



Managed Wetlands Can Benefit Juvenile Chinook Salmon in a Tidal Marsh

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Abstract

Loss of estuarine and coastal habitats worldwide has reduced nursery habitat and function for diverse fishes, including juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Underutilized off-channel habitats such as flooded rice fields and managed ponds present opportunities for improving rearing conditions and increasing habitat diversity along migratory corridors. While experiments in rice fields have shown enhanced growth rates of juvenile fishes, managed ponds are less studied. To evaluate the potential of these ponds as a nursery habitat, juvenile Chinook salmon (~2.8 g, 63 mm FL) were reared in cages in four contrasting locations within Suisun Marsh, a large wetland in the San Francisco Estuary. The locations included a natural tidal slough, a leveed tidal slough, and the inlet and outlet of a tidally muted managed pond established for waterfowl hunting. Fish growth rates differed significantly among locations, with the fastest growth occurring near the outlet in the managed pond. High zooplankton biomass at the managed pond outlet was the best correlate of salmon growth. Water temperatures in the managed pond were also cooler and less variable compared to sloughs, reducing thermal stress. The stress of low dissolved oxygen concentrations within the managed pond was likely mediated by high concentrations of zooplankton and favorable temperatures. Our findings suggest that muted tidal habitats in the San Francisco Estuary and elsewhere could be managed to promote growth and survival of juvenile salmon and other native fishes.

Keywords Fish nurseries · Diked wetlands · Habitat management · Restoration · Fitness · Tidal flow

Introduction

Estuaries provide essential nursery habitat for diverse juvenile fishes, but many have been degraded by human activities (Rountree and Able 2007; Borja et al. 2010; Barbier et al. 2011). Tidal wetland habitat has decreased 25–50% globally due to land use conversion (Pendleton et al. 2012; Kirwan and Megonigal 2013) and other remaining habitats are critically vulnerable (Costanza et al. 1997; Edgar et al. 2000; Gedan et al. 2009). Habitat loss and fragmentation result in myriad negative effects on the structure, function, and productivity of nearshore marine ecosystems and their fisheries (Valentine-

Rose et al. 2007; Rypel and Layman 2008). In severely human-dominated aquatic ecosystems, the ability to fully restore habitat can be limited by land ownership, funding, dams and other water infrastructure, flood control projects, water diversions, subsidence, and invasive species (Lund et al. 2007; Durand 2017). In these circumstances, ecological rehabilitation may be needed to help re-establish functional nursery habitats (Nagelkerken et al. 2015), but studies needed to inform rehabilitation efforts are often lacking.

The San Francisco Estuary (SFE) in California, USA, is highly altered, having lost approximately 80% of its historical tidal marsh habitat (Monroe et al. 1999; Brophy et al. 2019). This loss, coupled with dams, degradation of upstream habitat, overfishing, and altered hydrology, has contributed to long-term declines in Chinook salmon (*Oncorhynchus tshawytscha*) populations (Yoshiyama et al. 1998). Juvenile Chinook salmon use of estuarine tidal marsh habitats in the SFE is poorly understood compared to more northern estuaries (Nehlsen et al. 1991; Simenstad and Cordell 2000; Williams 2012), but tidal marsh is identified as critical habitat and an important component of salmon recovery plans. Limited studies suggest SFE brackish tidal marshes provide

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nursery habitats for Chinook salmon (Healey 1980; Levy and Northcote 1982) in which to forage and take refuge (Shreffler et al. 1992; Williams 2012; Enright et al. 2013). Juveniles which use both estuarine and freshwater rearing habitats typically have higher survivorship than those which rear primarily in one environment (Reimers 1971; Levy and Northcote 1982).

Increasing rearing habitat in tidal marshes can boost overall survivorship and population resilience when freshwater rearing habitats are unfavorable, such as during drought (Bottom et al. 2005; Hering et al. 2010; Volk et al. 2010). This “portfolio effect” is increasingly recognized as an important aspect of managing diverse fish populations, including salmonids (Schindler et al. 2010; Carlson and Satterthwaite 2011). Managing for a portfolio effect might include conservation of diversity in salmonid run timing (Satterthwaite and Carlson 2015), as well as habitat (Goertler et al. 2018; Herbold et al. 2018). For example, habitat diversity promotes diversification of life-history strategies, allowing for population asynchrony over space and time at evolutionary scales, but stability at higher levels of ecological organization (Rypel et al. 2012). Suisun Marsh, the largest contiguous tidal marsh remaining on the west coast of North America, may contribute to a diverse habitat portfolio. However, human use has fragmented portions of the marsh, limiting connectivity between tidal channels and the surrounding marsh plain.

Beginning in the late nineteenth century, much of Suisun Marsh’s historic wetlands were converted to managed ponds for hunting migratory waterfowl. Similar alterations along migratory corridors worldwide provide bird habitat for sport and conservation (Tamisier and Grillas 1994; Ma et al. 2010; Sass et al. 2017). These conversions move considerable tidal fish habitat into tidally muted, levee-lined ponds which limit fish access and reduce edge habitat. Most managed ponds in Suisun Marsh are inundated with shallow water from late fall through early spring to promote feeding and resting locations for hunted waterfowl (Moyle et al. 2014). Hydrologic connectivity between managed ponds and adjacent sloughs is controlled with a system of gates and levees, which mute the tidal range. Reduced connectivity between sloughs and marsh plains has decreased the extent and complexity of available habitat for native aquatic species, including salmon (Mount et al. 2012). Currently, 21,000 ha of habitat are managed in Suisun Marsh, compared with 2550 ha of unmanaged tidal habitat.

We designed this study to address two important questions surrounding the role of Suisun Marsh’s fragmented habitats in SFE fisheries: (1) Do Chinook salmon growth rates differ among natural tidal sloughs, tidal leveed sloughs, and muted tidal habitats (i.e., inlets and outlets of managed ponds) in Suisun Marsh? and (2) if growth differs, what environmental variables are responsible for the difference? To answer these questions, we held juvenile Chinook salmon in cages within each of these locations for 7 weeks from March to April of

2017. We then quantified and compared salmon growth within each habitat using mass growth rates, a metric commonly used to evaluate scope for fisheries productivity (Simenstad and Cordell 2000; Rypel and Layman 2008). We expected salmon to grow fastest in the natural tidal slough because it best represents historic salmon habitat in the marsh.

Methods

We conducted this study from 3/1/2017 to 4/21/2017 in Suisun Marsh, where juvenile salmon (30–75 mm FL) are generally found from January through May, with peak abundances in February and March (O’Rear et al. 2019). Our study locations, described below, were situated in the northwestern portion of the marsh, which includes managed ponds, preserved marsh, and a matrix of natural and leveed sloughs (Fig. 1).

First Mallard Slough (FM) This natural, tidal slough in the Rush Ranch Ecological Reserve is relatively undisturbed and meanders through historic wetlands, terminating at an ephemeral creek (Fig. 1; Table 1). There are several small sloughs branching from this mainstem ranging from 0.1 to 0.5 km in length. Invasive common reed (*Phragmites australis*) and tules (*Schoenoplectus* spp.) line the slough (O’Rear and Moyle 2018) and the adjacent low-lying marsh plain overtops during ~15% of high tides (Enright et al. 2013).

Sheldrake Slough (SD) This leveed, tidal slough is situated between two large managed wetlands (Fathen and Sheldrake duck hunting clubs), both of which exchange water with Sheldrake Slough from fall through spring (Fig. 1; Table 1). These exchanges occur by way of two major and one minor gated culverts. No side channels exist besides short extensions to gated culvert inlets/outlets. Vegetation on levee margins predominantly consists of up to a 1-m border of common reed and tules (O’Rear and Moyle 2018).

Wings Landing Duck Club (WL_IN and WL_OUT) This managed, muted tidal wetland is located between Peytonia and Suisun Sloughs (Fig. 1; Table 1) and is slated for open tidal restoration. We used two locations located in the club’s perennially flooded broodstock pond, which is smaller and separate from the main pond and intended to provide waterfowl habitat when the main pond is drained. The broodstock pond maintained water levels high enough for fish survival throughout the study, without negatively impacting the duck clubs pond management timeline. The inlet is on the western side of the pond, 1.5 m deep, and relatively exposed. Water enters from Peytonia Slough over a flashboard gate during daily high tides. The outlet is on the eastern side of the pond, ~0.75 m deep, and partially shaded by emergent vegetation. Water

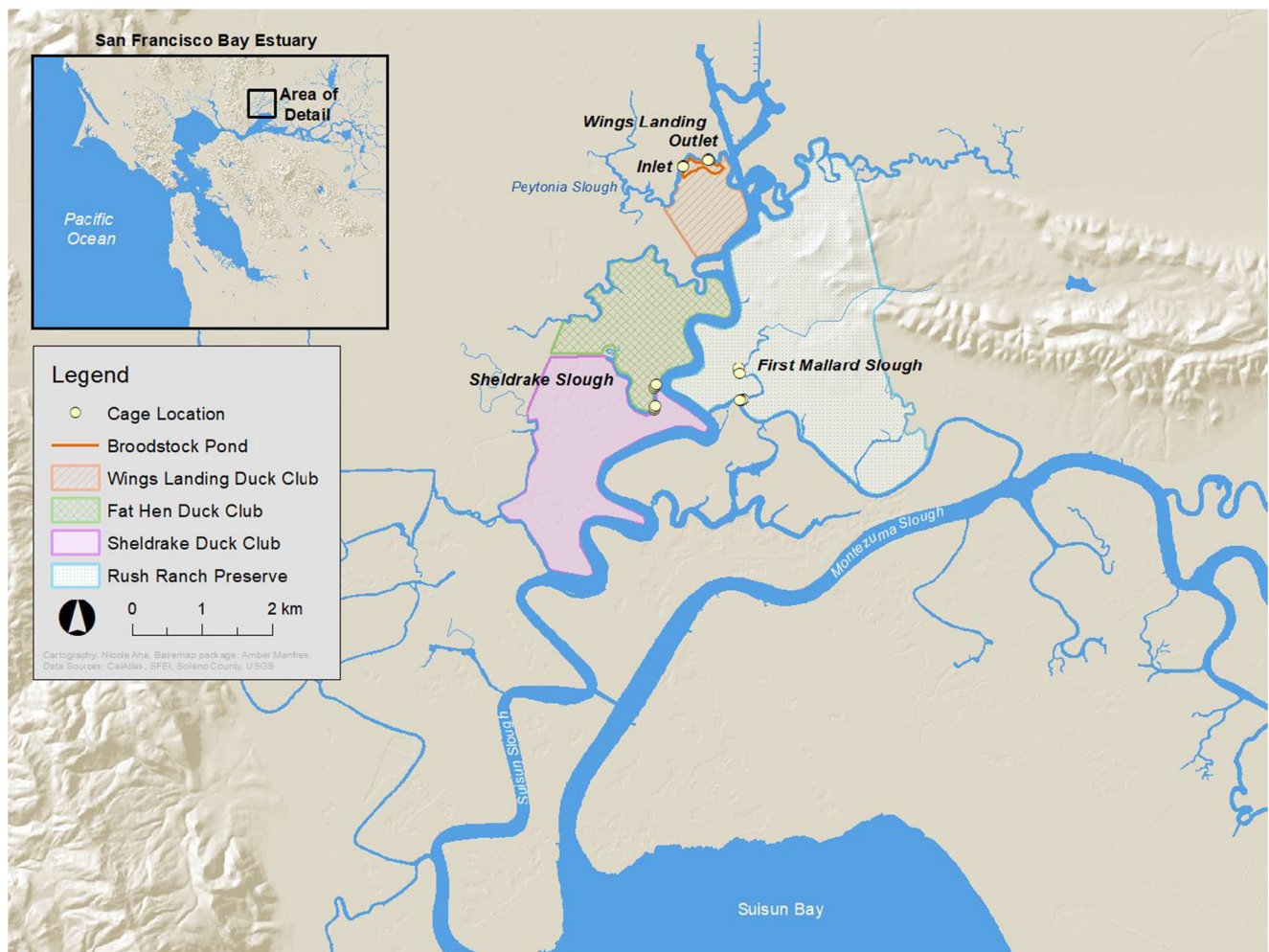


Fig. 1 Map of study area. Cage locations and managed/protected properties are denoted according to the legend

moves from the inlet to the outlet via dendritic channels and small ponds and may concentrate near the outlet during the ebb flow before passing over another flashboard control structure back into Peytonia Slough.

Water at all locations is relatively fresh during the months of March and April, with Suisun Marsh 37-year averages of 1.8 and 2.0 ppt respectively (O'Rear et al. 2019). During 2017, a year with higher than average precipitation (Lund 2017), increased riverine outflows produced higher water levels and lower than average salinities across the marsh (1.0 ppt in March and 0.8 ppt in April).

We deployed cages to hold juvenile salmon at a fixed location with access to natural prey and exposure to ambient environmental conditions (Forrester et al. 2003). We constructed cylindrical cages out of 6.35 mm black extruded plastic mesh and floated them near the surface with floats providing approximately seven kilograms of buoyancy. Each cage measured 0.5 m in diameter and 0.75 m tall and was weighted on the bottom with a 19-mm diameter steel stock hoop. Cages attached to a 25.4-mm diameter Schedule 40 PVC pipe sleeve

which slid over a 6-m piece of 12.7 mm diameter rebar driven into the marsh substrate. The assembly allowed cages to stay near the surface and move up and down the rebar support as the tide ebbed and flooded. To sample variation within First Mallard and Sheldrake sloughs, we placed cages in two clusters separated by about 0.8 km, each containing three replicate cages. We placed cages at the Wings Landing Duck Club in an inlet and an outlet location, which received three cages each. Multiple clusters at the inlet and outlet locations were not feasible due to space and depth limitations.

Fall-run juvenile Chinook salmon were obtained from Coleman National Fish Hatchery (Anderson, CA USA) and reared in tanks at the UC Davis Center for Aquatic Biology. They were fed 100% dry Skretting feed and maintained at 12 °C, consistent with concurrent water temperatures in Suisun Marsh. After 1 month, we transported 252 fish (mean ~2.8 g, 63 mm FL) to the experimental locations in an insulated tank of rearing water aerated with pure filtered oxygen. We measured, weighed, and placed 14 fish into each of the 18 cages. Because smaller fish more easily evaded collection

Table 1 General description of habitat types in Suisun Marsh included in this study

Habitat	Key features
Natural slough	These dendritic terminal, or seasonally terminal, tidal sloughs resemble historic form and function. Water may remain on the marsh plain with limited connectivity to adjacent sloughs via a series of dendritic channels or disconnect entirely and evaporate (Moyle et al. 2014).
Leveed slough	These are generally remnants of historical tidal creeks or sloughs which were straightened and leveed during the creation of managed wetlands. They are often terminal and leveed on either side, with fringe marsh lining the slough and subsided managed wetlands behind the levees. Overtopping does not occur except during levee failure. Hydraulic connectivity to surrounding managed wetlands is manipulated through a variety of different water control structures.
Managed pond	<p>These ponds are managed to produce desirable food resources for hunted waterfowl species. Managed wetlands are generally dried in summer for vegetation management, flooded beginning in September or October, and subsequently drained by April or May after the conclusion of hunting season. Several “leach cycles” of filling and draining help remove accumulated salts between hunting seasons (Moyle et al. 2014). Water movement is controlled by duck club managers through a series of gates using a system of gravity and/or pumps and are considered “muted tidal” systems.</p> <p>Inlet: The first access point for slough water when entering a managed wetland usually via a gate, culvert, or pump.</p> <p>Outlet: The exit point for water that has passed through the managed wetland and is returned to the adjacent slough generally via a gate, culvert, or pump.</p>

during fish out-planting, those placed in the final clusters (Sheldrake Slough) had smaller initial sizes (mean ~ 2.7 g, 62 mm FL). Fourteen fish per cage created densities as low as possible while also allowing for three fish/cage to be sampled every other week for diet analysis. Increasing cage size to match natural densities would have posed significant impediments to boat traffic. High winds and rough water conditions made initial measurements of fish mass unreliable. These were corrected by length using linearly regressed log-transformed mass-length relationships collected within 24 h of outplant from the same tank and brood stock ($n = 52$, $R^2 = 0.9097$) in which y is estimated weight and x is measured length,

$$\ln y = 2.76(\ln x) - 4.01. \quad (1)$$

We sampled cages every 2 weeks from 3/1/2017 to 4/21/2017. During sampling, all fish were netted and transferred to an aerated cooler, weighed (g) in a tared container of water with an Ohaus Scout Pro 200 mg scale, and measured to fork length (mm). We then haphazardly netted and euthanized three fishes per cage for later dissection and diet analysis (IACUC Protocol #19672). Euthanized fish were placed on ice and transferred to a -18 °C freezer upon return from the field. This sampling reduced the total number of fish in each cage as the study progressed. While reduction in density confounds inter-week comparisons across site, it maintained relative weekly site comparison, and enabled us to collect valuable incremental diet data over the study period. Reducing density over time also balanced finite cage resources with increasing metabolic needs of growing fish. When caged fish occasionally died between sampling events, we removed the carcasses and euthanized fewer live fish in order to maintain consistent numbers of salmon in each cage and reduce the potential for density dependent effects between cages. We assessed cages twice per week for biofouling and cleaned as necessary to allow free water exchange.

All experimental fish that survived until euthanasia ($n = 180$) were examined for external abnormalities and internal organ condition. We measured stomach fullness on a scale of 0–5, with zero indicating an empty stomach and five a full stomach. Fullness estimates were made based on the ratio of stomach contents to stomach size to account for differences in fish size (Hyslop 1980). Individual prey items were counted and identified to order or genus for zooplankton, genus for amphipods, and order for less common terrestrial and aquatic insects.

We collected zooplankton once per week from March through April adjacent to each cage cluster and in the up-slough reaches of Sheldrake and First Mallard Sloughs. Zooplankton samples were collected using a SEA-GEAR conical 50 cm \times 200 cm plankton net with 50 μ m mesh with 1 L plastic codend and a General Oceanics flowmeter suspended from the mouth. We suspended the net below the surface of the water between a buoy and 57 g spherical lead weight and hand-towed it 20 m. On three occasions, we were unable to collect a sample due to low water levels. Tows at Wings Landing Inlet were hand-towed approximately 10 m on average due to pond width restrictions at this location. Samples were stored in 500 ml wide-mouth Mason jars, preserved with 5% formaldehyde and stained with 1% rose bengal. In the laboratory, we suspended zooplankton from each tow in a known volume of water (s), sub-sampled in 5 ml increments (a) and identified to order for juveniles and genus for adults. For each sample, all individuals were counted until 150 individuals from the most common taxa were reached. In the case of sparse samples, individuals present in 20% of the total sample volume were counted. The following equation was used to calculate density (d):

$$d = \frac{\frac{s}{a} * c}{v} \quad (2)$$

where d is the density of individuals per meter cubed, s is known volume of water in which the sample was suspended, a is the total volume of counted subsamples, c is the number of individuals counted, and v is the estimated water volume (m^3) sampled by the tow. In cases of flow meter error, we calculated volume using averages of tows collected in similar flow conditions and locations (e.g., downstream slough, mid-slough, upstream slough, managed pond inlet, and managed pond outlet).

Dry-to-ash weight differences found in the literature and from direct measurements of SFE organisms (Dumont et al. 1975; data: W. Kimmerer) were used to calculate the biomass of observed zooplankton. For unknown values, we used the biomass value of the most comparable known taxon. When no comparable taxa were available, known biomass values of zooplankton found in this study were averaged to create a conservative estimate applied in place of the unknown values. This estimate contributed to < 4% of total zooplankton biomass.

ONSET Hobo loggers continuously measured temperature ($^{\circ}\text{C}$) at each location. Loggers were placed near the bottom of one cage at each location except for the downstream cluster in First Mallard slough, which used data from the National Estuarine Research Reserve System's long-term water quality station. The station was located between the middle and most downstream cages in the cluster. We used a YSI Pro 2030 to collect salinity (psu), specific conductivity (μS), and dissolved oxygen (% saturation) measurements twice per week, during cage checks or fish sampling at each set of cages. We also took water grabs at these locations for measurement of pH, turbidity (ntu), total phosphorus (mg/L), total dissolved phosphorus (mg/L), ortho-phosphate (mg/L), total nitrogen (mg/L), total dissolved nitrogen (mg/L), ammonium nitrogen (mg/L), nitrate + nitrite nitrogen (mg/L), dissolved organic carbon (mg/L), chlorophyll a (ppb), phaeophytin a (ppb), total suspended solids (mg/L), and volatile suspended solids (mg/L) (R. Dahlgren Lab, UC Davis, CA USA). To account for daily temporal changes in water quality, we altered the order in which each location was visited and sampled throughout the study.

We used mass (g) to evaluate salmon growth rate for each location (Meeuwig et al. 2004; Lusardi et al. 2019). Mass is preferred over fork length as salmonids can maintain skeletal growth at the expense of tissue growth, leading to low body mass in relation to length (Nicieza and Metcalfe 1997). However, fork lengths are also reported in the discussion to allow comparison to other salmon growth studies, many of which report only fork length. Because fish were not individually marked, cages were treated as the experimental units. We calculated growth rate as:

$$Y = \frac{\left(\overline{F}_w\right) - \left(\overline{F}_{wp}\right)}{\Delta d} \quad (3)$$

where Y is the growth rate of a specific cage, F is the mass or fork length of individual fish in each cage, w is sampling week, wp is prior sampling week of interest, and d is number of days.

For statistical analyses, we used the program R (R Core Team 2020). Using the package lme4, we analyzed growth data as a two-way repeated measures analysis of variance (Bates et al. 2015). We modeled mass growth rate as the response variable, location and time (i.e., "sampling week") as fixed variables, and cage as a random effect term. Shapiro-Wilk tests were used to test for normality, and Levene tests used to test for patterns of homoscedasticity. When model results were less than $p = 0.05$, we performed a Tukey HSD post hoc test to determine which locations differed. Bonferroni adjustments reduced potential type I errors due to multiple comparisons. Five of the 18 cages were compromised, resulting in loss of some or all experimental fish in affected cages (Table 2). Compromised cages were not included in the analysis.

To explore environmental drivers of salmon growth, we used a series of mixed effect growth models informed by principal components analysis (PCA). To reduce collinearity, we used PCA to develop a new set of synthetic and uncorrelated environmental variables or principal components (PCs) to aid in exploring key variables. Prior to running the PCA, we scaled environmental variables (using the base R 'scale' function) to achieve a similar magnitude among measurement values (Lusardi et al. 2019). The PCA produced three PCs that described 80% of environmental variation across habitat types (Table S1). Key PCs were identified with a scree plot and the top environmental variables that loaded on each of these key PCs identified as environmental variables of interest for our growth models (Gotelli and Ellison 2004). In this way, the list of candidate environmental driver variables was reduced from 21 to 3 variables. The environmental variables which explained the most variability in PC1, PC2, and PC3 were volatile suspended solids (10.7%), total phosphorus (13.6%), and nitrate + nitrite nitrogen (16.6%), respectively. We added to this list other key environmental variables known to directly influence salmon growth, including zooplankton biomass, temperature, and dissolved oxygen (Herrmann et al. 1962; Marine and Cech 2004; Jeffries et al. 2008; Katz et al. 2017). Salinity was not included due to how low salinity was in the marsh and the lack of substantial variability between sites and throughout the study period.

A series of mixed effect growth models were created with each of these scaled candidate environmental variables (Burnham et al. 2011; Lusardi et al. 2019). First, to determine which temperature metric to use, we compared maximum temperature, mean temperature, and temperature spread (daily maximum - daily minimum) models. Using the package lme4, we modeled mass growth rate as the response variable, an individual temperature metric and its interaction with time

Table 2 Experimental design. Asterisks denote cages that were compromised and subsequently removed from all analysis

Habitat	First Mallard						Sheldrake Slough						Wings Landing					
	Upstream			Downstream			Upstream			Downstream			Inlet			Outlet		
Cage	1	2	3	1	2*	3*	1*	2	3*	1	2	3	1	2*	3	1	2	3

(i.e., “sampling week”) as the independent variables, and cage as a random effect term to account for cage effects within location. Normality of residuals was evaluated using QQ-plots and Akaike’s information criteria (adjusted for small sample size, AIC_c) was used to compare the models (Burnham et al. 2011). Relative model ranks (models considered dissimilar when displaying a delta AIC_c value > 2 ; Bolker 2008) and 95% confidence intervals were used to evaluate the effect of the explanatory variables on mass growth rate. The mean temperature model predicted growth the best and was therefore used in subsequent steps of analysis.

Next, using the same structure as the above, we compared a zooplankton biomass model, a dissolved oxygen model, a volatile suspended solids model, the mean temperature model, a total phosphorus model, a nitrate + nitrite nitrogen model, and an intercept model (Table S2). The model which fit the data best was then used as the basis for a new set of models in which the best fit model was edited to include additive and/or interactive effects of another environmental variable (Table S2). The interaction of time (i.e., “sampling week”) with each environmental variable was always included to account for repeated measures. The top model from this step was then similarly adjusted to include additive and/or interactive effects with a third environmental variable. Finally, models from each step which had an AIC_c value > 2 were compared to one another using AIC_c to see how these increasingly complex models related to simpler models from earlier steps.

We evaluated spatial and temporal variances in mean zooplankton biomass and mean stomach fullness using two-way repeated measures ANOVAs. We modeled zooplankton biomass using location and time (i.e., “sampling week”) as fixed variables. For stomach fullness, we modeled fullness as the response, with location and time as fixed variables and cage as a random effect term. We ran a Tukey HSD post hoc test when model results were less than $p = 0.05$ to explore which locations differed from one another. The normality of residuals was confirmed using Shapiro-Wilk tests and homoscedasticity checked using Levene tests.

Results

Fish at Wings Landing Outlet grew the most over the 7-week duration of the experiment (Fig. 2). Growth was affected by

location (ANOVA, $F(3, 44) = 5.36$, $p = 0.003$), time (ANOVA, $F(1, 44) = 12.01$, $p = 0.001$), and the interaction of location and time (ANOVA, $F(3, 44) = 9.58$, $p = 5.50 \times 10^{-5}$). Wings Landing Outlet had higher growth rates than the other three locations, while First Mallard Slough, Sheldrake Slough, and Wings Landing Inlet fish all had similar growth rates (Tukey HSD test, $p < 0.05$). Fish in Sheldrake Slough experienced the highest observed growth between week zero and two, followed by a sharp decline thereafter. Fish held at Wings Landing Outlet had the greatest survival between sampling weeks (100%; Table 3).

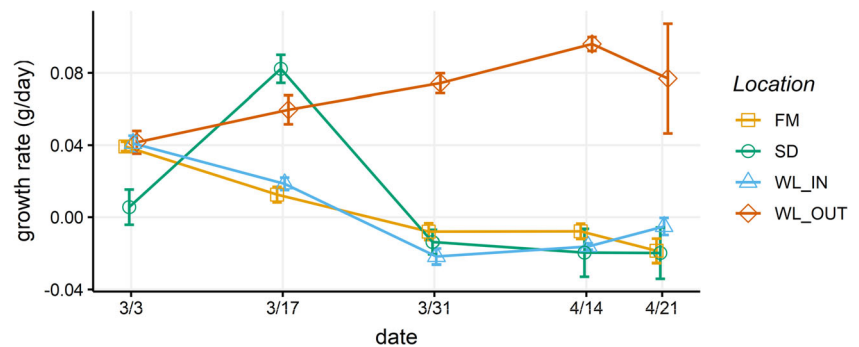
The top performing model included zooplankton biomass, dissolved oxygen, volatile suspended solids, and the interaction of each of these with time to explain mass growth rate over time ($\Delta AIC_c = 0$, weight = 29%; Table 4). The second top performing model included zooplankton biomass, dissolved oxygen, mean temperature, and the interaction of each with time ($\Delta AIC_c = 0.5$, weight = 22%; Table 4). The third best included zooplankton biomass and dissolved oxygen and the interaction of time with each ($\Delta AIC_c = 0.7$, weight = 20%; Table 4). The remaining models each received $< 20\%$ weight. For the top-fitting model, the strongest positive relationship was between zooplankton biomass and growth rate with the strongest negative relationship between dissolved oxygen and growth rate; estimates for these parameters were positive and negative, respectively, and did not overlap zero (Table 5). There was a weak negative relationship between time and growth rate, volatile suspended solids and growth rate, and zooplankton*time with growth rate. These relationships were similar in the second and third models, with the second model also highlighting a slight negative relationship between temperature and growth rate (Table 5).

Zooplankton biomass ($\mu\text{gC}/\text{m}^3$) differed across locations (ANOVA, $F(3, 8) = 7.79$, $p = 0.009$; Fig. 3) but not by

Table 3 Indirect mortalities at each location. Numbers represent fish that died between the listed sampling date and the sampling date prior. All fish were placed in cages on March 3rd, 2017

	March 17th	March 31st	April 14th	April 21st
First Mallard Slough	0	1	1	4
Sheldrake Slough	0	0	2	8
Wings Landing Inlet	0	0	1	2
Wings Landing Outlet	0	0	0	0

Fig. 2 Mean growth rates (\pm SE) at each location over the course of the study. $N=4$ cages at First Mallard (FM), $N=4$ cages at Sheldrake (SD), $N=2$ cages at Wings Landing Inlet (WL_IN), and $N=3$ cages at Wings Landing Outlet (WL_OUT)



sampling week (ANOVA, $F(1, 8) = 1.36$, $p = 0.28$). However, there was a strong interaction between location and sampling week on zooplankton biomass (ANOVA, $F(3, 8) = 14.63$, $p = 0.001$). First Mallard had slightly higher mean biomass in the beginning of the study, tapering by mid to late March. Zooplankton biomass at the Wings Landing Inlet remained consistently low throughout the study. Wings Landing Outlet had higher zooplankton biomass compared to First Mallard Slough and the Wings Landing Inlet (Tukey HSD test, $p < 0.05$), with mean biomass spiking between week three and four of the study and increasing through April (Fig. 3). Sheldrake Slough, which saw high zooplankton biomass in the beginning of the study but declining thereafter, fell statistically between the other locations (Tukey HSD test, $p < 0.05$).

The relative composition of taxa also differed among locations, with *Daphnia* being a large (84%) contributor to biomass at the Wings Landing Outlet while rarely (1%) contributing biomass at other locations (Fig. 4). Other Cladocera genera found in the tows included *Bosmina*, *Chydorus*, and *Ceriodaphnia*, which were distributed across locations, albeit in low numbers ($< 1\%$ total biomass). Copepods were found at all locations (53% total biomass) and were composed of the genera *Acanthocyclops*, *Limnithona*, *Eurytemora*,

Pseudodiaptomus, and *Sinocalanus*. Other commonly found taxa included harpacticoid copepods and *Eucypris* ostracods.

Stomach fullness differed across locations (ANOVA, $F(3, 44) = 7.66$, $p = 0.0003$; Fig. 5). Fish held at the Wings Landing Outlet were fuller than fish from First Mallard and Sheldrake sloughs; Wings Landing Inlet were similar to those from other locations (Tukey HSD test, $p < 0.05$). Sampling week did not appear to affect stomach fullness by itself (ANOVA, $F(1, 44) = 1.22$, $p = 0.28$). However, stomach fullness was affected by the interaction between location and sampling week (ANOVA, $F(3, 44) = 7.53$, $p = 0.0004$). Proportions of prey items varied across locations but most commonly included cyclopoids, calanoids, gammarids, and corophiids. Generally, the zooplankton taxa with the highest biomass in the environment corresponded to taxa with the highest biomass in the diets (Fig. 4). Of all locations, stomach contents from Wings Landing Outlet contained the greatest zooplankton biomass. Wings Landing Outlet was also the only location where the zooplankter *Daphnia* was found consistently in stomachs. Fish stomachs from Sheldrake Slough contained high copepod biomass during the first weeks of the study, corresponding to a period of adjacent managed wetland exports into the slough and declining thereafter. Stomachs from Wings Landing Inlet contained more terrestrial insects versus other locations and, during the first sampling period, one fish notably consumed a large number of ostracods (Fig. 4). Other taxa consumed but rarely found included (in order of abundance): ostracods, chironomid larvae, harpacticoid copepods, isopods, and cumaceans.

Wings Landing Outlet had lower average daily mean and mean maximum temperatures compared to First Mallard Slough, Sheldrake Slough, and the Wings Landing Inlet (Table 6). Both the Wings Landing Outlet and Inlet displayed less diel fluctuation than Sheldrake and First Mallard sloughs. Additionally, bi-weekly discrete samples of dissolved oxygen concentrations were lower at Wings Landing Outlet than First Mallard Slough, Sheldrake Slough, and the Wings Landing Inlet (Table 6). While dissolved oxygen concentrations were uniformly low across all locations, Wings Landing Outlet had the lowest recorded value, at 2.0 mg/L, compared to minimum measured values of 4.8, 5.4, and 3.1 mg/L for First Mallard

Table 4 Juvenile Chinook salmon mass growth rate (MGR) model development comparison. W represents sampling week. Each model included a cage effect expressed as (1|Cage). Variable abbreviations are as follows: *Mean Temp* daily mean temperature ($^{\circ}\text{C}$), *Zoop* zooplankton biomass ($\mu\text{gC}/\text{m}^3$), *DO* dissolved oxygen (mg/L), *VSS* volatile suspended solids (mg/L), *NO3N* nitrate + nitrite nitrogen (mg/L), *TP* total phosphorus (mg/L). More details on the model selection process can be found in Table S2

Model	df	ΔAIC_c	AIC_c weight
$\text{MGR} \sim (\text{Zoop} + \text{DO} + \text{VSS}) * W$	10	0.0	0.29
$\text{MGR} \sim (\text{Zoop} + \text{DO} + \text{Mean temp}) * W$	10	0.5	0.22
$\text{MGR} \sim (\text{Zoop} + \text{DO}) * W$	8	0.7	0.20
$\text{MGR} \sim (\text{Zoop} + \text{DO} + \text{NO3N}) * W$	10	1.2	0.15
$\text{MGR} \sim (\text{Zoop} + \text{DO}) * \text{VSS} * W$	14	1.4	0.14
$\text{MGR} \sim \text{Zoop} * W$	6	20.8	< 0.001
$\text{MGR} \sim \text{intercept} * W$	4	57.2	< 0.001

Table 5 Model summaries for the 3 top performing models listed in Table 4

Model	Parameter	Estimate	Standard error	<i>t</i> value	95% CI
1. MGR ~ (Zoop + DO + VSS)* <i>W</i>	Zoop	0.087	0.017	5.043	[0.053, 0.121]
	DO	-0.085	0.021	-3.988	[-0.127, -0.042]
	VSS	-0.032	0.017	-1.878	[-0.065, 0.002]
	Week	-0.016	0.002	-8.895	[-0.020, -0.013]
	Zoop*Week	-0.007	0.003	-2.514	[-0.012, -0.001]
	DO*Week	0.015	0.005	2.991	[0.005, 0.026]
	VSS*Week	0.004	0.004	0.918	[-0.004, 0.012]
2. MGR ~ (Zoop + DO + Mean temp)* <i>W</i>	Zoop	0.050	0.010	5.103	[0.030, 0.069]
	DO	-0.109	0.020	-5.595	[-0.148, -0.070]
	Mean Temp	-0.022	0.009	-2.516	[-0.039, -0.005]
	Week	-0.012	0.003	-3.714	[-0.018, -0.006]
	Zoop*Week	-0.001	0.002	-0.464	[-0.005, 0.003]
	DO*Week	0.019	0.005	4.111	[0.010, 0.029]
	Mean Temp*Week	0.002	0.002	1.233	[-0.001, 0.006]
3. MGR ~ (Zoop + DO)* <i>W</i>	Zoop	0.0512	0.010	5.100	[0.032, 0.072]
	DO	-0.096	0.020	-4.863	[-0.135, -0.057]
	Week	-0.017	0.002	-8.819	[-0.020, -0.129]
	Zoop*Week	-0.002	0.002	-1.004	[-0.006, 0.002]
	DO*Week	0.015	0.004	3.413	[0.006, 0.024]

Slough, Sheldrake Slough, and Wings Landing Inlet, respectively. Mean volatile suspended solids were lowest in Wings Landing Outlet and highest in Sheldrake Slough (Table 6).

Discussion

This is the first study in the SFE to demonstrate that a productive tidally muted managed pond can benefit rearing salmon. Contrary to our expectation, salmon grew considerably faster in the managed pond outlet relative to the other locations, with observed growth rates that were comparable to other

productive habitats (Table 7). Limited studies suggest that juvenile Chinook salmon in the SFE show less estuarine dependency than other populations, with shorter juvenile residence time and correspondingly slower growth rates (Kjelson et al. 1982; MacFarlane and Norton 2002). Whereas juvenile salmon in more northern populations use estuary rearing habitats into August, most salmon leave the SFE by June to avoid warming water temperatures in the estuary. Reduced estuarine dependence and growth rates in the SFE may be due to habitat loss, flow alterations, and changes to prey communities (Alpine and Cloern 1992; MacFarlane and Norton 2002; Jassby 2008; Kimmerer et al. 2012). However, growth rates

Fig. 3 Zooplankton biomass over the course of the study at each location. Tows were collected once per week at all locations. Biomass was measured as milligrams of carbon per meter cubed

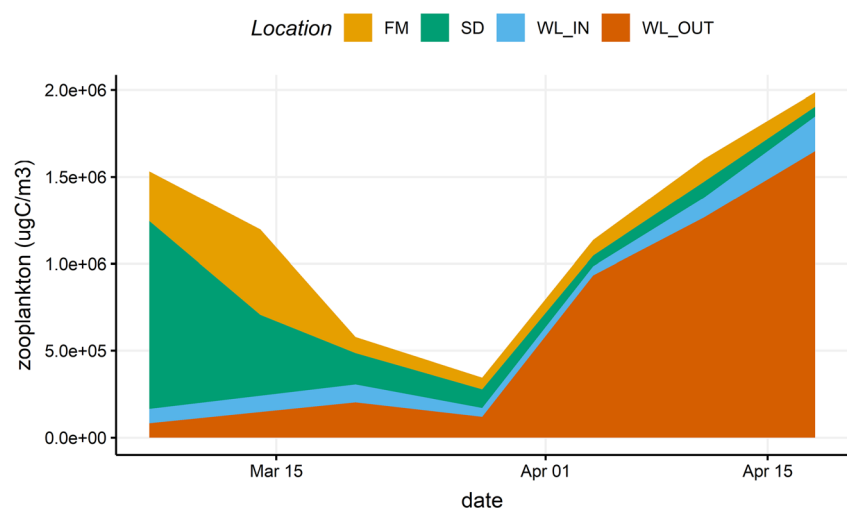


Fig. 4 Proportional taxa composition of zooplankton biomass collected via tows (a) compared to zooplankton biomass in the diets (b). Taxa found in the diet other than zooplankton are not included. “Other” categories include both taxa not covered in more specific groupings and those too deteriorated to identify further. All juvenile calanoid and cyclopoid copepods are included under “Other Copepoda” category while adults were differentiated further

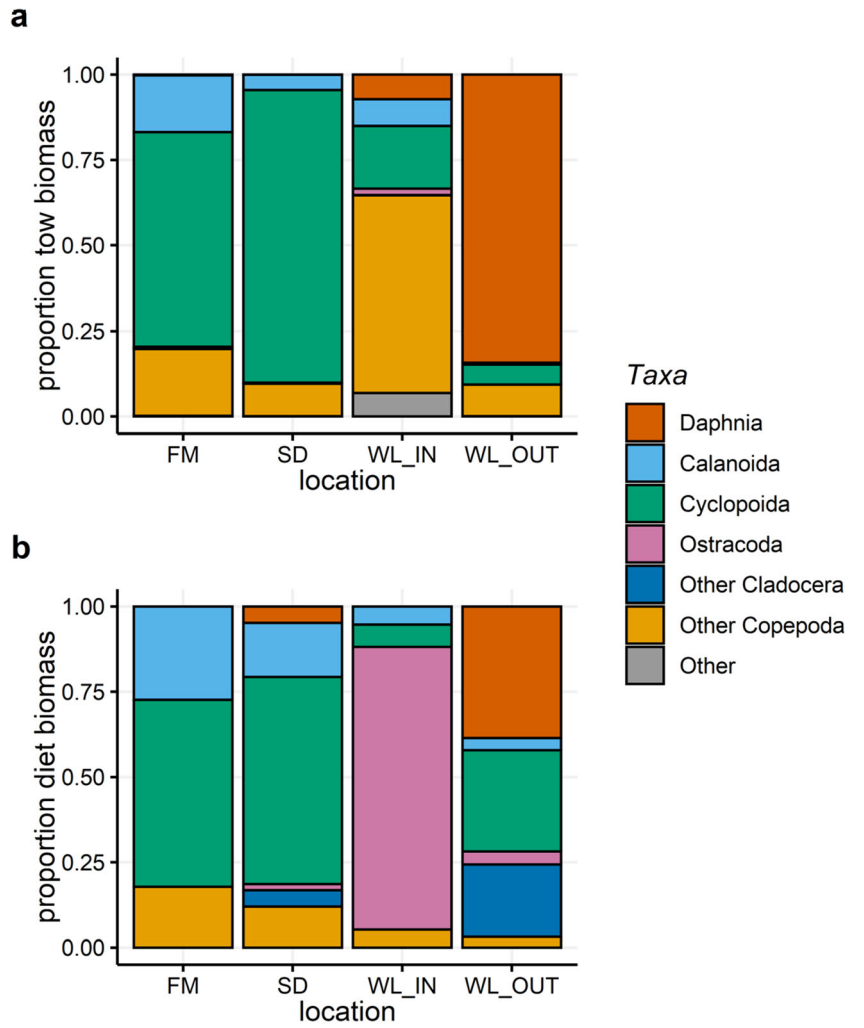


Fig. 5 Stomach fullness (\pm SE) at each location over time. Stomach fullness of individual fish was averaged across each cage

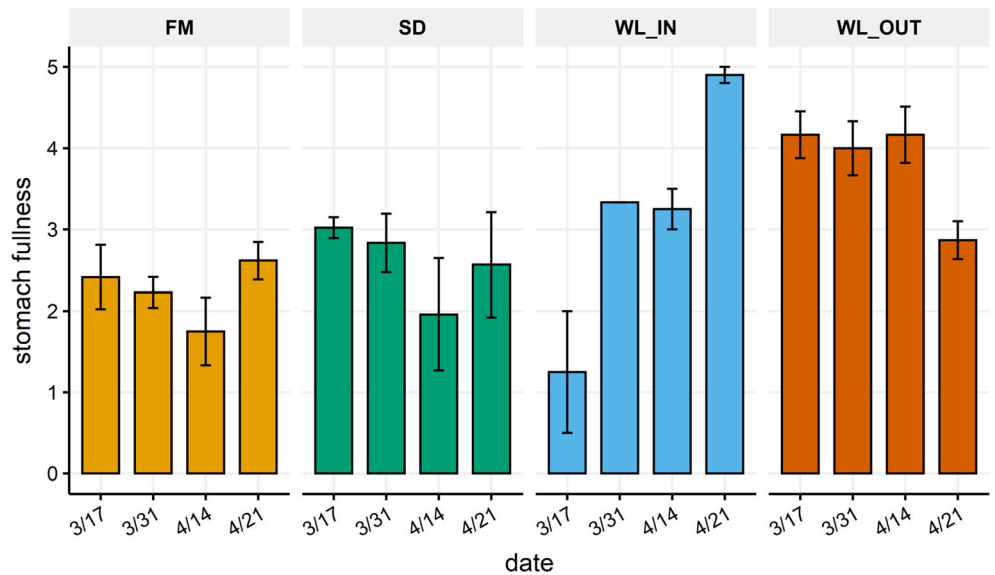


Table 6 Temperature values, dissolved oxygen concentrations, and volatile suspended solids at each location. Values represent mean \pm 1 SE

	Daily mean temperature (°C)	Daily maximum temperature (°C)	Diel temperature fluctuation (°C)	Dissolved oxygen (mg/L)	Volatile suspended solids (mg/L)
First Mallard Slough	15.7 \pm 0.02	17.5 \pm 0.34	3.3 \pm 0.22	6.6 \pm 0.21	8.47 \pm 0.29
Sheldrake Slough	16.0 \pm 0.02	17.9 \pm 0.29	3.0 \pm 0.24	6.9 \pm 0.14	9.79 \pm 0.47
Wings Landing Inlet	15.4 \pm 0.02	16.0 \pm 0.19	1.3 \pm 0.08	5.6 \pm 0.36	7.39 \pm 0.37
Wings Landing Outlet	14.7 \pm 0.02	15.6 \pm 0.19	1.7 \pm 0.12	3.9 \pm 0.53	5.50 \pm 0.35

observed at the managed wetland pond in this study generally fall within (and occasionally exceed) reported ranges from more northern estuaries (Healey 1980; Shreffler et al. 1992; Moore et al. 2016; Table 7).

Of the factors we measured, the high growth rates in the managed pond outlet were most attributable to considerably greater zooplankton biomass in the managed pond, relative to other locations. Fish held in the managed pond outlet were the fullest, with higher zooplankton biomass in their diets compared to other locations, verifying that the fish took advantage of the abundance of zooplankton in their environment. We speculate that volatile suspended solids (a measure of organic matter in the water) was included in the top performing model as it covaried with zooplankton biomass. The managed pond outlet, which had the highest zooplankton biomass, had the lowest amount of volatile suspended solids likely because these solids were being consumed or used by zooplankton or other higher trophic processes. We also saw 100% survival of fish between all sampling periods at the managed pond outlet location. While mortality between sampling events at other locations late in the study would presumably improve resource availability for the remaining fish, the managed pond outlet displayed the greatest growth even with the maximum amount of fish sharing the cage resources. We observed high growth rates in Sheldrake Slough in the first weeks of the study, when adjacent managed ponds were regularly releasing water into the slough to make room for water gained through precipitation. This corresponded to a spike in zooplankton biomass and fish growth in Sheldrake Slough which subsequently dissipated when inputs ceased.

The observed zooplankton productivity at the managed pond outlet is consistent with the positive relationship between phytoplankton (a food source for zooplankton) and longer water residence time that has been observed in rivers, lakes, floodplains, estuaries, and lagoons when nutrients are not limited (Alpine and Cloern 1992; Lucas et al. 2009; Peierls et al. 2012). These habitats are engines of productivity that increase food production, allowing fish to feed successfully while minimizing energy expenditures on foraging (Corline et al. 2017). Freshwater floodplain habitats above the tidal

excursion of the SFE have shown elevated levels of zooplankton biomass and correspondingly high Chinook salmon growth rates compared to local riverine habitats (Sommer et al. 2001; Jeffres et al. 2008; Katz et al. 2017). While these upriver floodplain habitats have been recognized for their benefits to salmon, wetland habitats in the tidal estuarine portion of this large deltaic ecosystem have received less attention. The few studies which have measured managed pond productivity in the SFE have found similar periods of high zooplankton abundance (Williamson, Durand, Phillips, and Tung, personal communication), suggesting that the pond in this study is likely not an outlier in the system. Additionally, as was observed in Sheldrake Slough, this study suggests that drainage of water from managed ponds, which overlaps with peak juvenile Chinook salmon outmigration (Kjelson et al. 1982), can export food resources into less productive surrounding waterways and benefit salmon indirectly. Similarities in ecological function among floodplains, tidal wetlands, and managed ponds indicate that productive managed ponds could provide rearing benefits for salmon.

Aside from food abundance, temperature and dissolved oxygen are important factors influencing growth and survival of juvenile salmon (Geist et al. 2006) and were included in the top performing growth rate models. The managed pond had lower mean temperatures and less diel temperature fluctuation relative to the tidal sloughs. This may be attributable to the combination of a relatively high ratio of emergent vegetation to channel width, inputs of slough water during high tides, and evaporative cooling at night (Heath et al. 1993; Enright et al. 2013; Hemes et al. 2018). Habitat features that produce thermal refugia are generally viewed as positive for coldwater fishes like salmonids (McCullough et al. 2009); thus, we believe these pond features provided additional benefits to salmon in this study.

While dissolved oxygen levels were low in the managed pond and reduced growth rate potential, the stress of low dissolved oxygen was likely offset by lower thermal stress and higher food abundance. This benefit of food abundance and lower thermal stress in the managed wetland outlet, which also had the lowest dissolved oxygen, is likely why we found a negative effect of increased dissolved oxygen on salmon

Table 7 Growth rates (GR) recorded for juvenile Chinook salmon. Values represent mean growth rates \pm 1 SE

Location	Mass GR (g/day)	Length GR (mm/day)	Source
First Mallard Slough	-0.004 ± 0.003	0.057 ± 0.021	This study
Sheldrake Slough	0.011 ± 0.004	0.193 ± 0.011	This study
Wings Landing Inlet	-0.006 ± 0.002	0.077 ± 0.004	This study
Wings Landing Outlet	0.077 ± 0.004	0.408 ± 0.005	This study
Yolo Rice Fields	0.11 ± 0.01	0.70 ± 0.01	Katz et al. 2017
Yolo Rice Field enclosures	0.10 ± 0.00	0.68 ± 0.01	Katz et al. 2017
Sacramento River	–	0.33	Kjelson et al. 1982
Central Valley Rivers	–	0.57	Williams 2012
Sacramento-San Joaquin Delta	–	0.53–0.86	Kjelson et al. 1982
Sacramento-San Joaquin Delta	–	0.54	Williams 2012
San Francisco Estuary	–	1.01	Kjelson et al. 1982
San Francisco Estuary	0.02	0.18	MacFarlane and Norton 2002
Chippis Island to Farallons	–	0.33	Williams 2012
Nanaimo River Estuary, BC	–	1.32	Healey 1980
Puyallup River Estuary, WA	0.52	0.37	Shreffler et al. 1992
Skeena River Estuary, BC	–	0.48 ± 0.09	Moore et al. 2016

growth in our mixed effect model. Dissolved oxygen was higher in the sloughs; however, both the leveed and natural slough experienced greater diel fluctuation and higher maximum temperatures, especially in late April. The spike in mortality at these locations during the final week of the study likely resulted from the physiological stress of temperature fluctuation in combination with too few prey resources to meet the increased metabolic needs resulting from warmer temperatures. Most fish that died during the study appeared emaciated.

While this field experiment suggests managed ponds may benefit rearing salmon, the use of cages limits full interpretation of growth rates and diet. For example, caging fish in the tidal sloughs may have subjected the juvenile salmon to water velocities from which they would otherwise seek refuge. Fish reared in the managed pond may have expended less energy as the tidal flow was muted by gates. Additionally, cage effects likely dampened true growth potential as study fish were held at higher densities than free-swimming fish would likely be found and were limited to consuming only what passed through the cages. This could have amplified competition for resources, magnified reliance on zooplankton, created an artificial structure for amphipods to colonize, and decreased access to other common prey items such as terrestrial insects (David et al. 2016). For example, First Mallard Slough has been recognized as valuable fish nursery habitat within Suisun Marsh (Colombano et al. 2020), although salmon in this study grew poorly there. Food resources at this location may be dominated by epibenthic invertebrates (O'Rear and Moyle 2018) rather than zooplankton; such invertebrates were less available in cages, especially cages in deeper locations which had less interaction with the benthos. The cages likely also

limited access to insect fallout from overhanging vegetation due to the mesh material covering the top of the cages.

The uncertainties in this field experiment do not change the conclusion that it is possible for salmon to benefit from managed wetland zooplankton productivity. As a test of the comparative zooplankton resources available to juvenile salmon across different marsh locations, the study provided robust results that bear further investigation. While this study took place during a single year and differing environmental conditions may change the magnitude of zooplankton productivity and fish growth, these results uphold that there are conditions in which managed wetlands can provide valuable food resources. To reduce uncertainties, future studies should consider deploying instruments to measure water velocity as part of a bioenergetic model, find locations in which larger enclosures could be safely deployed, and study multiple years with varied environmental conditions. Additionally, the cage structure itself appeared to attract amphipods, which were found consistently in the diets across all sites. Future growth rate modeling would benefit from the inclusion of these prey resources, which will require new techniques for quantifying invertebrate cage colonization.

In altered estuaries, such as the SFE, it may not be possible to achieve conservation goals through tidal restoration alone, as the size of planned and feasible restoration is often limited (Moyle et al. 2018). Under these circumstances, exploring alternative options may be necessary to aid declining populations. The high fish growth rates in this study, resulting from muted tidal pond productivity, demonstrate the potential of an altered estuarine habitat

to benefit rearing juvenile salmon. Managed wetlands could be used to supplement in-slough zooplankton during critical times, such as peak salmon outmigration. Additionally, productive managed ponds could be outfitted with water control structures to improve volitional passage of fish into these typically inaccessible habitats. Improvement to lateral movement of fishes from rivers and sloughs into floodplain and wetland habitats is an important element of restoration in impacted watersheds and connected river ecosystems (Junk et al. 1989; Jones and Stuart 2008; Baumgartner et al. 2014) and increase available rearing habitat. However, different salmon populations and run types have varied migration periods and life-history strategies that may complicate the utility of the managed habitats explored in this study. In addition, uncertainty about the ability of fish to navigate through these ponds, avoid avian predation, and find exits merits further research.

Actions that increase productivity and improve connectivity can increase the value of estuarine marshes for outmigrating juvenile salmon, especially in the SFE where salmon are in decline. Repeated studies of more northern Pacific Coast salmon populations demonstrate the value of estuaries as key stopover habitats along migratory routes and show that wetland restoration increases rearing opportunities (Bottom et al. 2005; Volk et al. 2010; Moore et al. 2016). Increasing habitat and ecosystem function in estuaries can expand rearing opportunities for out-migrating salmon and encourage diversification of life-history strategies. When restoration is not possible, taking advantage of underappreciated productive habitats could provide an opportunity to manage for multiple ecosystem services (Needles et al. 2015) and create a desirable mosaic of habitat (Ritter et al. 2008) for varied foraging opportunities. Novel or managed habitats in other coastal and estuarine ecosystems may have similar capacities to provide nursery benefits to juvenile fishes (Jude and Pappas 1992) and these possibilities should be further explored.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-020-00880-4>.

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