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# Juvenile Chinook salmon use of sandbar willows in a large-scale, simulated riparian floodplain: microhabitat and energetics

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**Abstract** Outmigrating, juvenile Chinook salmon *Oncorhynchus tshawytscha*, with access to floodplains (e.g., Yolo Bypass California, USA), grow faster than those restricted to the main channel of the Sacramento River. How these young salmon might use rooted, vegetative structure (e.g., to decrease

energy expenditures) while holding positions in flowing water on floodplains and flooded riparian zones is unknown. We conducted daytime experiments in a large (24.4 m long) flume containing a planted area (9.76 m × 1.22 m) of sandbar willows, *Salix interior*. Flume water was maintained at 1.5 m depth and 16 °C over a 15–90 cm s<sup>-1</sup> test velocity range. Fish were videoed using 19 cameras to determine positional behavior, including their depth, use of vegetation, and tail-beat (body-undulation) frequencies (TBFs). These TBFs were replicated with similarly-sized salmon in a calibrated, Brett-type swimming respirometer, where oxygen consumption rates were measured. Using these laboratory measurements, we estimated their swimming velocities and energetic costs associated with occupying sandbar willow habitats in the flume. As flume velocities increased and the leafy canopies of the willows were bent over from the flow, salmon occupied deeper water, among the thick stems of the willows, and maintained their positions. Even at the highest (90 cm s<sup>-1</sup>) nominal flume velocities, their estimated swimming velocities were only 35.6 cm s<sup>-1</sup>, within the bottom 15 cm of the water column. This resulted in unchanged energetic costs, compared with those estimated at lower nominal water velocities. The use of vegetated (e.g., with sandbar willow common to the riparian zone) floodplains, rather than non-vegetated ones, can potentially provide energy-saving, growth-promoting daytime habitat for migrating juvenile salmonids during river-flow periods that include floodplain inundation.

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## Introduction

Many freshwater ecosystems worldwide have been heavily altered by anthropogenic modifications for flood protection and reliable water delivery for increasing human populations (Mount et al. 2002; Singer 2015). Consequently, valuable habitat for larval and juvenile fishes has been lost, either directly through the upstream diversion of water and construction of levees to prevent or limit river flooding or indirectly through the loss of connectivity between habitat types (e.g., via river channelization; Mount 1995, Tockner and Stanford 2002). Historically, floodplain habitats served as important rearing grounds for the early-life-history stages of migrating anadromous fishes (Brown and Hartman 1988, Moyle 2002), and research has increasingly focused on the role of these habitats in promoting juvenile survival in fishes (i.e., Sommer et al. 2001; Jeffres et al. 2008). For example, outmigrating juvenile Chinook salmon (*Oncorhynchus tshawytscha*) that have access to the Yolo Bypass floodplain (California, USA) show faster growth (i.e., increased body mass  $d^{-1}$  in rearing area) than those restricted to the main channel of the Sacramento River (Sommer et al. 2001). Similar results have been found for juvenile Chinook smolts in other California rivers using natural floodplains/riparian zones (Jeffres et al. 2008), and Chinook smolts reared on agricultural floodplains have shown growth rates among the highest recorded in freshwater systems in California (Holmes et al. 2020; Jeffres et al. 2020; Katz et al. 2017).

The mechanisms driving increased growth and survival of salmonids within floodplains may be attributed to interactions between abiotic and biotic factors, such as increased water temperatures and productivity (Sommer et al. 2001; Jeffres et al. 2020), or the promotion of phytoplankton and zooplankton densities from reduced water velocities associated with vegetative structure (Jeffres et al. 2008). In northern California, floodplains and their associated riverbanks, flooded riparian zones, and levees can be vegetated with willow (*Salix* spp., Harris 1987) and other vegetative structure that may facilitate increased growth

rates in fishes. In addition to increases in prey availability, the vegetation's hydraulic drag may provide low-velocity zones for small fishes (Pu et al. 2019). Many fish, including salmonids, have been shown to occupy lower-velocity zones created by physical structures, including large woody debris, large rocks, and even other fish (Herskin & Steffensen 1998; Crook and Robertson 1999; Chun et al. 2011), to their apparent advantage (e.g., provide cover, decrease energetic costs associated with locomotion). Presumably, these fish can therefore invest more energy into other processes, such as somatic growth, and achieve relatively higher growth rates compared to those individuals that cannot find or do not have access to such zones.

Increased growth and shorter migration times in juveniles could have large-scale implications for population persistence of salmonids. The ability to achieve a large body size at an earlier age decreases the probability of predation by piscivorous predators, with smaller individuals experiencing higher mortality due to predation than larger-size cohorts (Hurst and Conover 1998; Lundvall et al. 1999). Similarly, faster migration rates may decrease the length of time juveniles are exposed to predators (Anderson et al. 2005), and ultimately increase the probability of survival. Therefore, the presence of vegetative structure within floodplain and flooded riparian habitats may contribute to overall population persistence by increasing the potential of juvenile salmonids to reach larger sizes and survive to reproduce.

In California, salmon are a priority for conservation, with management and restoration actions being driven primarily by Chinook populations. There are three evolutionarily significant units (ESUs) of Chinook salmon that spawn and rear within the Sacramento-San Joaquin watershed of California's Central Valley. These include the Central Valley Fall and Late Fall-runs, Central Valley Spring-run, and Sacramento Winter-run. These ESUs were listed under the federal Endangered Species Act as a species of concern (2004), threatened (1999), and endangered (1994), respectively (NMFS 2016). Understanding the ways in which juvenile Chinook salmon growth and survival may be impacted by access to floodplain and flooded riparian habitats is crucial for successful management. Furthermore, the effects of specific variables associated with floodplain habitats on salmonid behavior and swimming efficiency, such as

the presence of vegetative structure, need to be evaluated to more effectively guide management actions, including the creation or restoration of floodplains.

To investigate how young Chinook salmon use such vegetative structure on floodplains over a range of water velocities, we conducted daytime experiments in a large (24.4 m long  $\times$  1.22 m wide) flume containing a 9.76 m long  $\times$  1.22 m wide planted area of sandbar willows (*Salix interior*). We observed fish behavior and measured their tail-beat frequencies (body-undulations, TBFs) using video recordings and analyses. We hypothesized that these fish would spend more time within the submerged, sandbar willows (e.g., as low-velocity, hydraulic refuges), especially at increased water velocities, in this simulated floodplain. The flume-fish TBFs were replicated with similarly-sized salmon in a calibrated, Brett-type swimming respirometer, where oxygen consumption rates were measured. Using these laboratory data, we estimated fish swimming velocities and energetic costs associated with occupying sandbar willow habitats in the flume.

## Methods

### Fish source and care

Age-0 Chinook salmon, *Oncorhynchus tshawytscha*, from the California Department of Fish and Wildlife Nimbus Fish Hatchery were transported in 11-l polyethylene bags filled with hatchery water (ca 75%) and oxygen (ca 25%) to the University of California, Davis' Center for Aquatic Biology and Aquaculture (CABA). Fish were divided into two 557-l cylindrical tanks equipped with air-equilibrated  $12 \pm 0.5$  °C flow-through well water, with in-tank water velocities ranging from 0 to 6.6 cm/s. Any fish with obvious injuries (e.g., skin lesions, “cloudy” eyes, frayed fins) were separated from the others and not used in experiments. Tank covers allowed sufficient natural light to maintain fish on a natural photoperiod. Tank temperatures were raised  $1$  °C  $d^{-1}$  to  $16 \pm 0.5$  °C to acclimate the fish to temperatures that replicate late-spring river water temperatures, while pH and dissolved oxygen concentrations (DO) remained at 8.0–8.2 and 8.0–10.0  $mg\ l^{-1}$ , respectively. All fish were fed daily ad libitum rations of 12-mm Rangen commercial

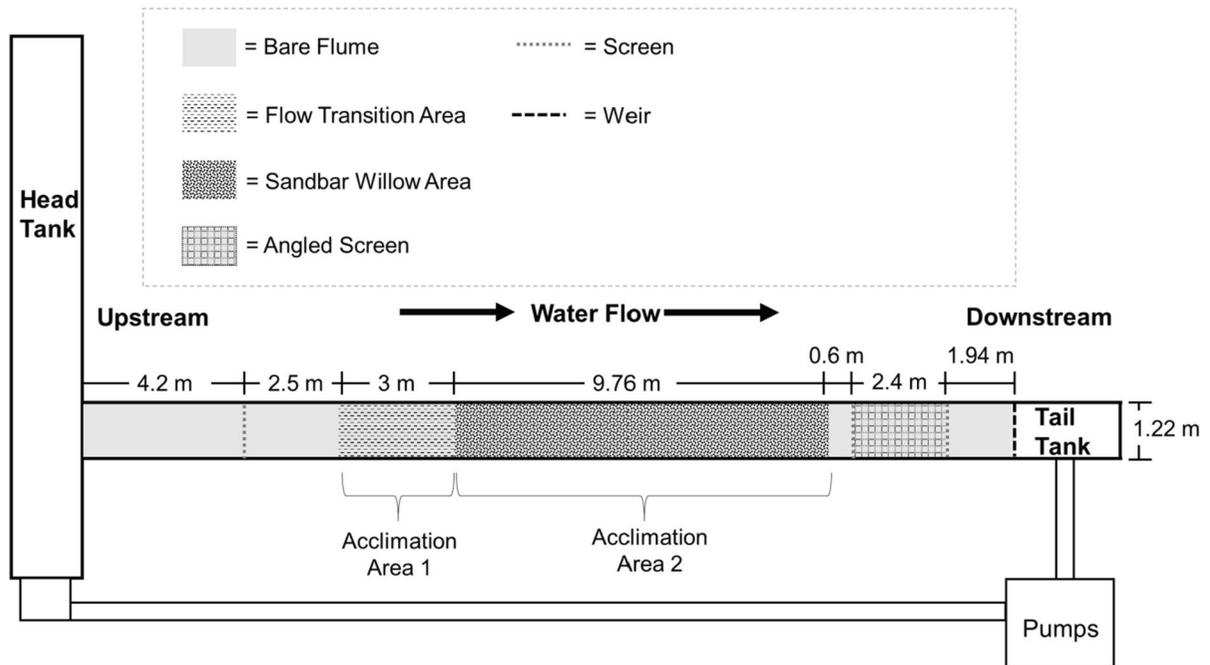
pellets (Rangen, Inc., Buhl, Idaho). Uneaten food and fish waste were removed daily.

### Experimental flume

Experiments were conducted in a large (24.4 m long by 1.22 m wide) re-circulating steel flume with 2.4-m-high painted walls (Fig. 1). Flow entered the vegetated experimental section downstream of a 4.2-m-long flow stabilization zone, and an additional 5.5 m of bare flume surface. The vegetated section was 9.76 m long, consisting of eight, 1.22-m-long  $\times$  1.22-m-wide planted bins of sandbar willows (*Salix interior*) at ca. 15 plants  $m^{-2}$ . The bin's soil (0.61 m deep) was covered with river gravel (ca. 2-cm diameter), to be level with the flume's false floor, upstream and downstream of the vegetated section. The willow's foliage (ca. 1.2–1.5 m tall) was more concentrated at the top leafy canopy versus the bottom stems. Downstream of the vegetated section, a 2.4 m long, 45° angled screen (0.63-cm stainless steel mesh) protected fish from the recirculation pumps and aided in collecting fish. Water depth in the flume was maintained at 1.5 m using a downstream overflow weir for each velocity condition (15, 45, and 90  $cm\ s^{-1}$ ). Flume water temperature was maintained at  $16 \pm 0.5$  °C to approximate that in the Sacramento River in the late spring. Flume pH and dissolved oxygen concentration were maintained at 8.0–8.2 and 8.0–9.0  $mg\ l^{-1}$  respectively.

### Fish transport and acclimation to flume

Juvenile salmon ( $n=40$  fish per experiment, to simulate aggregations observed in California rivers, McElroy et al. 2018) were transferred 0.5 km from CABA to the flume (<5 min trip) using a large ice chest (ca. 100 l) filled with water from their holding tank. Fish were placed into either one of the flume's two acclimation areas delineated by net panels across the flume's channel. One acclimation area (3 m long, 1.22 m wide, 1.5 m deep) was located upstream of the planted section of the flume, while the other (9.76 m long, 1.22 m wide, 1.5 m deep) was in the planted section of the flume (Fig. 1). Two acclimation areas were used to determine if fish exhibited positional bias due to their location in the flume when the flow was initiated. No positional bias was found. After a



**Fig. 1** Top view of the experimental flume. Fish were confined between the flow-stabilization zone and the angled screen

30-min acclimation at  $0 \text{ cm s}^{-1}$  water velocity, net panels were removed, and the flume's flow was initiated, starting the experiment.

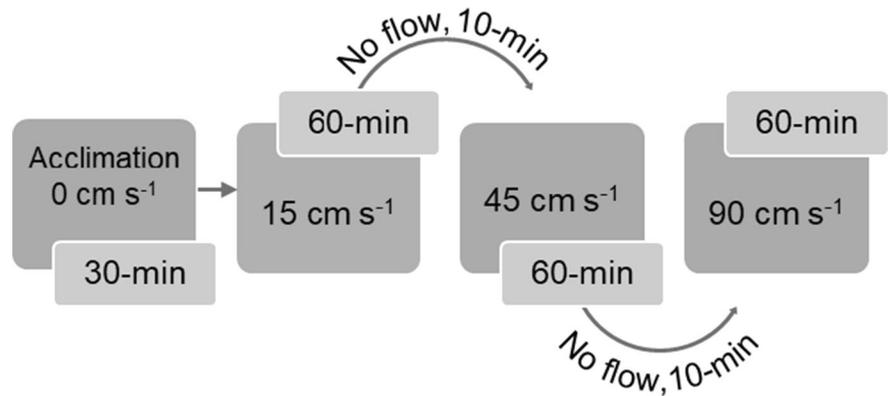
#### Flume experiments

Water velocities of 15, 45, and  $90 \text{ cm s}^{-1}$  were chosen to expose the salmon to a low, moderate, and high velocity challenge (Cech and Myrick 1999). Water velocities were validated for the three experimental flows using a SonTek Acoustic Doppler Velocimeter (ADV) down-looking probe at 10 Hz, over 30 s when fish were not in the flume. Velocities were measured upstream, in the center, and downstream of the vegetated section (Fig. 1; denoted XS-1, XS-2, and XS-3 respectively). The velocity-measurement grids were chosen from preliminary observations of apparent effects of flow on the vegetation with depth. A  $3 \times 3$  grid was used for the  $15 \text{ cm s}^{-1}$  test condition with measurements taken at 0.25, 0.75, and 1.14 m from the flume bottom and 0.15, 0.61, and 1.07 m from the flume wall. Unfortunately, data recordings for cross-Section 1 of the  $15 \text{ cm s}^{-1}$  condition were unusable due to file corruption. For the 45 and  $90 \text{ cm s}^{-1}$  test conditions, velocity measurements were taken at 0.15,

0.46, 0.76, 1.07, and 1.37 m from the flume bottom at 0.15, 0.38, 0.61, 0.84, and 1.07 m from the flume wall.

After acclimation, experiments ( $n=13$ ;  $n=40$  fish per experiment) consisted of three, test-velocity periods interspersed with short, no-flow periods. Specifically, for the first 6 experiments conducted, we used a 60-min period at  $15 \text{ cm s}^{-1}$ , 10 min at  $0 \text{ cm s}^{-1}$ , 60 min at  $45 \text{ cm s}^{-1}$ , 10 min at  $0 \text{ cm s}^{-1}$ , and 60 min at  $90 \text{ cm s}^{-1}$  (Fig. 2). In experiments 7 through 13, the periods of non-zero velocity were shortened from 60 to 30 min due to decreased water-temperature control caused by a local heat wave. We did not detect any indicators of “fatigue” (e.g., higher impingement rates) among fish in the 30- or 60-min test period experiments. Estimated swim speeds for fish in the flume did not exceed their aerobic performance envelope nor were higher than 50% of their  $U_{\text{crit}}$  for fish of this size (ca.  $70 \text{ cm s}^{-1}$ , Cech and Myrick 1999). The general “increasing velocity” pattern for the experiments most closely simulates that following storm and subsequent runoff events (or pulsed-flow events in California rivers with hydro-electric dams). Throughout each experiment, observations of fish

**Fig. 2** Explanatory diagram of the timeline of the flume experiments



location and swimming patterns (including positive or negative rheotaxis, i.e., fish swimming into or with the current, respectively) were made for each velocity at 5-min intervals. Video clips (mean = 8 per experimental interval of fish, which were swimming but holding station for greater than 6 s) were recorded for fish TBF, behavior, and position in the water column, from nineteen cameras placed above the flume and on the flume wall for subsequent analyses (see below). If fish impinged (> 2/3 of its body pinned against the screen for > 30 s) on the angled screen, they were removed using a dip net, measured for mass (electronic balance) and fork length (FL), and moved to a 70-l holding tank. Following each experiment, fish were collected from the flume, measured for mass and FL, and ten fish were randomly selected for a visual health assessment. None of the 520 fish used in these experiments were re-used, and any fish impinged on the angled screen was not included in post-experiment health assessments. Fish used in flume experiments were mean ± SE mass: 6.2 ± 0.1 g; mean ± SE fork length: 7.4 ± 0.1 cm.

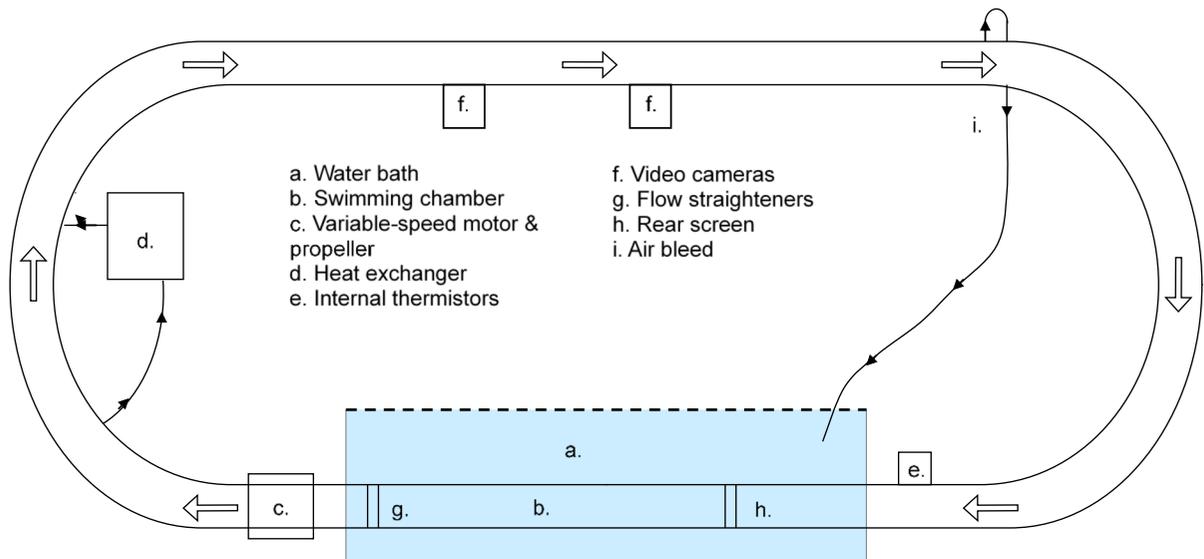
After experiments in the experimental flume, TBFs (n = 320 individual fish) at all velocities were determined via digitizing (Videowave ver. 4 software) the videos (30 frames s<sup>-1</sup>) of each experiment and counting tail beats. Each video was scanned for fish activity using Windows Media Player. Tail beats (full propulsive motions of the caudal fin) were counted, frame-by-frame, using Adobe Premiere software. Each tail-beat-video segment (10–30 s long) was counted four times to calculate a mean TBF.

### Laboratory MO<sub>2</sub> experiments

Swimming oxygen consumption (aerobic metabolism) rates at 16 ± 0.5 °C were measured using groups of juvenile Chinook salmon at six flume-relevant velocities in a custom-built, recirculating-flow, 150-l Brett-type (Brett 1964) swimming tunnel, immersed in a thermally stable water bath (Fig. 3). To quantitatively assess the three-dimensional flow field in the tunnel, we measured water velocities at five points on each of three cross-sections of the cylindrical swimming chamber: at the upstream end, middle, and the downstream end, with a calibrated, Marsh-McBirney flow probe (Model 201D).

Prior to experiments, the respirometer was flushed with water from an aerated bath to increase the PO<sub>2</sub> to > 18.7 kPa, and fish (n = 10, simulating natural aggregations, McElroy et al. 2018 and consistent with our observations of fish behavior in the flume) were placed into the respirometer for a 30-min acclimation. Although 30 min is a relatively short acclimation time for fish used in swimming metabolism experiments, it minimized injuries from their efforts to escape or from inter-fish interactions, and it replicated the acclimation period used for our flume experiments. Curtains surrounding the respirometer prevented experimenter influence on fish behavior; swimming fish were viewed remotely via two video cameras (Fig. 3). During acclimation, water from the bath was continuously flushed through the respirometer to maintain the > 18.7 kPa PO<sub>2</sub> level.

After acclimation, recirculatory flow generated from a propeller, and its variable-frequency drive unit was slowly introduced in the respirometer until



**Fig. 3** Side view of the Brett style swimming chamber used in  $MO_2$  experiments

a velocity of  $12 \text{ cm s}^{-1}$  was reached, and positive rheotaxis (i.e., the majority of fish swimming into the current) was observed. The water velocity was slowly increased to one of the six velocities (12, 16.5, 21, 32.1, 36.9, or  $44.4 \text{ cm s}^{-1}$ ) encompassing the range of swim velocities estimated for fish swimming in the flume. A 3-ml water sample from the respirometer was taken for the initial  $PO_2$  determination, and the experiment began by sealing the respirometer. Heat exchangers in the water bath maintained the respirometer's water temperature at  $16 \pm 0.5 \text{ }^\circ\text{C}$ . Sequential  $PO_2$  samples were taken every 30 min until a  $PO_2$  decrease of at least 1.3 kPa was reached (i.e., 1–2 h). Water  $PO_2$  values were converted to oxygen concentrations using a solubility nomogram (Green and Carritt 1967). Mean fish oxygen consumption rates were measured by quantifying the oxygen concentration decrease in the sealed respirometer due to the aerobic respiration of the fish. We calculated aerobic respiration according to the following:

$$MO_2 = [(O_2(A) - O_2(B)) * (V/T)/(M)] / (10)$$

where  $MO_2$  was  $O_2$  consumption rate ( $\text{mg } O_2 \text{ kg}^{-1} \text{ h}^{-1}$ ),  $O_2(A)$  was the oxygen concentration ( $\text{mg } O_2 \text{ l}^{-1}$ ) at the start of the measurement period,  $O_2(B)$  was the oxygen concentration at the end of the measurement period,  $V$  was the respirometer's volume

(150 l), minus the total fish volume (assumed to be equal in ml to total mass in grams [Virani and Rees 2000]),  $T$  was the elapsed time during the measurement period (h),  $M$  was the total fish mass (kg), and 10 was the number of fish used, to calculate the mean, individual fish  $MO_2$  (Cech 1990). Adjusting for fish mass by using  $M^{-1}$  in this equation is appropriate for swimming fish (Brett and Glass 1973). Experiments at each of the six water velocities were tested with at least 3 groups of salmon. Video recordings from the cameras mounted above the transparent swimming chamber facilitated subsequent TBF analyses, which paralleled those from the experimental flume. After experiments, fish were removed and measured for mass (g) and fork length (FL), and placed into a post-test holding tank. No fish were re-used in these experiments. Fish used in flume experiments were slightly, though significantly smaller than those used in the laboratory swimming oxygen consumption experiments (mean  $\pm$  SE mass:  $6.2 \pm 0.1$  vs.  $9.4 \pm 0.2$  g, respectively; mean  $\pm$  SE fork length:  $7.4 \pm 0.1$  vs.  $9.3 \pm 0.1$  cm, respectively;  $p < 0.05$  for both comparisons). Using the equations in Brett and Glass (1973), we also confirmed that differences in fish size between our flume and respirometry fish likely had a minimal effect on metabolic rates (estimated error of 1.5% for active, ca. 6- and 9-g sockeye salmon at  $15 \text{ }^\circ\text{C}$ ).

## Statistical analyses

Data were analyzed using R Studio version 2.15.2 software (R-CoreTeam 2016) and the *car* (Fox and Weisberg 2011), *plyr* (Wickham 2011), and *multcomp* (Hothorn et al. 2008) packages, while data were visualized using *ggplot2* (Wickham 2009). TBFs (flume and laboratory) were analyzed as a function of water velocity using a generalized linear model (GLM) analysis with a hierarchically nested design and a negative binomial distribution for count data. Subsequent post-hoc tests comparing TBFs observed for each velocity step were conducted using multiple comparisons of means for general linear hypotheses with single-step adjusted p-values. Oxygen consumption values were analyzed as a function of water velocity using a nested ANOVA. Fish mass (g) and fork length (cm) data for fish used in the flume and laboratory experiments were compared using Student's t-tests, and a Grubb's test was conducted to verify that fish mass within each experiment was homogeneous. Statistical significance was considered at  $\alpha=0.05$ .

## Results

### Flume fish swimming behavior

Fish swimming behavior was described for those within the vegetated area, where they spent the vast majority of their time. No fish impinged on the downstream screen at  $15 \text{ cm s}^{-1}$ , and only two fish impinged during one experiment at  $45 \text{ cm s}^{-1}$ . However, a mean of 17.1 fish per experiment ( $\pm 1.9$  SE, range: 9–33 fish per experiment) impinged at  $90 \text{ cm s}^{-1}$ . Interestingly, the majority of the impingements at the highest test velocity occurred within the first minute of the experiment, when the plants' canopies started to bend over from the increased flow, producing the steep, vertical water-velocity gradients in the vegetative section. Therefore, the impinged fish at  $90 \text{ cm s}^{-1}$  likely had insufficient time to react to the hydraulic changes (e.g., to locate low-velocity zones) before interacting with the angled screen.

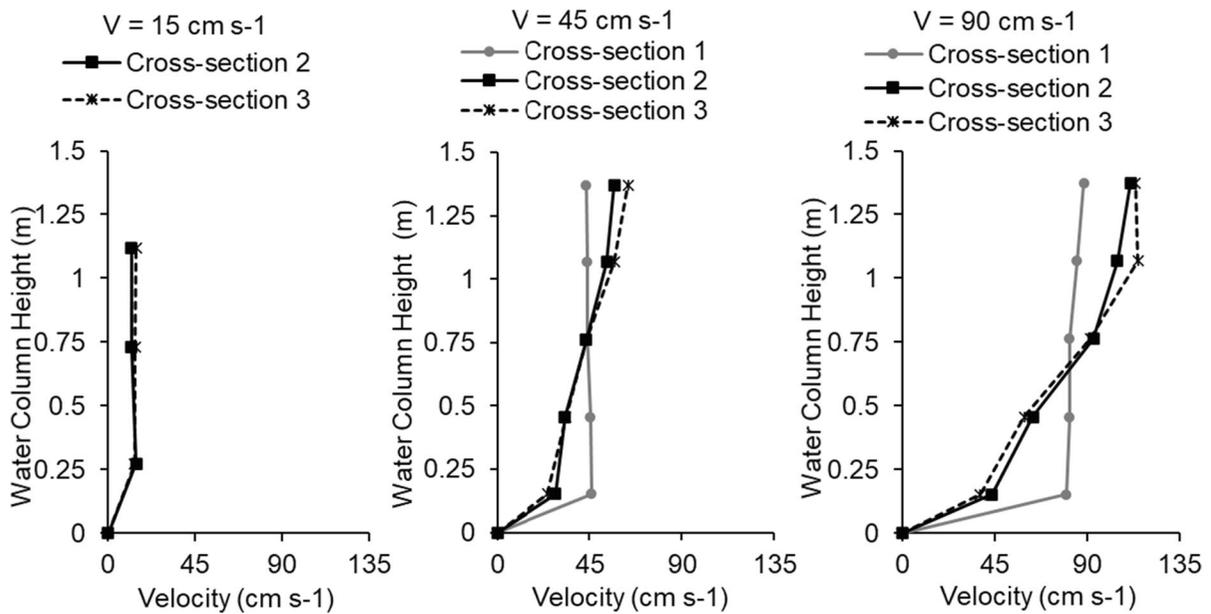
Juvenile Chinook salmon positions in the flume varied with flume velocity. At  $15 \text{ cm s}^{-1}$ , fish were distributed throughout the water column, from the bottom of the flume to within 10 cm of the water surface, and displayed no consistency in rheotaxis. At 45

and  $90 \text{ cm s}^{-1}$ , all fish occupied the deepest 15 cm of the water column, among the thickest part of the willow stems, and oriented into the current with positive rheotaxis. At the higher velocities, fish also tended to occupy the downstream region of the willows. At the 45 and  $90 \text{ cm s}^{-1}$  treatments, velocities in the bottom 60 cm of the water column decreased with distance downstream, relative to their respective upstream (cross-Sect. 1) velocities (Fig. 4). Thus, mean velocities at the lowest depth (0.15 m) decreased 47% between cross-Sects. 1 and 3 in the  $45 \text{ cm s}^{-1}$  treatment, and 52% in the  $90 \text{ cm s}^{-1}$  treatment (Fig. 4). Indeed, to stay off the angled screen at the rear of the flume, our fish required lower-velocity hydraulic refuges at the  $90 \text{ cm s}^{-1}$  treatment, because this velocity exceeded the  $U_{\text{crit}}$  of juvenile Chinook salmon of this size (Cech and Myrick 1999). The first-minute “washout” of 17.1 fish per replicate to the angled screen, at the  $90 \text{ cm s}^{-1}$  treatment, supports the value of low-velocity zones, especially near the bottom of the flume where velocities were lowest in the vegetated area.

### Flume fish TBFs and swimming velocities

Fish TBFs in the willows significantly increased ( $p < 0.0001$ ), as water velocities increased, from  $218.4 \pm 2.0 \text{ beats min}^{-1}$  (mean  $\pm$  SE) at  $15 \text{ cm s}^{-1}$  to  $393.9 \pm 13.1 \text{ beats min}^{-1}$  at  $90 \text{ cm s}^{-1}$  (Table 1). By using TBFs of fish measured in the laboratory experiments (see below), we estimated the water velocities where the fish were swimming in the experimental flume. A significant ( $p < 0.0001$ ,  $R^2 = 0.74$ ) linear model was fitted to the laboratory TBFs:  $y = 186.3 + 5.83x$ , where  $y = \text{TBF}$  and  $x = \text{velocity (cm s}^{-1}\text{)}$  in the swim chamber. By rearranging this equation to:  $x = (y - 186.3)/5.83$ , fish swimming velocities in the flume were estimated from their TBFs (Table 1).

Fish swimming in the willows had estimated swimming velocities that were roughly 63, 41, and 60% lower than flume nominal water velocities of 15, 45, and  $90 \text{ cm s}^{-1}$ , respectively, supporting our hypothesis that vegetation provided low-velocity zones (hydraulic refuges) for these juvenile fish (Table 1). Due to its configuration, the Sontek ADV probe could not measure velocities directly behind the willow stems without disturbing those microhabitats. However, the close correspondence of the measured water



**Fig. 4** Average velocities ( $\text{cm s}^{-1}$ ) plotted against water column height (m) at the three measurement cross-sections. (1-upstream, non-vegetated, 2-midstream, vegetated,

3-downstream, vegetated), for the nominal water velocities ( $V$ ):  $15 \text{ cm s}^{-1}$ ,  $45 \text{ cm s}^{-1}$ , and  $90 \text{ cm s}^{-1}$ . The flume bottom is at 0 m

**Table 1** Mean ( $\pm$ SE) tail-beat frequencies (TBF) in the experimental flume, estimated mean flume swimming velocities, and estimated oxygen consumption ( $\text{MO}_2$ ) rates at each velocity segment in the flume. The mean estimated swimming velocities were calculated using the equation:  $x=(y - 186.3)/5.83$ , where  $x$ =swimming velocity and  $y$ =TBF, and expected oxygen consumption rates were calculated using the equation:  $y = -41.3 + 0.33x$ , where  $y$ = $\text{MO}_2$  and  $x$ =TBF, for velocities above  $15 \text{ cm s}^{-1}$ . No  $\text{MO}_2$  values could be calculated for the  $15 \text{ cm s}^{-1}$  velocity treatment due to the poor fit of the relationship between TBF and  $\text{MO}_2$  in the laboratory at slower velocities (range:  $12.2$ – $21.3 \text{ cm s}^{-1}$ )

Velocity treatment ( $\text{cm s}^{-1}$ )	TBF (beats $\text{min}^{-1}$ )	Estimated Swimming Velocities ( $\text{cm s}^{-1}$ )	Estimated $\text{MO}_2$ ( $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ )
15	$218.4 \pm 2.0$	5.5	n.a
45	$341.1 \pm 5.9$	26.6	71.3
90	$393.9 \pm 13.1$	35.6	88.7

velocities at 0.15 m from the bottom in the vegetated area (cross-Sections. 2 and 3;  $28.4$  and  $24.6 \text{ cm s}^{-1}$  at  $45 \text{ cm s}^{-1}$  treatment;  $43.7$  and  $38.2 \text{ cm s}^{-1}$  at  $90 \text{ cm s}^{-1}$ ) with their respective, estimated swimming velocities ( $26.6$ ,  $35.6 \text{ cm s}^{-1}$ ) supports our

TBF-derived estimates (Fig. 4, Table 1). Thus, TBF and water-velocity data strongly infer that the vegetation provided low-velocity, hydraulic refuges, especially as fish moved further downstream and into the vegetated area and away from the margins, increasing their hydraulic protection. Finally, despite the loss of the  $15 \text{ cm s}^{-1}$  treatment water-velocity data at cross-Sect. 1, the significantly decreased TBF data, compared with those at the higher water velocities, support the low, estimated swimming velocity at the  $15 \text{ cm s}^{-1}$  treatment.

There were no obvious differences among all the post-experimental fish from our visual health assessments.

#### Laboratory TBF and $\text{MO}_2$

We found a significantly positive relationship between treatment velocity and TBF ( $p < 0.0001$ , Table 2). Although we did not detect a significant effect of velocity on  $\text{MO}_2$  ( $F = 19.25$ ,  $p = 0.1700$ ), fish swimming patterns apparently affected the  $\text{MO}_2$  results (Table 2). At lower velocities (i.e., between  $12.2$  and  $21.3 \text{ cm s}^{-1}$ ), swimming activity was noticeably less directed into the current and included fish turning

**Table 2** Mean ( $\pm$ SE) tail-beat frequencies (TBF; beats  $\text{min}^{-1}$ ) and oxygen consumption rates ( $\text{MO}_2$ ;  $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ ) of groups of juvenile Chinook salmon ( $n=10$ ) in a Brett-style swimming chamber. Significant differences among velocity

treatments are indicated with different letters;  $n$  values refer to the number of trials for which oxygen consumption or tail-beat frequencies were quantified, plus either non-rheotactic (NR) or highly rheotactic (HR) swimming styles are indicated

Water velocity (cm $\text{s}^{-1}$ )	Swim style	$\text{MO}_2$ ( $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ )	$n$	TBF (beats $\text{min}^{-1}$ )	$n$
12.2	NR	114.1 $\pm$ 21.4 <sup>a</sup>	3	223.8 $\pm$ 2.5 <sup>a</sup>	8
16.8	NR	122.0 $\pm$ 31.2 <sup>a</sup>	3	284.3 $\pm$ 2.0 <sup>b</sup>	5
21.3	NR	172.4 $\pm$ 47.5 <sup>a</sup>	3	331.3 $\pm$ 4.3 <sup>c</sup>	4
32.6	HR	81.8 $\pm$ 9.4 <sup>a</sup>	4	377.6 $\pm$ 3.2 <sup>d</sup>	3
37.5	HR	98.4 $\pm$ 10.2 <sup>a</sup>	5	427.5 $\pm$ 4.2 <sup>e</sup>	5
45.1	HR	113.9 $\pm$ 24.4 <sup>a</sup>	3	424.1 $\pm$ 4.8 <sup>e</sup>	5

around in the swimming chamber, swimming cross-wise to the current, and apparently seeking (unavailable) hydraulic refuge or escape from the apparatus. These data were characterized by comparatively high and variable  $\text{MO}_2$  values at relatively slow TBFs (Table 2). However, at higher velocities (i.e., between 32.6 and 45.1  $\text{cm s}^{-1}$ ), swimming was steadier and highly rheotactic, without apparent escape attempts. Swimming  $\text{MO}_2$  values at the three higher velocities showed an increasing trend with increasing velocity, although they were statistically indistinguishable. Interestingly, these higher-velocity  $\text{MO}_2$  values were all somewhat, though non-significantly, lower than those measured at the three lower velocities. Thus, at swimming velocities between 21.3 and 32.6  $\text{cm s}^{-1}$ , juvenile salmon apparently transitioned to a more energetically efficient swimming behavior.

Due to this apparent behavioral and physiological transition exhibited by juvenile Chinook salmon at intermediate water velocities (Table 2), TBFs associated with “slower” water velocities (12.3–21.3  $\text{cm s}^{-1}$ ) were analyzed separately from those associated with “faster” water velocities (32.6–45.1  $\text{cm s}^{-1}$ ). Because no significant (i.e.,  $p > 0.05$ ) linear model could be fitted to the TBFs and  $\text{MO}_2$  data obtained from laboratory swimming tests at the slowest velocities, no  $\text{MO}_2$  values were estimated for fish swimming in the flume at comparable conditions (15  $\text{cm s}^{-1}$ ). However, because the relationship between  $\text{MO}_2$  and TBFs at the higher velocities in the laboratory approached significance ( $p=0.09$ ;  $R^2=0.19$ ), the equation:  $y = -41.3 + 0.33x$ , where  $y = \text{MO}_2$  and  $x = \text{TBF}$ , was constructed, and salmon  $\text{MO}_2$ s in the flume were estimated. The estimated flume-fish  $\text{MO}_2$  was only 63% of that measured for

laboratory fish at the similar velocity treatment (ca. 45  $\text{cm s}^{-1}$ , Tables 1 and 2), and argues for supporting our hypothesis that vegetation-associated velocity refuges decrease a juvenile salmon’s energetic costs of maintaining its floodplain position. The small, but significant size differences between the flume and laboratory experimental fish may have contributed to the variability in these estimates.

### Discussion/Conclusions

#### Fish behavior in a simulated floodplain

Our juvenile Chinook salmon selected vegetated microhabitats in a simulated floodplain habitat. At the higher nominal water velocities (45 and 90  $\text{cm s}^{-1}$ ), our salmon used the bottom 15 cm of the water column, occupying low-velocity zones and possibly minimizing their energetic costs of holding station. This behavior also, presumably, prevented downstream displacement (Cech and Myrick 1999). In this region, water velocities were slower due to the hydraulic drag associated with the vegetation, and the bed shear stress of the bottom of the flume (Bennett et al. 2002; Stoesser et al. 2010). Fulton et al. (2001) found that wrasses (Labridae), small teleosts which commonly inhabit coral reefs, avoided high water flows by placing themselves deeper in the water column, often taking advantage of the boundary layer near the substratum where water flows were lower. Herskin and Steffensen (1998) showed that considerable energy can be saved for fishes swimming behind other fishes (e.g., at the rear of a school), compared with those swimming at the front of the school, another form

of velocity refuge. Sea bass *Dicentrarchus labrax* decreased their TBF by 9–14% and their  $MO_2$  by 9–23% when swimming at the rear of the school compared when swimming at the front (Herskin and Steffensen 1998). Similarly, the use of physical structures (e.g., larger rocks, large woody debris) as hydraulic refuges by juvenile salmonid fishes in streams has been documented in the laboratory (Chun et al. 2011), in outdoor stream channels (McMahon and Hartman 1989), and in the field (Crook and Robertson 1999). When nominal water velocities were increased in a swimming respirometer, Strailey et al. (2021) showed that smallmouth bass (*Micropterus dolomieu*) swam in the wake of cylindrical structures, maintaining an unchanged mean  $MO_2$ , while control (without structures) bass increased their mean  $MO_2$ . Wild juvenile steelhead (*O. mykiss*) were more likely to seek velocity refuge when it was coupled with some forms of visual isolation (i.e., physical structure that obscured the fish; Fausch 1993). The fine branches (and later in the spring, leafy canopy) of planted willows presumably provide juvenile fish with increased predator protection, as well. This combined effect of physical structure decreasing predation risk and energy expenditure has been previously documented for juvenile salmonids (Fausch 1984; Tabor and Wurtsbaugh 1991), and our results provide further evidence in support of this hypothesis.

#### Laboratory TBF and $MO_2$

In our laboratory, fish generally increased their TBFs as water velocities increased, allowing them to increase their swimming velocity and hold their position in the water column. The positive relationship between increased TBF and increased swimming velocity has been previously documented in several fishes. Bainbridge (1958) described the linear increase in swimming velocity with increasing TBF for three teleosts: dace (*Leuciscus leuciscus*), rainbow trout (*O. mykiss*), and goldfish (*Carassius auratus*), and Fangue et al. (2015) showed a similar pattern in hardhead (*Mylopharodon conocephalus*). The virtually unchanged TBFs in our salmon at the two highest velocities in the swimming tunnel are perplexing. It could be that these fish were reaching their preferred maximum TBF at  $37.5 \text{ cm s}^{-1}$ , and that they were able to hold position in the respirometer at

$45.1 \text{ cm s}^{-1}$  by swimming in the wakes of other fish (cf., Herskin and Steffensen 1998).

Increased swimming velocities at increased TBFs typically are associated with increased  $MO_2$  values as fish increase muscular contraction frequencies to counter associated, increased hydrodynamic drag forces (see reviews by Webb 1995; Brett 1995). For example, adult sockeye salmon (*O. nerka*) increased TBFs and consumed more oxygen when encountering higher river velocities while proceeding upstream to spawn (Hinch & Rand 1998). Similarly, increased TBFs were significantly correlated with increased oxygen consumption in both saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*; Steinhäuser et al. 2005).

Although our juvenile Chinook salmon showed no significant  $MO_2$  changes with water velocities, an apparent  $MO_2$  breakpoint was noted as water velocities increased, and fish transitioned from a non-directed swimming type (i.e., lateral, non-rheotactic movements in the flume) to a directed (i.e., highly rheotactic) type at velocities  $\geq 32.6 \text{ cm s}^{-1}$ . Presumably, the rheotactic swimming was more efficient, precluding  $MO_2$  increases at the higher TBFs. Because fish at the two higher velocities in the flume exhibited highly rheotactic swimming, this adds confidence that our model estimates provide solid numbers. Schakmann et al. (2020) measured the swimming metabolic costs in goldring surgeonfish (*Ctenochaetus strigosus*), a marine teleost that inhabits wave swept, reef habitats characterized by oscillatory (i.e., unsteady, bi-directional) flows. Using a swimming respirometer that could produce either linear or oscillatory flows, the surgeonfish's net swimming costs to hold station in the respirometer increased by two-fold under a combination of oscillatory flows, compared with those under linear ones (Schakmann et al. 2020). Although this surgeonfish used a labriform (pectoral-fin) swimming mode, Marcoux and Korsmeyer (2019) made similar oxygen consumption measurements in oscillatory flows on four reef species, including one (*Kuhlia* spp. *Kuhliidae*) using body/caudal-fin swimming, similar to that used by our juvenile salmon. Their *Kuhlia* spp. increased its net cost of swimming to hold station in the oscillatory flows by up to 50%, via its turning and re-acceleration behavior (Marcoux and Korsmeyer 2019). Because the turning and other non-rheotactic moves that our fish exhibited at the three lower velocities were quite erratic, the standard errors

around the mean  $MO_2$  values were mostly (up to five-fold) higher than those at the three higher velocities. These high variabilities may have contributed to the lack of significant differences among  $MO_2$  as TBFs increased. Within the three low velocities and within the three high velocities, mean  $MO_2$  showed steady numerical, though non-significant, increases with increasing water velocity.

### Fish energetic and conservation considerations

Decreased swimming-associated energetic costs could permit increases in growth of juvenile fishes. For example, Gregory and Wood (1998) found a negative relationship between the critical swimming velocity and the specific growth rate of rainbow trout fed reduced rations. Furthermore, Fausch (1984) found that juvenile salmonids increased their net energy gain (and therefore their growth rates) by positioning themselves in areas of low water velocity adjacent to rapidly moving currents carrying increased invertebrate drift, permitting decreased costs of maintaining position with increased foraging opportunities. Therefore, decreasing energy costs via a decrease in swimming effort could increase the somatic growth of juvenile salmonids and increase potential survival.

Juvenile salmonids are known to use habitats other than the main-channel of river systems, occupying areas such as seasonal floodplains (Sommer et al. 2001, 2005), natal and non-natal tributaries (Johnson et al. 1992; Murray and Rosenau 1989), and off-channel ponds (Limm and Marchetti 2009). Although we used sandbar willow, which is widely distributed in floodplains and other moist habitats in the USA, other rooted aquatic macrophytes could confer a similar hydraulic advantage to juvenile fishes subjected to strong currents. Both growth and survival of juvenile Chinook salmon are higher in areas such as seasonal floodplains (Sommer et al. 2001; Jeffres et al. 2008). While increased temperatures and higher productivity in these areas have been suggested as contributing factors for increased growth rates (e.g., Katz et al. 2017; Sommer et al. 2001), Jeffres et al. (2008) also hypothesized that increased vegetated structure is a significant factor affecting elevated salmonid growth through its effects on flow regimes. In their study, increased vegetation decreased water velocities in the floodplains, relative to the main-channel of the river,

increasing productivity via increased phytoplankton and zooplankton densities (Jeffres et al. 2008). We argue that by minimizing the energy to maintain position in high-velocity areas, juvenile salmon could increase the energy invested in somatic growth.

Chinook salmon populations are vulnerable to extinction (Katz et al. 2012; Moyle et al. 2017), and the efforts to conserve salmonid resources could be more effective if floodplain vegetation, including upland vegetation receiving seasonal inundation, were available for smolts throughout their migratory corridors. Less than 5% of pre-development floodplain habitat remains in California's Central Valley (Hanak et al. 2011), and indeed, floodplain restoration has been suggested as a priority for improving salmonid habitat (Beechie et al., 2013). Coupling floodplain restoration with agricultural management practices (Katz et al. 2017) can provide high quality salmon rearing habitat. Furthermore, vegetated (e.g., with sandbar willow) floodplains may provide energy-efficient, daytime habitat for migrating juvenile Chinook salmon when their migratory corridors include floodplain inundation.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

**Declarations**

**Ethics approval** All handling, care, and experimental procedures used were reviewed and approved by the University of

California Davis Institutional Animal Care and Use Committee (IACUC No. 12708).

**Conflict of interest/Competing interests** The authors declare no competing interests.

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