phi) = \beta_0(\text{Low Density}) + \beta_1(\text{Medium Density}) + \beta_2(\text{High Density})$$

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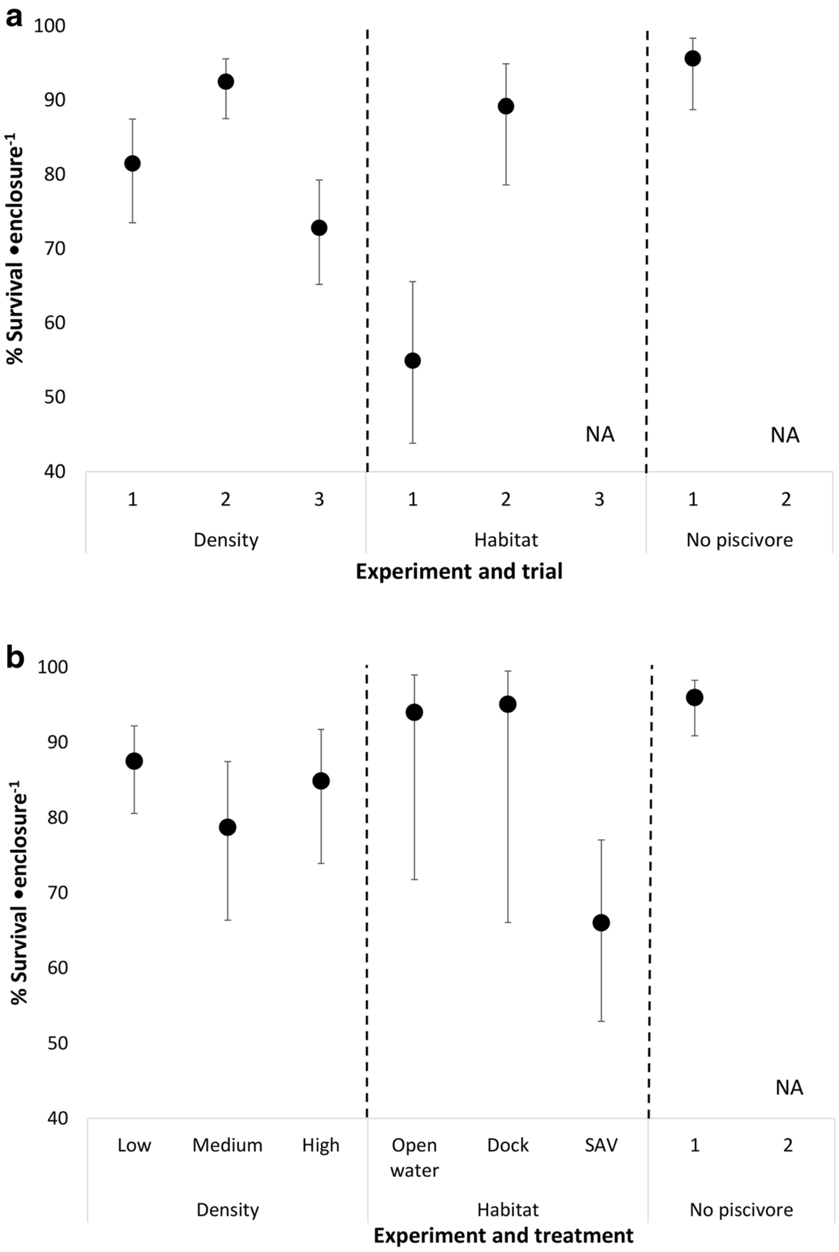

Fig. 4 Survival·enclosure^{-1} estimates with 95% confidence intervals for tagged Chinook Salmon in each trial (panel a) and treatment (panel b) from Cormack Jolly-Seber models. Coefficient estimates for pairwise comparisons among treatments can be found in Table 3

Thus, coefficient values for treatment effects were interpreted. There was good support for lower survival in the medium-density treatment relative to the low-density treatment enclosures whereas the difference in survival between the low-density and high-density treatment enclosures had little support (Table 3, Fig. 4b). Additionally, there was little support for a difference between medium- and high-density treatment enclosures (Table 3).

Median residence time of juvenile Chinook Salmon was greatest in the high-density treatment enclosures followed by the medium-density and low-density enclosures regardless of previous experience (Fig. 5). The Bayesian model did not identify any consistency in the varying effects of trial or individual. In addition to the well-supported effect of naiveté described above, there were consistent differences found in pairwise contrasts of the effects of treatment levels on residence time. Specifically, the high-density enclosure was associated with consistently higher residence times relative to the low-density (credible interval −1.15, −0.31) or medium-density (credible interval −1.16, −0.38) enclosures. The model did not identify any consistent difference in estimated residence times between the high-density and no-piscivore enclosures.

Habitat Experiment

Modeling of encounter histories for the habitat experiment only included data from the first two trials due to the issue

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Table 3 Coefficient estimates and 95% confidence intervals for the effects of Largemouth Bass density levels and habitat treatments on survival from Cormack Jolly-Seber mark-recapture models. Coefficients compare the effect on survival of the treatment in the "Comparison" column relative to the treatment in the "Base category" column. Coefficients with confidence intervals that do not include zero were considered effects with good support relative to the base category. LCI: lower confidence interval; UCI: upper confidence interval

Experiment	Base category (β_0)	Comparison (β_1)	Coefficient	LCI	UCI
Density	Low density	Medium density	−0.6362	−1.2669	−0.0056
	Low density	High density	−0.2215	−0.9036	0.4607
	Medium density	High density	0.4148	−0.1683	0.9978
Habitat	Open water	SAV	−2.0891	−3.9090	−0.2691
	Open water	Dock	0.2087	−2.3779	2.7954
	SAV	Dock	2.2978	0.0012	4.5944

with flotation described above. Mean survival·enclosure^{-1} was 54.9% in trial 1 and 89.2% in trial 2 (Fig. 4a) with detection probabilities ranging between 34.8 and 67.5%. The model including treatment covariates was a better fit to the data relative to an intercept-only model ($\Delta AIC_c = 14.0$):

$$\mathrm{logit}(\phi) = \beta_0(\mathrm{Open\ Water}) + \beta_1(\mathrm{SAV}) + \beta_2(\mathrm{Dock})$$

Coefficient values indicated good support for a negative effect of SAV in treatment enclosures relative to the open water and dock treatment enclosures (Fig. 4b, Table 3). Differences in survival between dock and open water treatment enclosures had little support.

Median residence time of juvenile Chinook Salmon was greatest in the open water treatment enclosures (2.5 h)

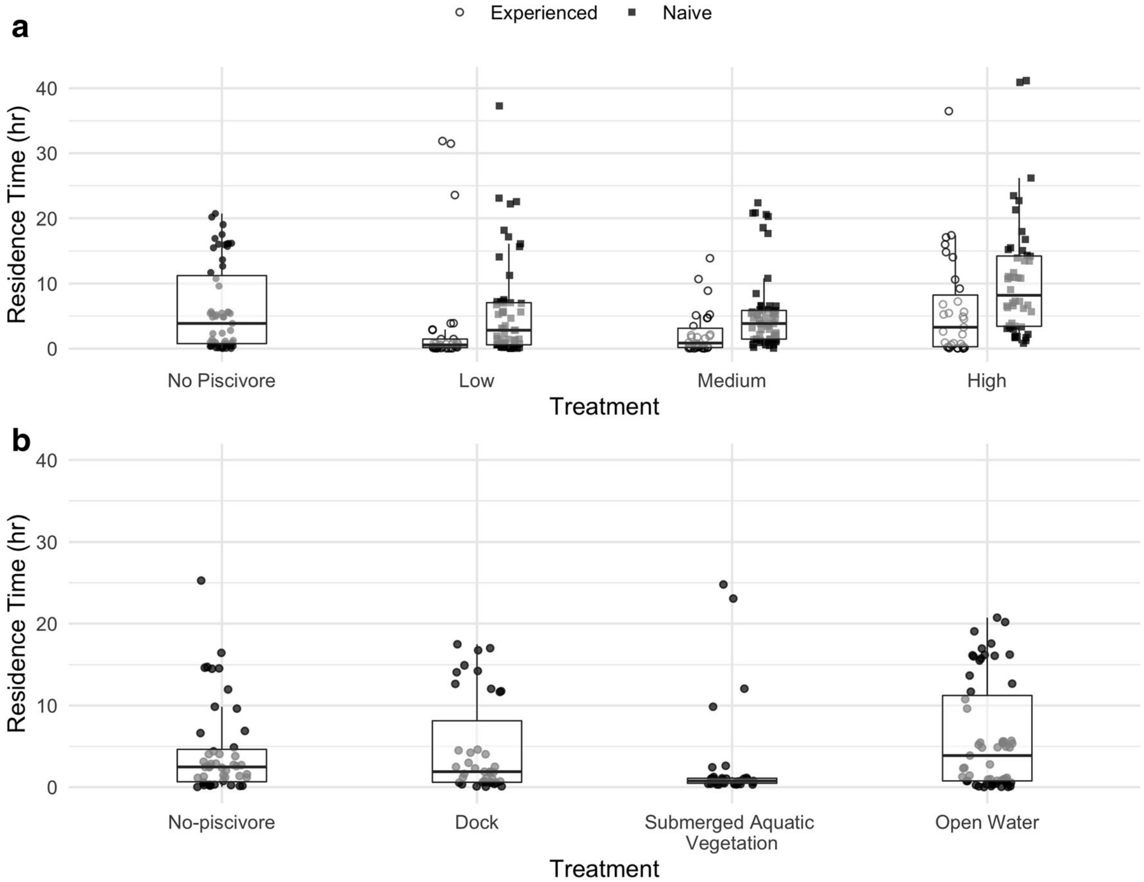

Fig. 5 Box and whisker plots overlaid on individual juvenile Chinook Salmon residence time observations in treatment enclosures. Boxes define the interquartile range and the horizontal line is the median value. Vertical lines define the largest value within 1.5 times the interquartile range. Bayesian hierarchical modeling identified consistently higher residence time in the high-density treatment relative to the low- and medium-density enclosures. Additionally, residence time was consistently higher for naïve fish across treatments in the density experiment. No differences among treatments, or between naïve and experinced fish, were well supported in the habitat experiment

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followed by the dock (1.9 h) and SAV enclosures (0.8 h) (Fig. 5b). The median value for the no-piscivore trials, where no predators were present, was 3.9 h. Box and whisker plots demonstrated overlap in the interquartile range of residence time for the dock and open water treatment whereas residence time was consistently low in the SAV enclosures (Fig. 5b). Across treatments and trials, the Bayesian negative binomial model identified five individuals with consistently higher residence time, but no other effect modeled (trial, habitat treatment) was found to consistently influence residence time. Pairwise contrasts between treatment effects did not yield any consistent differences.

Discussion

Understanding predation dynamics in estuarine ecosystems like the Sacramento-San Joaquin Delta is complicated by their large size, habitat heterogeneity, and environmental variability. Here, we used a novel experimental approach under field conditions to quantify the effects of piscivore density and habitat type on survival and movement behavior of juvenile Chinook Salmon. This strategy enabled balancing control over the context of predator-prey interactions with realistic field conditions. The results provide important implications for management strategies proposed to increase survival of juvenile Chinook Salmon migrating through the Delta including piscivore control and habitat restoration.

Juvenile Chinook Salmon survival was reduced in the presence of simulated SAV, whereas survival was similar in the presence of a simulated dock and open water. Increasing habitat complexity has been found to reduce predator capture success in previous studies (Savino and Stein 1982; Minello and Zimmerman 1983; Nelson and Bondsdorff 1990; Grabowski 2004) whereas our results conflict with those findings and survival was lowest in the most structurally complex habitat treatment (SAV). The predator and prey species used in the current study may have influenced this finding. Savino and Stein (1982) reported that increasing complexity of aquatic vegetation reduced the ability of Largemouth Bass to capture Bluegill *Lepomis macrochirus*. However, Bluegill are commonly associated with aquatic vegetation (Brown and Michniuk 2007; Young et al. 2018) that they use for foraging and predation refuge (Savino and Stein 1982). Juvenile Chinook Salmon are more likely to inhabit open water and respond to potential predation risks by reducing activity and spending more time near the substratum (Kuehne and Olden 2012). Thus, while higher complexity habitats may favor a prey species like Bluegill that can take advantage of them for defense against Largemouth Bass predation, it may not favor species like juvenile Chinook Salmon that do not use structurally complex structural habitat in the same way. Ferrari et al. (2014) reported that Largemouth Bass were significantly more likely to prey on open-water species than SAV-associated species. The analysis of residence time also supported the lack of affinity for SAV by juvenile Chinook Salmon with the lowest residence times observed in the SAV treatment.

The presence of a simulated dock did not have a detectable effect on juvenile Chinook Salmon survival relative to the open water treatment. Reviews by Carrasquero (2001) and Kahler et al. (2000) concluded that there was no quantitative or qualitative evidence that docks, piers, boathouses, or floats either increase or decrease predation on juvenile salmonids. Ward et al. (1994) reported that piles associated with piers, floating platforms, and wharves did not affect juvenile Chinook Salmon and steelhead migration and predation in the lower Willamette River, Oregon. Although the Delta has a different predator assemblage than the systems examined in the referenced reviews, our results were consistent with the conclusion of limited effects of piles associated with docks on survival and movements of juvenile Chinook Salmon. Lehman et al. (2019) estimated that 22% of the Delta water surface area is occupied by SAV, whereas docks cover only 0.44%, and from these results as well as further literature review, they concluded that SAV warranted the most immediate future investigation in the Delta. Our results suggest that even when the area of SAV and dock is comparable, SAV effects appear to have considerably greater importance on survival of juvenile Chinook Salmon.

Juvenile Chinook Salmon survival decreased as bass density increased from the low- to medium-treatment level. However, an additional doubling of bass density in the high-density treatment did not further reduce Chinook Salmon survival. A change in the number of predators per-unit-area is expected, based on theory, to change the frequency of predator-prey interactions and thus survival of prey (Anderson et al. 2005). However, the results presented here suggest that the relationship between bass density and Chinook Salmon survival may be non-linear. The range of Largemouth Bass densities used in the experiment was similar to, or greater than, densities observed in the Delta (Cavallo et al. 2013). This relatively high density could have resulted in limited effects in the high-density treatment as a result of Largemouth Bass interference competition (Skalski and Gilliam 2001). Further studies with a greater number and range of bass density treatments would be useful to describe potential non-linear relationships.

Chinook Salmon consistently spent more time in the high-density treatment relative to the low- and medium-density treatments. This pattern conforms well with previous work that indicates juvenile salmon reduce activity in response to predation threats (Kuehne and Olden 2012, Sabal et al. 2020). The only well-supported effect of Chinook Salmon naiveté was detected in the model of residence time during the density experiment. Naïve Chinook

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Salmon consistently spent more time in enclosures relative to experienced fish that moved in from adjacent enclosures. A study by Sabal et al. (2020) that found naïve juvenile Chinook Salmon traveled more rapidly than experienced conspecifics even when exposed to predation cues. The opposite movement pattern was detected in the density experiment and the effect may not be related to predator cues. The effect of naiveté was not well supported in the density experiment survival model indicating that the effect on residence time did not translate to an effect on survival.

The results of the density experiment indicate the abundance of predators at a candidate control site is likely to impact the ability of a predator removal action to produce an observable effect on Chinook Salmon survival. Without knowledge of the quantitative relationship between predator density and prey survival and the current predator density at a potential control site, the prospect for observable effects is unpredictable. Indeed, Lennox et al. (2018) reviewed the efficacy of manipulating predator abundance to protect prey species and concluded that outcomes were inconsistent and idiosyncratic across a diversity of vertebrate taxa. Some previous field studies in the Delta reported inconsistent or weak responses of juvenile salmonid survival to aquatic predator removals (Cavallo et al. 2013; Michel et al. 2019). These studies occurred in natural channels where predator density could not be precisely estimated or controlled resulting in uncertainty regarding the predator densities experienced by study fish. In open systems, predators can rapidly recolonize the removal area from adjacent habitats, which can reduce the efficacy of removals designed to increase survival without sustained removal effort (Cavallo et al. 2013). There is some evidence that predator removal in confined areas associated with water control structures may be achievable (Sabal et al. 2016).

The lack of evolutionary history between study species may have contributed to the observed survival responses to some treatments (Kuehne and Olden 2012). Both Largemouth Bass and the most abundant species of SAV in the Delta (Brazilian waterweed) are not native to the study area. Non-native species can have both consumptive and non-consumptive effects on the survival of native species (Sih et al. 2009). Kuehne and Olden (2012) reported that juvenile Chinook Salmon displayed attenuated antipredator responses when exposed to a non-native relative to a native piscivore which suggests Chinook Salmon in the Delta may be more susceptible to predation by non-native Largemouth Bass regardless of density. The presence of aquatic vegetation has been shown to reduce predation on juvenile Chinook Salmon by a native piscivore (Gregory and Levings 1996); however, Semmens (2008) found that juvenile Chinook Salmon in a Pacific Northwest estuary had a strong preference for native vegetation and no preference for non-native vegetation. Any potential protective effect of non-native aquatic vegetation may be lost if juvenile Chinook Salmon have no preference for it, it displaces preferred native species or enhances capture success of non-native piscivores.

There are several qualifications related to the experimental design and study species that should be considered when interpreting study results. Using enclosures provided greater control over the context of predator-prey interactions but also necessitated the use of a scaled down dock and artificial SAV that could be standardized among trials. Using simulated vegetation is a common technique for controlled experiments (Savino and Stein 1982; Winfield 1986; James and Heck 1994; Sirota and Hovel 2006) and although we observed strong responses in Chinook Salmon survival to the SAV treatment, natural materials may provide different ecological functions for predators or prey.

The experimental set up was intended to bridge the gap between studies using small mesocosms with total control over context but unnatural conditions, and observational studies with no control over context but natural conditions. Small mesocosms allow for many replicates but inference to natural systems is limited because species interactions are forced to occur in a limited area for a time determined by the investigator. In our experimental set up, the large size of enclosures and the ability of juvenile Chinook Salmon to volitionally move through the array better represented how fish move through a predator field in natural habitat while controlling the context of interactions (predator density and habitat type). The number of replicates in our study was limited by logistics and water temperatures. However, the tradeoff was greater inference to natural systems and relevance to management actions. Pre-project simulation indicated samples sizes were sufficient to estimate survival with enough precision to differentiate variation between treatments $\geq 10\%$. The open design may have allowed alternative prey species to enter the enclosure during the experiments. Our study did not explicitly evaluate the extent to which alternative prey was available during each trial and prey density has a well-known, yet often inconsistent, relationship with consumption rates (Berryman 1992; Abrams and Ginzburg 2000; Nilsson 2001). Examination of Largemouth Bass stomach contents revealed only small amounts of alternative prey, suggesting low occurrence.

Largemouth Bass was the only piscivore tested and results may differ for other piscivorous species with alternative habitat preferences and feeding behaviors (e.g., Striped Bass and catfishes). However, Largemouth Bass and other black bass species *Micropterus* spp. may offer the best prospect for depletion in localized areas given their tendency to occupy limited ranges, whereas residence time of Striped Bass tends to be short in any given location (Smith et al. 2017). The juvenile Chinook Salmon used in the experiment were all naïve, hatchery-origin fish. Multiple studies have reported hatchery salmonids have reduced fitness relative to wild conspecifics (Araki et al. 2008; Fraser et al. 2010; Jackson and Brown 2011). Studies on predation risk specifically have indicated

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effects of domestication tend to be small or undetectable (Dellefors and Johnson 1995, Fritts et al. 2007). However, reduced fitness should still be considered when interpreting results.

Our results indicated that juvenile Chinook Salmon survival was reduced in the presence of SAV. Invasive SAV and Largemouth Bass have both become widespread in the Delta over the last few decades (Brown and Michniuk 2007; Mahardja et al. 2017). Restoration strategies that control or remove non-native SAV could be profitable and studies at the spatial scale of potential actions (e.g., > 1 ha) would be a logical next step to better predict benefits. Largemouth Bass density strongly affected survival between some treatments, but relationships may be non-linear. This finding is largely consistent with the evidence from studies in the Delta (Cavallo et al. 2013; Michel et al. 2019), and predator control efforts in general where predator densities are not known, and results have been unpredictable (Lennox et al. 2018). This suggests that efforts to increase juvenile salmonid survival via predator abundance manipulation could have limited success. Possible exceptions may be at specific, relatively confined locations where manmade water control structures concentrate and potentially disorient salmonids as they move through or over the structure (Sabal et al. 2016). Results from the habitat experiment suggest that removing derelict docks, piers and pilings as part of habitat restoration may have limited or undetectable effects on juvenile Chinook Salmon survival. The scale of our dock treatment was limited to fit within the enclosure and data at larger scales may be informative (e.g., in association with multi-dock marinas and boating berths). The potential for manipulation of predator-prey interactions to increase juvenile Chinook Salmon survival is likely to be site-, predator species-, and context-dependent and it is unlikely that a single strategy will be effective in all situations.

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