

Original Articles

Variability in foodscapes and fish growth across a habitat mosaic: Implications for management and ecosystem restoration

Flora Cordoleani^{a,b,*}, Eric Holmes^c, Miranda Bell-Tilcock^c, Rachel C. Johnson^{b,c}, Carson Jeffres^c

^a Institute of Marine Sciences, Fisheries Collaborative Program, University of California Santa Cruz Santa Cruz, 1156 High Street, Santa Cruz 95064, USA

^b National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center, 110 McAllister Way, Santa Cruz 95060, USA

^c University of California Davis, Center for Watershed Sciences, One Shields Ave, Davis 95616, USA



ARTICLE INFO

Keywords:

Salmon
Floodplain
Chlorophyll-a
Water temperature
Invertebrate
Landscape

ABSTRACT

Riverine ecosystems in their natural state are complex mosaics of habitats whose conditions vary across space and time as landscape features filter prevailing hydrologic forcing. Yet, through anthropogenic alteration many large river systems have become simplified through the construction of levees and dams that reduce lateral connectivity and flow variability. The extent to which shifts in habitat mosaics create conditions that support different trophic responses that manifest in differences in fish growth across the landscape remains largely untested. This is primarily due to limitations in linking habitat features, dynamic physical processes, and trophic transfer of energy to higher taxa at the landscape scale. Here, we conducted large-scale enclosure experiments across varying habitats on a fluvial floodplain as a model system to measure factors that influence habitat-specific growth rates in multiple Chinook Salmon (*Oncorhynchus tshawytscha*) stocks important to fisheries and of conservation concern. Using an ecosystem approach, we reveal that landscape context, water residence time, and habitat type (agricultural, wetland, river channel) result in different hot-spots of primary and secondary food production. This variation in the aquatic foodscape resulted in significant variation in salmon growth rates and ultimate size and morphology across the landscape. Floodplain habitats generally exhibited higher water residence times as highlighted by higher specific conductance, salinity, and chlorophyll-a values. Pelagic invertebrate abundance was 10 to 100 times more abundant in the off-channel habitats compared to the river channels. The average daily growth rates of the juvenile Chinook Salmon ranged from 0.15 mm day⁻¹ and 0.01 g day⁻¹ in the riverine habitat to 0.55 mm day⁻¹ and 0.07 g day⁻¹ in the off-channel habitat. These data were used to build mixed effects models that showed the influence of chlorophyll-a concentration, water temperature and pelagic invertebrate composition on fish growth across locations throughout the experiment. As landscapes become increasingly simplified there is increased risk of losing the mosaic of habitats necessary to achieve enhanced fish growth and phenotypically diverse and sustainable salmon populations. This in-situ experimental and modeling approach can be applied to other systems to develop ecosystem indicators such as habitat-specific fish growth rates to manage landscapes and processes to support resilient fish populations.

1. Introduction

One of the greatest challenges in restoration ecology is linking specific restoration actions to demographic responses in higher trophic organisms. Globally, riverine ecosystems are under severe threat from human activities and a warming climate (Ward et al., 1999), and are the focus of significant restoration efforts due to the ecological services they

provide (Sabater et al., 2018; Dudgeon, 2019). However, the effectiveness of many restoration actions remains highly variable, due to the inability to first identify the mechanisms involved in the response of the river's biota to changes in habitat features and physical processes (Kail et al., 2015; Friberg et al., 2016). In particular, the extent to which the simplification of a river's habitat mosaic affects the food web structure and ultimately fish growth and survival across the landscape remains

* Corresponding author at: National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center, 110 McAllister Way, Santa Cruz 95060, USA.

E-mail address: flora.cordoleani@noaa.gov (F. Cordoleani).

<https://doi.org/10.1016/j.ecolind.2022.108681>

Received 8 July 2021; Received in revised form 9 February 2022; Accepted 11 February 2022

Available online 15 February 2022

1470-160X/© 2022 The Authors.

Published by Elsevier Ltd.

This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

largely untested. Therefore, identifying process-based indicators that can rapidly track changes in freshwater environmental conditions could help quantify how habitat modifications affect the river's ecological processes and help design management actions that will best restore ecosystems functions. Fish growth is a valuable ecological indicator to assess habitat quality because it integrates several abiotic and biotic factors such as water quality and abundance and quality of prey. Monitoring fish growth across multiple river habitats, including floodplains which have been shown to play a significant role in fish recruitment (Humphries et al., 1999; Górski et al., 2011; Scharbert and Borcherting, 2013), could then provide critical information on how to manage river landscapes to support resilient fish populations and ecosystems.

Measuring habitat-specific fish growth rates at landscape scales and identifying the environmental factors promoting high growth can be difficult, particularly for migratory species using highly dynamic landscapes. While fish size in different habitats can be assessed by capturing and measuring fish in targeted locations, apparent differences in size could be attributed to differences in factors other than habitat quality such as fish ages, size selective mortality, density dependence, or other confounding factors (Staggs and Otis, 1996; Jodun et al., 2002). To track changes in fish sizes over time (individual growth rates) in different habitats often requires extensive mark and recapture efforts that can be particularly challenging to implement in large areas with low recapture probabilities. Fish growth rate estimates are thus often derived from laboratory experiments in controlled settings that do not account for the habitat complexity (e.g., substrate diversity, multi-trophic interactions) that fish might experience in their natural environment. This approach strongly limits the predictive capability of those estimates under natural conditions. In contrast, experimental fish enclosures deployed across the landscape provide a unique opportunity to track fish growth rates through space and time and to directly link those growth rates to local and regional environmental conditions (Jeffres et al., 2008; 2020).

California's Sacramento-San Joaquin River watershed (USA) serves as a model system for understanding how fish growth indicators could help resource managers optimize their investments in habitat restoration of a highly modified riverine landscape. More than 95% of floodplains and wetlands in the California Central Valley (CCV), that were once accessible to native fish, have been lost due to human development (Whipple et al., 2012). Further, the remaining riverine habitats have been simplified through the construction of levees that have channelized the rivers and disconnected them from adjacent floodplains. This disconnection has negatively altered the food web and contributed to the decline of many fish species (Sommer et al., 1997; Feyrer et al., 2006; Opperman et al., 2017), especially anadromous species like Chinook Salmon (*Oncorhynchus tshawytscha*). The majority of the remaining floodplains that are accessible to juvenile Chinook Salmon now exist in the form of flood bypasses. Those bypasses are large flood control infrastructures constructed to mitigate flood risk to developed areas in the CCV (Kelley, 1989; Sommer et al., 2001). The nutrient-rich soils in the bypasses have been converted to a mosaic of agricultural plots and managed wetlands with Sacramento River water spilling into the bypasses, during high flows, through passive weir structures (Whipple et al., 2012; Goertler et al., 2018). The diversity in physical habitat features and the seasonal flooding dynamic make flood bypasses an ideal system to quantify the extent to which habitat mosaics contribute to the development of multiple trophic responses that manifest in differences in fish growth.

This study was centered on the Sutter Bypass, a crucial piece of the Central Valley Project relieving pressure on the levees of the Sacramento and Feather Rivers ([CVFMPP] Central Valley Flood Management Planning Program, 2010), and an important rearing habitat for threatened CCV Chinook Salmon populations (McReynolds et al., 2006; Johnson & Lindley, 2016). Here, we established an experimental and modeling framework to quantify factors and processes that influence juvenile salmon growth at local, regional, and landscape-scales. Based

on previous studies of juvenile salmon growth in the CCV (Sommer et al., 2001; Jeffres et al., 2008; Katz et al., 2017; Jeffres et al., 2020; Holmes et al., 2021) we hypothesized that the various habitat types found across the landscape support different food webs which ultimately lead to different juvenile salmon growth patterns. We measured the spatial and temporal dynamics of juvenile Chinook Salmon growth using experimental enclosures stratified among representative habitat types. We concurrently collected system hydrology, water quality, chlorophyll-a concentration, and ambient pelagic invertebrate abundance and composition. Using those data, we sought to 1) characterize habitat productivity, foodscape, and juvenile salmon growth differences across habitat types, and 2) identify drivers of salmon growth across the landscape. Additionally, wild juvenile Chinook Salmon were sampled, and a diet analysis of both enclosure and wild juvenile salmon was conducted to determine whether enclosure salmon diet was representative to that of free-swimming salmon. This spatio-temporal analysis allowed us to garner critical information for evaluating how flood bypass management, such as increased local flooding or floodplain-to-river water transfer, might positively influence process-based indicators such as fish growth, and ultimately improve salmon population-level dynamics (Hendrix et al., 2017; Cordoleani et al., 2020; Peterson and Duarte, 2020)

2. Materials and methods

2.1. Study system

The Sacramento River is the largest river and watershed of California, USA, and drains the northern half of the CCV (Buer et al., 1989). The headwaters are located just south of Mount Shasta in the southern Cascade Range, and the river enters the Sacramento-San Joaquin Delta south of the city of Sacramento. The lower Sacramento River is heavily channelized and leveed, and flood bypasses have replaced a portion of the historical floodplains, receiving surplus river water during high winter and spring flow events. Parallel to the lower Sacramento River, the Butte Sink and Sutter Bypass, encompassing approximately 214 km², are part of the uppermost flood bypass in the Sacramento Valley, and constitute a crucial piece of the Central Valley Project relieving pressure on the levees of the Sacramento and Feather Rivers ([CVFMPP] Central Valley Flood Management Planning Program, 2010). The area from the Butte Sink in the north to the confluence of the Sutter Bypass with the Feather and Sacramento Rivers near Verona in the south receives water from various watersheds (Fig. 1). The lower Butte Creek watershed - a Sacramento River tributary of approximately 2,103 km² which originates on the western slopes of the Sierra Nevada mountains, in the Lassen National Forest - flows into the Butte Sink just north of the Sutter Buttes (McReynolds et al., 2006) (Fig. 1). Additionally, the Butte Sink and Sutter Bypass receive floodwaters from the Sacramento River at Moulton, Colusa, and Tisdale weirs. Flooding generally occurs between December and May, when Sacramento River water overtops the three passive weirs. The Sutter Bypass's low-lying topography and weir structures allows the bypass to be inundated in most years, including some drought years. Flood flows from Sutter Bypass subsequently drain into the Sacramento River and Yolo Bypass, a similar large seasonal floodplain (Sommer et al., 2001). Apart from flood protection, this region provides important agricultural and wildlife benefits. In particular, the Butte Sink and Sutter Bypass are thought to provide important rearing habitat for the threatened Butte Creek spring-run Chinook Salmon population, especially in years of extensive winter and spring flooding when fish can access the mosaic of flooded agricultural plots and managed wetlands (McReynolds et al., 2006; Johnson & Lindley, 2016). Other populations of Chinook Salmon from the Sacramento River, such as the endangered Sacramento River winter-run, and the Central Valley fall- and late fall-run which are listed as species of concern (Yoshiyama et al., 1998) also use this habitat when access is permitted during flooding events.

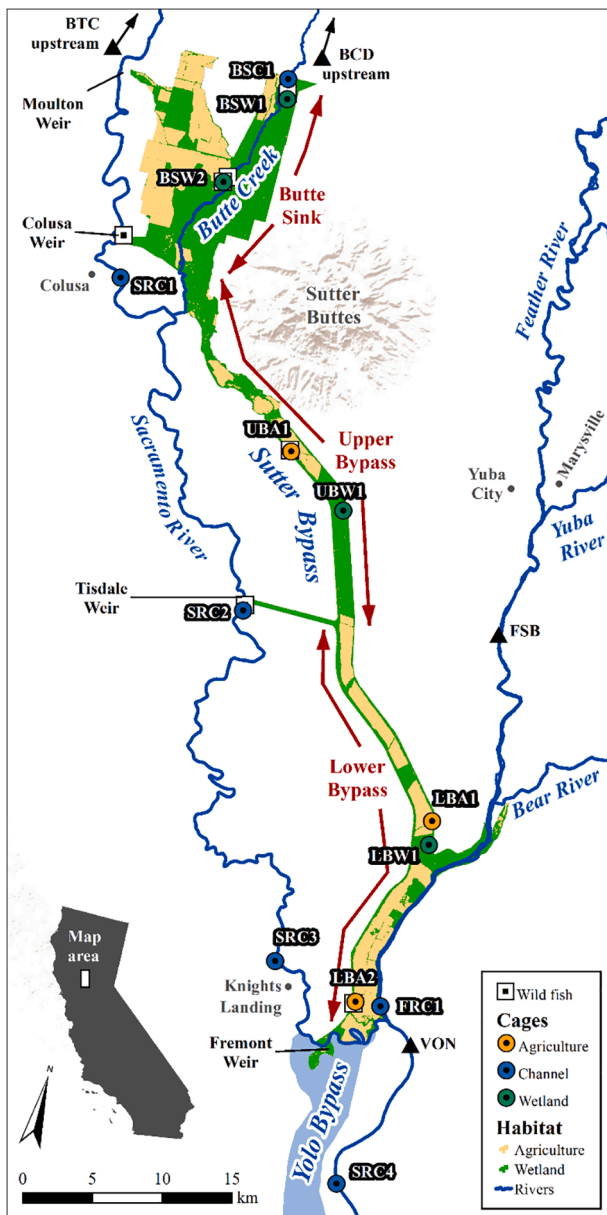


Fig. 1. Study area map with the different regions and the fish cage locations. The Butte Creek watershed is separated into three regions: 1) Butte Sink: North of Colusa weir, 2) Upper Bypass: Colusa weir to Tisdale weir, 3) Lower Bypass: Tisdale weir south to Sacramento River. Triangle symbols represent flow gaging stations (BTC

= Sacramento River at Butte City, BCD = Butte Creek at Durham, and FSB = Feather River at Boyd’s Landing above Star Bend, VON = Sacramento River at Verona).

2.2. Study habitats

To better characterize the mosaic of habitats available to juvenile salmon for rearing, 13 locations were selected across 5 regions defined as: 1) Butte Sink: North of Colusa weir, 2) Upper Bypass: Colusa weir to Tisdale weir, 3) Lower Bypass: Tisdale weir south to Sacramento River, 4) Sacramento River, and 5) Feather River (Table 1, Fig. 1). Three different habitat types were identified; channel, off-channel wetland, and off-channel agricultural substrate. The Butte Sink and Sutter Bypass, had both wetland and agriculture habitat types, while the Sacramento and Feather River were only characterized by one type of habitat (channel). Two enclosures were deployed at each site.

Table 1
Enclosure site locations across the different regions.

Region	Site	Habitat type
Butte Sink	BSW1	Wetland
	BSW2	Wetland
	BSC1	Channel
Upper Bypass	UBA1	Agriculture
	UBW1	Wetland
Lower Bypass	LBW1	Wetland
	LBA1	Agriculture
	LBA2	Agriculture
Sacramento River	SRC1	Channel
	SRC2	Channel
	SRC3	Channel
	SRC4	Channel
Feather River	FRC1	Channel

2.3. Experimental enclosure design and salmon growth estimation

The salmon enclosure experiment was implemented from 2/19/2019 to 4/3/2019 (i.e., 42 or 43 days per enclosure) to study site-specific juvenile Chinook Salmon growth rates during winter months (Table 1), which corresponds to their peak rearing time period in the CCV (Williams, 2006). Enclosures were utilized to maintain fish within a specific habitat for the duration of the study, and provided access to the top 0.5 m of the water surface. While enclosure fish could not directly access benthic resource, similar salmon growth studies have shown that juvenile salmon diets are mostly composed of pelagic organisms or benthic organisms which have a pelagic lifestage that could be transported during high flow events (e.g, drift invertebrates like chironomids; Sommer et al., 2001; Jeffres et al., 2008; Corline et al., 2017). Therefore, we assumed that, despite movement restrictions, enclosure salmon were able to access their preferred food resource (this assumption was further tested by comparing enclosure versus wild juvenile salmon diet composition, see section 2.4.4). Each site had two 122 cm long × 61 cm wide × 61 cm depth floating enclosures constructed with 2.5 cm pvc pipe frames enclosed with 0.6 cm plastic mesh material (Fig. 2). This enclosure design has been used extensively for similar studies throughout the CCV (Jeffres et al., 2008, 2020). The enclosures allowed for re-measurement of individually marked fish at a specific location as well as allowing for food resources to enter the enclosure that are of a

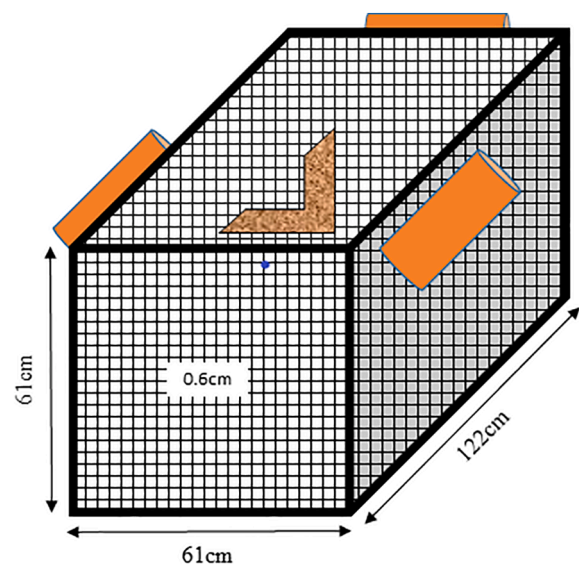


Fig. 2. Schematic of enclosure used for the salmon growth study. Orange cylinders represent floats to maintain the enclosure near the surface and the mottled brown “L” represents the closure structure where fish can be put in and removed from the enclosure.

suitable size for juvenile salmon. Each enclosure was stocked with five juvenile fall-run Chinook Salmon sourced from the Feather River Hatchery (Oroville, CA) and individually tagged with a Passive Integrated Transponder (PIT). The enclosure salmon were weighed to the nearest 1/100th of a gram (g) with an Ohaus Scout Pro scale and measured for fork length (FL) to the nearest millimeter (mm) at a two-week interval (week 2: 3/4/2019–3/6/2019, week 4: 3/18/2019–3/21/2019, week 6: 4/1/2019–4/3/2019). The only exception to the two-week interval was during week 2 at one of the Butte Sink locations (BSW2) which was delayed a week until 3/12/2019 due to limited access during a flooding event. When fish weight could not be recorded due to difficult field conditions (e.g., inability to tare a scale due to unstable sampling platform of a boat and/or high winds), we used the juvenile Chinook Salmon weight prediction model developed by Holmes and Jeffres (2021), which used morphometrics analysis on images that were collected from live fish in the field. Salmon density within enclosures was maintained by adding “placebo” hatchery fish when escape or mortality occurred among the marked fish (Table A1). At the end of the 6 weeks, all remaining fish were euthanized and a subset were analyzed for gut contents.

We used individual fork length (FL) and wet weight measurements performed at week 0, 2, 4 and 6 to estimate a site-specific mean daily growth rate (expressed in millimeters per day (mm d^{-1}), and grams per day (g d^{-1})) during each two-week interval and over the entire 6-week study. Mass specific growth rates ($\text{SGR}_i = 100 \times \ln(\text{end_mass}_i) - \ln(\text{start_mass}_i)/t$) were also estimated for each enclosure fish (i) at each two-week interval (where t = days between sampling events), to remove the influence of body size on absolute growth.

2.4. Hydrologic, physical and biological data collection

2.4.1. System hydrology

River flow data for the three main inputs; Sacramento River, Feather River, and Butte Creek, and for the Butte Sink and Sutter Bypass was downloaded from the California Data Exchange Center (CDEC, <http://cdec.water.ca.gov/>). Sacramento River flow data was collected from the Sacramento River at Butte City (BTC) gaging station, Feather River flow was obtained at the Boyd’s Landing above Star Bend (FSB) station, and Butte Creek flow data was obtained from the Butte Creek at Durham (BCD) station (Fig. 1). Moulton (MLW), Colusa (CLW) and Tisdale (TIS) weirs overtopping information was also collected from CDEC (<http://cdec.water.ca.gov/>).

2.4.2. Water quality sampling

Water quality sampling was performed from 1/7/2019 to 4/29/2019. Continuous water temperature ($^{\circ}\text{C}$) was collected at all sites and dissolved oxygen (mg L^{-1}) was collected at one site in each region (except the Butte Sink region which had two), using submersible Onset U26 loggers continuously recording at a 15-minute interval and suspended approximately 0.5 m below the water surface. Point water quality data was also collected weekly at all sites with a YSI Exo2 multi parameter sonde. The parameters collected were: turbidity (NTU), electrical conductivity ($\mu\text{g cm}^{-1}$), salinity (PSU), pH, chlorophyll-a concentration ($\mu\text{g L}^{-1}$) and relative blue-green algae concentration ($\mu\text{g L}^{-1}$).

2.4.3. Ambient pelagic invertebrate sampling

Pelagic invertebrate sampling was performed weekly at all sites, from 1/7/2019 to 4/29/2019, using a 30 cm diameter 150 μm mesh zooplankton net thrown five meters and retrieved through the upper 0.5 m of the water column four times from the stream bank. To account for differences in sampled volume due to variable water velocities, a flow meter attached to the zooplankton net was used to estimate the volume of water sampled. All samples were preserved in a solution of 95% ethanol. The dilution volume, number of splits, and number of aliquots removed was recorded and used to obtain total estimates of

invertebrates which were divided by the total volume of water sampled to estimate density.

Subsampling was necessary due to the high density of invertebrates within the samples. Invertebrates were identified with the aid of a dissecting microscope at 4x magnification to the lowest taxonomic level possible using keys from pertinent ecological literature (Merritt et al., 2008; Thorp and Covich, 2009; Karanovic, 2012). Copepods were only identified to family level. Samples were sorted into two groups of one hundred. One group was for the taxonomic group with the highest number of individuals counted. A second group was for the total individual counts of each of the other taxonomic groups added up such that they met or exceeded a hundred in their total numerical count. If a hundred count of the single highest taxonomic group was reached, but not a hundred of the remaining total individuals, then in the following aliquots the highest taxonomic group was not counted.

2.4.4. Wild fish sampling and salmon diet composition

To determine how well enclosure salmon diets represent those of free-swimming fish, we used either a beach seine or fyke nets to capture juvenile salmon at locations along the Sutter Bypass and Butte Sink that were in the proximity of enclosure sites (i.e., BSW1, BSW2, UBA1, Colusa Weir/SRC1, Tisdale Weir/SRC2, and LBA2; Fig. 1). This sampling was conducted when the Sacramento River flowed over flood weirs into the Sutter Bypass starting in January and continuing until flood waters receded in May. Chinook Salmon were measured for fork length to the nearest mm and weighed to the nearest 0.01 g, and a subset of young-of-the-year fish were lethally sampled following the guidelines of our scientific collecting permit (CDFW permit SC-13029).

Stomach contents from euthanized enclosure and wild juvenile Chinook Salmon were identified to their lowest possible taxonomic group with the aid of a dissecting microscope at 4x magnification. The same taxonomic keys from the ambient invertebrate identification were used to identify the stomach contents. Because we didn’t have information on potential differences in digestion rate across prey taxa we made the assumption that what was found in the salmon stomachs during the dissection was representative of what they were feeding on in the environment.

2.5. Statistical analyses

2.5.1. Pelagic invertebrate composition analysis

We compared pelagic invertebrate composition across the various habitat types using a non-metric multidimensional scaling (NMDS) analysis (using the *vegan* package in R; Kruskal, 1964a;b). This approach allowed us to visualize how study sites clustered across habitat types and how those clusters were correlated to the various invertebrate taxa. Pelagic invertebrate taxa were aggregated into higher taxonomic units (HTUs; Table A2) for the analysis, to increase statistical power. Pelagic invertebrate total densities (organisms m^{-3}) were standardized prior to analysis (using a range standardization in the *decostand* function in R; Legendre and Gallagher, 2001).

2.5.2. Enclosure vs wild juvenile salmon diet comparison

We estimated the mean invertebrate HTU’s abundances and the proportion of each invertebrate HTU found in both euthanized enclosure and wild salmon guts. We performed an analysis of similarities (using *ANOSIM* function in R) on the site-specific invertebrate HTU proportions to evaluate whether the diet compositions of enclosure and wild salmon sampled in the proximity of an enclosure were statistically similar.

2.5.3. Salmon growth modelling

We developed a series of juvenile salmon growth models to explore the environmental drivers of enclosure salmon growth. Specifically, we used mixed effects models to account for the three nested levels of correlation among fish growth estimates that resulted from the experimental framework – 1) 13 enclosure locations, 2) two enclosures per

Table 2

List of simple candidate growth models. The “Biological Assumption” column briefly describes the reason why each environmental variable is considered in this study.

Models	Biological Assumption
$1 + 1 Fish_ID + 1 Location$	None of the environmental variables considered significantly influence juvenile salmon growth.
$meanCHL + 1 Fish_ID + 1 Location$	Chl-a concentration can be used as a proxy for system’s primary productivity which might indirectly influence juvenile salmon growth through its role in the development of invertebrate biomass, including juvenile salmon prey.
$meanEC + 1 Fish_ID + 1 Location$	Electrical conductivity can be used as a proxy for water residence time which might indirectly influence juvenile salmon growth through its impact on primary and secondary production development.
$meanTemp + 1 Fish_ID + 1 Location$	Water temperature might indirectly influence juvenile salmon growth through its impact on primary production development and directly through its impact on fish physiology.
$sdTemp + 1 Fish_ID + 1 Location$	Variability in water temperature, observed as the result of a dynamic system hydrology, combines the influence of water temperature and residence time changes on juvenile salmon growth.
$logCladocera + 1 Fish_ID + 1 Location$	Cladocera density might directly influence juvenile salmon growth
$logInsecta + 1 Fish_ID + 1 Location$	Insecta density might directly influence juvenile salmon growth
$logOstracoda + 1 Fish_ID + 1 Location$	Ostracoda density might directly influence juvenile salmon growth
$logRotifera + 1 Fish_ID + 1 Location$	Rotifera density might directly influence juvenile salmon growth
$logCopepoda + 1 Fish_ID + 1 Location$	Copepoda density might directly influence juvenile salmon growth
$logTotInvert + 1 Fish_ID + 1 Location$	The total density of pelagic invertebrate might directly influence juvenile salmon growth
$NMDS1 + 1 Fish_ID + 1 Location$	The composition of the pelagic invertebrate community defined by NMDS1 axis might directly influence juvenile salmon growth
$NMDS2 + 1 Fish_ID + 1 Location$	The composition of pelagic invertebrate community defined by NMDS2 axis might directly influence juvenile salmon growth

location, 3) three time periods (period 1 = weeks 1 & 2, period 2 = weeks 3 & 4, period 3 = weeks 5 & 6 of the experiment). Fish mass specific growth rates (SGR) estimated for each time period were used as the response variable. Fish that escaped or died during the first two weeks of the experiment were removed from the analysis, resulting in the use of 83 marked fish (see Table A3 for details). To account for time dependency structure within individual fish growth rates and for within-location correlations among individuals, random intercepts $1|Fish_ID$ and $1|Location$ were used in each model. Since preliminary results showed no significant SGR differences across enclosures for most of the locations and time periods (see results from paired t-tests between SGRs grouped by location and time period in Table A4), we decided to not include a within-enclosure correlation term in our modelling. Finally, the following environmental factors were included as fixed variables: mean water temperature (meanTemp), water temperature standard deviation (sdTemp), mean electrical conductivity (meanEC), mean chlorophyll-a concentration (meanCHL), each pelagic invertebrate HTU’s density (i.e., Cladocera, Copepoda, Insecta, Ostracoda and Rotifera), total invertebrate density (TotInvert; organisms m^{-3}), and first and second NMDS axis scores (NMDS1 and NMDS2). Each variable was averaged by sampling period to coincide with the bi-monthly growth measurements. Based on preliminary data exploration invertebrate densities were log-transformed to improve comparison across locations. Moreover, prior to fitting the models to the growth data, all the continuous variables were standardized.

The growth models were developed in R (R Core Team, 2017), and model parameters were estimated using the *lmer* function (from *lme4* package; Bates et al., 2015). We developed simple models that included each environmental variable taken separately (Table 2), as well as more complex models that tested the combined influence of various variables, through either additive (i.e., $var1 + var2$) or interactive (i.e., $var1 \times var2$) effects. Variables that were highly correlated with each other (i.e., Pearson correlation coefficient value > 0.6 , Fig. A1) were not included in the same model. Akaike’s Information Criterion corrected for small sample sizes (AICc; Akaike, 1973; Burnham and Anderson, 2002) was used to identify the environmental variables that had a significant effect on fish growth.

3. Results

3.1. System hydrology and residence time relationship with site productivity

The 2019 water year was wetter than average (“above normal”: <https://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST>) with an extraordinary number of cold weather systems during February and March which led to a substantial snowpack. There were numerous weir overtopping events in the Butte Sink and Sutter Bypass at all three weirs (Moulton, Colusa and Tisdale, Fig. 3). Large, rapid tributary flooding dominated the early season hydrograph while increased reservoir releases from Shasta dam on the Sacramento River sustained significant flooding events during March into April. During the sampling season the maximum observed flow in the Sacramento River, Feather River, and Butte Creek reached 2577, 1086 and 301 $m^3 s^{-1}$ respectively, while minimum flows were as low as 153, 73, and 2 $m^3 s^{-1}$.

Overall, water temperature increased throughout the course of the experiment, but a more pronounced increase was observed in wetland and agriculture off-channel sites (Fig. 3 and Fig. A2). Dissolved oxygen levels were generally high with little fluctuation in the river channel locations (i.e., Butte Creek, Feather River and Sacramento River). Wetland sites showed a larger range of dissolved oxygen, with some periods of low dissolved oxygen when flood waters receded and temperatures increased later in the season (Fig. A2). We note that dissolved oxygen was not recorded in agriculture sites but likely exhibited the same trend than in wetland sites.

Off-channel conductivity (EC) was similar to channel conductivity during high flow events but diverged under lower flows when the wetlands and agriculture off-channel sites were contained within the off-channel habitat (Fig. 3 and Fig. A3). Conductivity in certain flow and habitat conditions can be used to indicate residence time differences in the sites with the same water source. Thus, during these containment periods, conductivity increased in off-channel sites likely because of longer residence time during which evaporation concentrates solutes.

Chlorophyll-a levels remained at relatively low concentrations in the channel sites for the duration of the study (Fig. 3 and Fig. A3). Chlorophyll-a concentrations were generally higher in off-channel sites except during high flow events when concentrations were similar to the channel sites. Chlorophyll-a concentrations were also higher in wetland than in agricultural off-channel sites. Blue Green Algae (BGA) followed

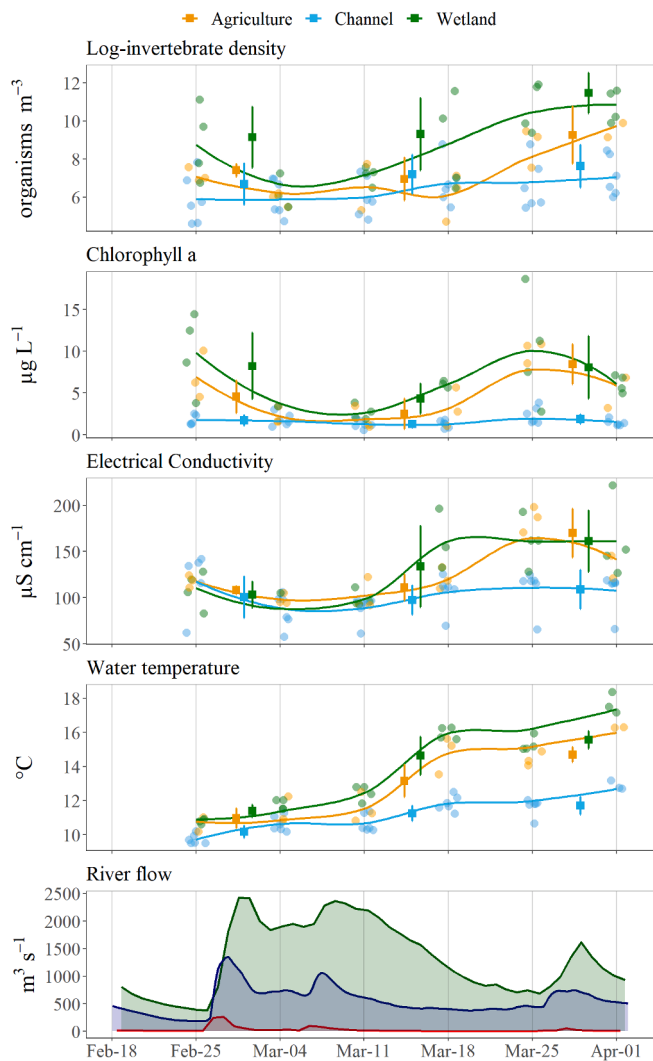


Fig. 3. River flow, water temperature, electrical conductivity, chlorophyll a, and pelagic invertebrate density stack plot, grouped by habitat type. The bottom graph shows Butte Creek (red), Feather River (blue) and Sacramento River (green) hydrograph. The dots show actual data sampled each week and the lines show a loess regression. The squares and associated error bars show each variable mean and 1SD values, where variables are averaged over the two weeks bracketing each square (i.e., data averaged over Feb 25-Mar 04, Mar 11-Mar 18, and Mar 25-Apr 01), to match with growth data used in the mixed effect modelling analysis.

the same pattern as chlorophyll-a concentration (Fig. A3).

Highest log-transformed pelagic invertebrate density was observed in wetland off-channel sites in comparison to the agriculture off-channel and channel sites for the entire sampling period (Fig. 3). During flooding events in the first two weeks of March a slight decrease in invertebrate densities was observed in off-channel sites, while the density in channel sites slightly increased. As the floodwaters receded in the last two weeks of March and water residence time increased in off-channel sites, invertebrate abundance largely increased. On the contrary, log-transformed invertebrate densities in channel sites only slightly increased and remained much lower than in off-channel sites.

3.2. Habitat-specific pelagic invertebrate resource and salmon diet composition

Overall, off-channel wetland, agriculture and channel sites were all defined by high proportions of Rotifera, Cladocera and Copepoda and

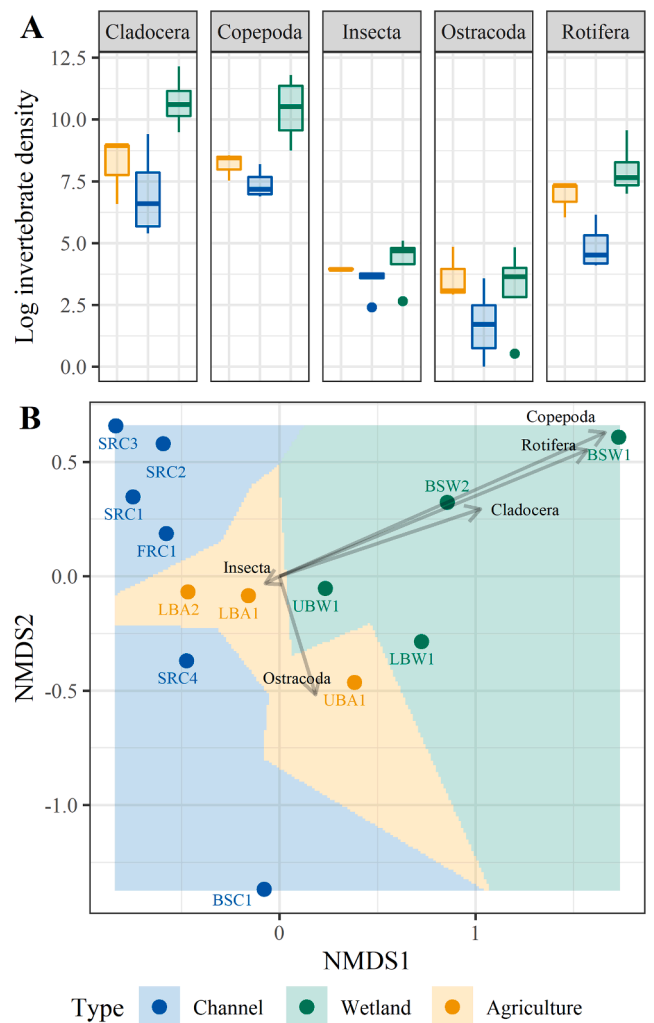


Fig. 4. (A) Boxplot displaying the distribution of ambient pelagic invertebrate HTU's densities averaged over the entire experiment period (i.e., 6 weeks). (B) NMDS results of ambient pelagic invertebrate community for the last sampling period.

low proportions of Insecta and Ostracoda (Fig. 4A and Fig. A4). Wetland sites had the highest densities of Rotifera, Cladocera and Copepoda, while channel sites had the lowest densities for all HTUs. Additionally, Insecta densities were similar for all habitat types and Ostracoda densities were similar for wetland and agriculture sites.

Most wetland sites grouped together and were defined by Rotifera, Cladocera and Copepoda food resources, except for UBW1 and LBW1 sites that grouped close to UBA1 agriculture site which was associated with Ostracoda HTU. Most Channel sites grouped together and were associated with Insecta HTU, except for SRC4 and BSC1 sites which had a larger contribution of Ostracoda taxa (Fig. 4B). Pelagic invertebrate composition in agriculture sites was intermediate between the wetland and channel sites.

A total of 28 young-of-the-year juvenile Chinook Salmon that were lethally sampled at BSW1, BSW2, Colusa Weir/SRC1, and LBA2 sites were used for wild versus enclosure diet composition comparison. Three or four enclosure fish were used for diet analysis at each site. Additionally, only wild juveniles that were sampled close to when enclosure salmon were euthanized (i.e., from March 20th to April 16th) were used for the analysis. Although the total invertebrate abundance was usually higher in enclosure salmon guts (Fig. 5), we found that, for all the sites, the diet compositions of enclosure and wild juvenile salmon sampled close to the enclosure site were not statistically different (BSW1

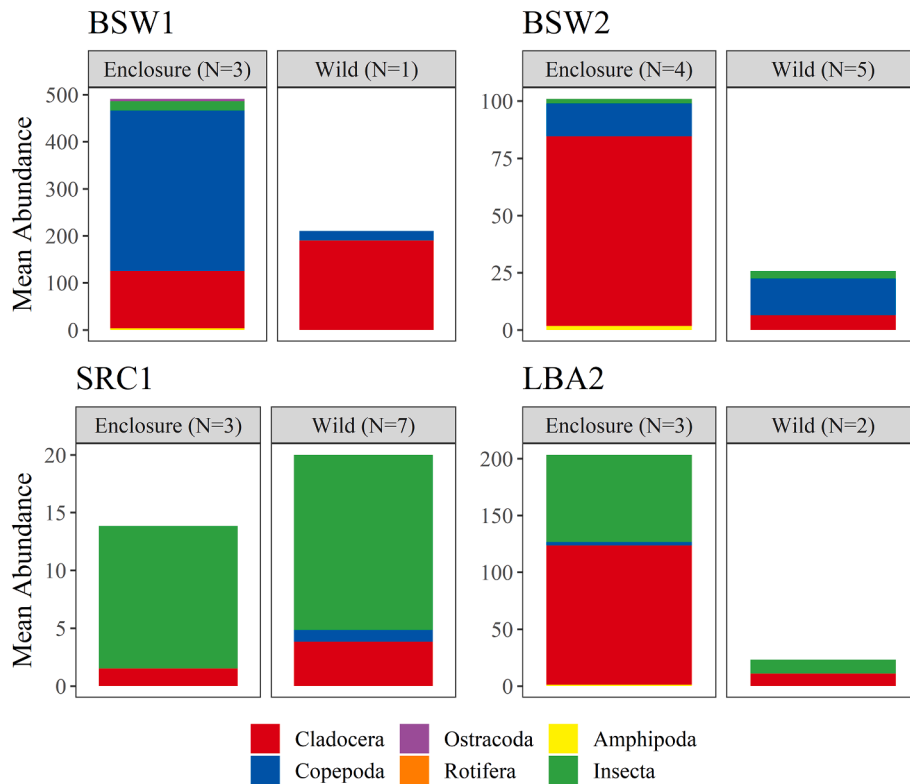


Fig. 5. Enclosure versus wild juvenile diet's mean abundances colored by invertebrate HTU. Gut content comparison was performed for wild young-of-the-year fish that were sampled in the proximity of enclosure sites BSW1, BSW2, SRC1 and LBA2, at the end of March and beginning of April.

ANOSIM significance = 0.25, BSW2 ANOSIM significance = 0.10, SRC1 ANOSIM significance = 0.68 and LBA2 ANOSIM significance = 0.10). Similar to ambient pelagic invertebrate composition we also observed differences in fish diet composition across habitat types. Copepoda and Cladocera were the most common taxa found in salmon diets in the wetland habitats (BSW1 and BSW2 sites), while Insecta was the most common taxa in salmon diets in the channel (SRC1), and salmon diets in

the agricultural site (LBA2) were intermediate between diet composition in the wetland and channel habitats (Fig. 5).

3.3. Enclosure juvenile salmon growth across habitat types

Initial salmon fork length (mm) and weight (g) at the time of enclosure stocking was 47.7 +/- 3.2 mm SD and 1.20 +/- 0.28 g SD. At the end of the six-week experiment, sizes ranged from 53.8 +/- 3.2 mm SD and 1.7 +/- 0.40 g SD at SRC3 (Sacramento River site) to 70.7 +/- 4.2 mm SD and 4.28 +/- 0.74 g SD at BSW2 (Butte Sink site). The average daily growth rates ranged from 0.15 mm d⁻¹ and 0.01 g d⁻¹ at SRC3 to 0.55 mm d⁻¹ and 0.07 g d⁻¹ at BSW2 (Fig. 6). Percent changes in fork length and weight ranged from 12.5% and 28.9% respectively at SRM3 to 47.2% and 255.8% respectively at BSW2.

Overall, growth rates were higher in both wetland and agriculture off-channel sites compared to channel sites. Wetland sites from the Upper Sutter Bypass and Butte Sink (i.e., UBW1, BSW1, and BSW2) had the highest growth rates measured among all fish (Fig. 6). Interestingly, the lowest Sutter Bypass agricultural site (LBA2) and the Sacramento River at Tisdale site (SRC2) showed very similar growth rates. Additionally, the growth rate in Butte Creek channel (BSC1) was higher than in the other channel locations (i.e., from the Sacramento and Feather rivers), and also higher than at LBA2 site.

3.4. Environmental factors influencing juvenile salmon growth

The best AICc model included the interaction between Chlorophyll-a concentration, temperature standard deviation and NMDS2 score (AICc = 0, weight = 60%; Table 3). The second best model included the same variables but with an additive effect (ΔAICc = 2.87, weight = 14%; Table 3). The third top model, which included Chlorophyll-a concentration and temperature standard deviation interactions with NMDS1 score instead of NMDS2, was also found to significantly influence juvenile salmon growth (ΔAICc = 3.32, weight = 11%; Table 3). The top-

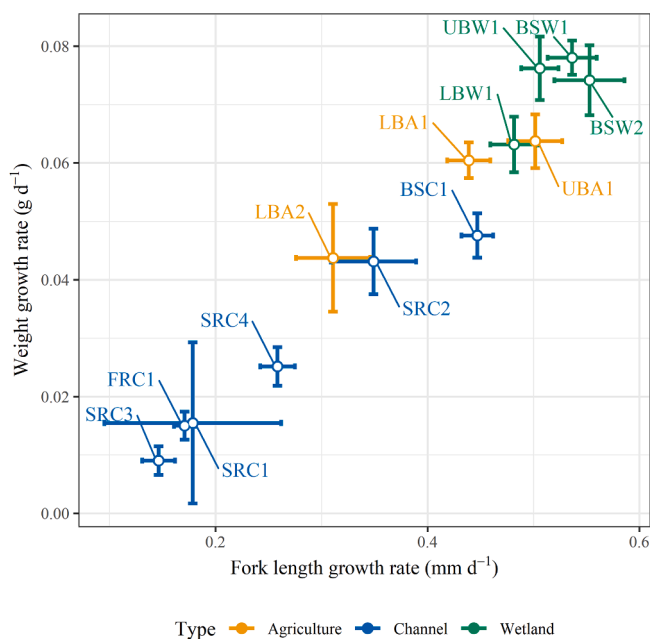


Fig. 6. FL (mm/day) and weight (g/day) 6-weeks growth rates biplot, for each site location. Circles represent mean values and bars represent standard errors.

Table 3

Comparison of SGR mixed effect models. AICc = Akaike's information criterion corrected for small sample size; Δ AICc = difference in AICc score between the given model and the most parsimonious model. AICcWt = model weights. Models are ordered from lowest to highest AICc. Lower AICc scores indicate greater relative model parsimony. Only the first 20 models are shown in this table.

Model	AICc	Δ AICc	AICcWt
NMDS2 \times sdTemp \times meanCHL + (1 Fish_ID) + (1 Location)	617.20	0	0.60
meanCHL + sdTemp + NMDS2 + (1 Fish_ID) + (1 Location)	620.07	2.87	0.14
NMDS1 \times sdTemp \times meanCHL + (1 Fish_ID) + (1 Location)	620.53	3.32	0.11
NMDS2 \times meanCHL + (1 Fish_ID) + (1 Location)	620.78	3.58	0.10
meanCHL + sdTemp + NMDS1 + (1 Fish_ID) + (1 Location)	622.91	5.71	0.03
NMDS2 \times meanTemp \times meanCHL + (1 Fish_ID) + (1 Location)	626.78	9.58	0
NMDS2 + meanCHL + (1 Fish_ID) + (1 Location)	628.50	11.29	0
meanCHL + sdTemp + (1 Fish_ID) + (1 Location)	629.05	11.85	0
meanCHL + meanTemp + NMDS2 + (1 Fish_ID) + (1 Location)	629.81	12.61	0
meanCHL + meanEC + NMDS2 + (1 Fish_ID) + (1 Location)	630.61	13.41	0
meanCHL + meanEC + sdTemp + (1 Fish_ID) + (1 Location)	631.02	13.81	0
meanCHL + sdTemp + logCladocera + (1 Fish_ID) + (1 Location)	631.05	13.84	0
meanCHL + sdTemp + logInsecta + (1 Fish_ID) + (1 Location)	631.07	13.87	0
logInsecta \times sdTemp \times meanCHL + (1 Fish_ID) + (1 Location)	633.41	16.21	0
logCladocera \times sdTemp \times meanCHL + (1 Fish_ID) + (1 Location)	634.12	16.92	0
logCladocera \times meanTemp \times meanCHL + (1 Fish_ID) + (1 Location)	643.27	26.06	0
meanCHL + meanEC + NMDS1 + (1 Fish_ID) + (1 Location)	644.45	27.24	0
logInsecta \times meanTemp \times meanCHL + (1 Fish_ID) + (1 Location)	644.48	27.28	0
NMDS1 \times meanCHL + (1 Fish_ID) + (1 Location)	644.75	27.55	0
meanCHL + meanTemp + (1 Fish_ID) + (1 Location)	645.25	28.05	0

fitted model predicted 1) an increase in SGR with increased temperature standard deviation (i.e., larger temperature variation; sdTemp), 2) a decrease in the minimum SGR value but an increase in the range of SGR values with an increase in NMDS2 score (i.e., decreased contribution of Ostracoda in the pelagic invertebrate community), and 3) either an increase in SGR with increased mean Chlorophyll-a concentration (i.e., higher primary productivity; meanCHL) when $NMDS2 \geq -1$ and when $NMDS2 = -2$ and $sdTemp \leq 0.76$, or a decrease in SGR when $NMDS2 = -2$ and $sdTemp \geq 1.3$ (Fig. 7, Table A5).

4. Discussion

Pacific Salmon are an iconic anadromous species that utilize a mosaic of aquatic habitats to optimize growth, survival and reproductive success across their life cycle (Healey, 1991). This complex migration pattern is one of the things that makes them both exceptionally interesting yet difficult to understand and manage. Each of the variety of life stages and habitats has the potential to be a limiting factor for the species persistence and sustainability over time. Here, we established an experimental and modeling framework to better understand how the use of diverse habitat types during the juvenile salmon rearing stage, a small but very important period of time in the life of a salmon, can disproportionately contribute to their growth. Overall, we found that flooded wetland and agricultural off-channel habitats provided the best conditions for juvenile salmon growth. These results are consistent with recent studies showing floodplain and managed wetland 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; Jeffres et al., 2020). The off-channel mean growth rates found in this study were, however, lower than the juvenile salmon growths found in the Yolo Bypass (a similar flood bypass in the Central Valley), for both free-swimming and rice fields enclosure fish (0.41–0.53 mm/day in the Sutter Bypass versus 0.55–0.8 mm/day in Sommer et al., 2001; Katz et al., 2017) The channel sites' mean growth rate of 0.25 mm/day was also slightly lower than the growth found in a mark-recapture study in the Upper Sacramento River (mean growth rate of 0.33 mm/day; Kjelson et al., 1982). We hypothesize that the main differences in growth pertains to differences in the amount of natural flooding (this study was conducted during a year with extensive natural flooding compared with previous experimental years), and that a better understanding of the mechanisms involved in the

system productivity is key to identify optimal juvenile salmon growth conditions across the landscape.

4.1. Channel versus off-channel ecosystem mechanisms

The above normal water year in 2019 created hydrological conditions that allowed for a productive and dynamic food web in the Butte Sink and Sutter Bypass. Throughout our study period we observed both large high flow events as well a recession following the flow events that resulted in increased residence time and pelagic invertebrate abundance within the off-channel habitats. Dynamic hydrology creates conditions that allow for the production as well as the transport of food web productivity both within the floodplain as well as export locally derived production to downstream locations (Winemiller, 2004; Ahearn et al., 2006; Furst et al., 2014; Correa and Winemiller, 2018). Heterogeneity of habitats and hydrology can result in differing water quality, pelagic invertebrate production, and juvenile salmon growth rates (Bellmore et al., 2013; Górski et al., 2013; Pander et al., 2018; Jeffres et al., 2020; Corline et al., 2021). Despite the diversity of habitats used in our study, large flooding events created conditions where in-channel and off-channel habitats followed very similar patterns at high flows. However, when high flows receded, velocities slowed in the off-channel habitats and residence times increased. This resulted in an increase in water temperature and food web development in the off-channel habitats (Fig. 3). Numbers of pelagic invertebrate during this time were often 10 to 100 times more abundant in the off channel habitats compared to the river channels. These off-channel habitats were thus found to be strong engines of productivity allowing increased food production and enhanced fish growth. This is similar to other studies that found following large flood events primary and secondary production can be prolific (Van den Brink et al., 1992; Ahearn et al., 2006; Grosholz and Gallo, 2006; McInerney et al., 2017; Ndehedehe et al., 2021).

4.2. Biotic and abiotic factors affecting juvenile salmon growth across the landscape

Chlorophyll-a concentration, which inform on the system primary productivity was one of the three most important factor influencing juvenile salmon growth rates observed during the experiment, with increased productivity correlated to higher juvenile salmon growth. Channel sites, that were characterized by the lowest Chlorophyll-a

concentrations throughout the entire experiment, exhibited the slowest fish growth, while off-channel wetland sites, which had the highest Chlorophyll-a levels were associated to the highest growth rates. This is consistent with the idea that off-channel wetlands, and to a certain extent agriculture sites, can act as functional floodplain and enhance juvenile fish production by stimulating bottom-up production of phytoplankton carbon (Junk et al., 1989).

Water temperature standard deviation was the second important factor influencing fish growth, with an increase in water temperature variability positively correlated to salmon growth. Water temperature has been shown to be an important determinant of juvenile salmon growth, through a direct interaction with food density (Brett et al., 1969; Jonsson et al., 2001; Myrick and Cech, 2001; Lusardi et al., 2020). Furthermore, the large water temperature variability observed in off-channel habitats was the result of multiple flooding events followed by increased water residence time, which likely provided optimum environmental conditions for the development of a productive lower trophic food web and would explain the high juvenile salmon growth observed in those habitats.

NMDS2 which is associated with the proportion of Ostracoda HTU, and to a lesser extent NMDS1 which is associated with the relative contribution of Insecta versus Copepoda, Cladocera and Rotifera in the environment, were also found to locally influence juvenile salmon growth. Channel enclosure locations, which had large NMDS2 score and were associated with a lower contribution of Ostracoda and a higher contribution of Insecta in the pelagic invertebrate community, exhibited the lowest juvenile salmon growth rates, while off-channel wetland and agriculture sites, which were defined by a higher proportion of Ostracoda, as well as Cladocera, Copepoda and Rotifera, exhibited higher juvenile salmon growth rates. These results suggest that the relative contribution, more than the absolute abundance, of pelagic invertebrate taxa had an impact on salmon growth. Comparatively, gut contents of juvenile Chinook Salmon reared in Yolo Bypass' agricultural floodplain in 2012 contained over 85% of Cladocera species *Daphnia pulex*, and had some of the highest growth rates recorded for Chinook Salmon in the California Central Valley (Katz et al., 2017). Furthermore, multiple studies of juvenile salmon diet in other lentic water bodies also found that salmon selectively fed on large *Daphnia* spp. (Craddock et al., 1976; Morrison, 1983; Koehler et al., 2006). Similar to this study's agriculture sites, high Ostracoda abundances have also been observed in fallowed rice fields from the Yolo Bypass (Corline et al., 2017) and other plant-rich floodplains (Pereira et al., 2017; Szlauer-Lukaszewska and Pešić, 2020), providing an alternative food resource for juvenile salmon.

Importantly, we found that those three factors had an interactive effect on juvenile salmon growth rates. For instance, for low NMDS2 and high water temperature variability, SGR decreased with increased Chlorophyll-a concentration. One assumption could be that an increased hydrology dynamic in channel sites with low productivity might have

created less favorable conditions for juvenile salmon and led to a decrease in growth, even if Chlorophyll-a concentration increased. Additionally, the larger variability in SGR values observed with combined increase in NMDS2 and Chlorophyll-a concentration values could be explained by the fact that 1) an increase in Chlorophyll-a concentration correlates with higher growth, and 2) a higher NMDS2 score is associated with channel sites exhibiting more diverse SGRs (e.g., SRC2 had SGR closer to off-channel agriculture sites than other river sites, while SRC3 had the lowest SGR), thus resulting in the expression of a larger SGR range.

4.3. Inference from experimental framework to natural system and management implications

While we acknowledge that the use of enclosures restricted salmon movements, which could have influenced food access and competition for resources, the similarities found between wild and experimental salmon diets suggest that enclosure growth experiments can be considered as a powerful tool to reflect wild juvenile Chinook Salmon feeding and growth patterns.

This study also highlighted the potential for this managed flood bypass to act as a proxy for natural floodplain and can provide high quality rearing habitat for all CCV Chinook Salmon, when it is accessible to them. Our results are therefore consistent with similar results for the downstream Yolo Bypass, another large managed floodplain (Sommer et al., 2001; Katz et al., 2017). Currently the limiting factor to get water, including fish, into the off-channel floodplain habitat in the CCV is often the elevation of various weirs that allow water to spill from the river channel into the flood bypass system. The wet conditions in 2019 allowed multiple spilling events to occur, however drier years might not provide as much access to productive habitats. Being able to collect data across a variety of water year types will help to tell a better story of how the Butte Sink and Sutter Bypass function across a variety of hydrological conditions. These data will provide information to resource managers to think more holistically about how managed off-channel habitats can benefit juvenile salmon across various hydrological conditions.

Additionally, two channel sites (SRC2 and BSC1) were found to have relatively high juvenile salmon growth rates among channel enclosures (Fig. 5). Taxa identified in juvenile salmon's diet from the Butte Sink channel site (BSC1) were also found to differ from the ambient pelagic invertebrate community sampled there, and were more similar to adjacent off-channel salmon's diet. These results suggest that fish from those sites might have benefited from food resources being transported from productive off-channel sites during flood events. Resource subsidy, through aquatic and terrestrial nutrient input, has been found to improve aquatic fish production (Polis et al., 1997; Kawaguchi and Nakano, 2001; Correa and Winemiller, 2018), and this management action could be considered to enhance juvenile salmon growths, by

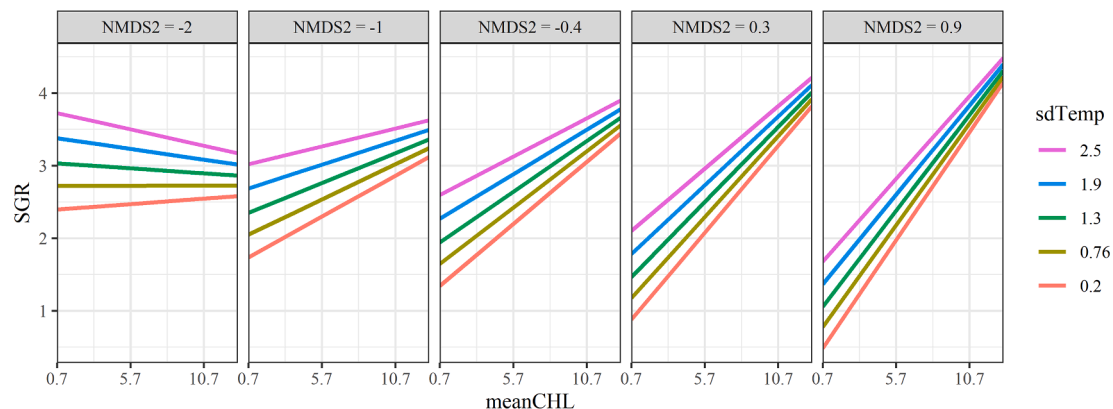


Fig. 7. Enclosure fish SGR predictions from the best AICc ranked mixed effect model in Table 3, for each combination of NMDS2, meanCHL and sdTemp values.

supporting the transfer of allochthon invertebrate species from the productive floodplain wetlands and agricultural fields to channel sites.

5. Conclusion

With strong modification of the CCV landscape, the access to the mosaic of aquatic habitats that California Chinook Salmon rely on throughout their lifetime has become more difficult, which has likely contributed to their decline (Yoshiyama et al., 2001). Particularly, floodplains and other off-channel habitats have drastically decreased, and the availability of the remnant ones is dependent on large fluctuations in river flows to push water out of the channel into the adjacent habitats. This study has highlighted the importance of those ephemeral habitats to the aquatic food web and subsequent growth of vulnerable CCV juvenile salmon across a diverse landscape. The experimental framework we presented here, and the use of fish growth as an indicator of habitat quality, can help resource managers prioritize and implement restoration actions that will support the physical and biological processes important for floodplains to resume functioning.

CRedit authorship contribution statement

Flora Cordoleani: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **Eric Holmes:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – review & editing. **Miranda Bell-Tilcock:** Investigation, Writing – review & editing. **Rachel C. Johnson:** Conceptualization, Methodology, Writing – review & editing. **Carson Jeffres:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Funding for this project was provided by the US Fish and Wildlife Service through a Central Valley Project Improvement Act (CVPIA) grant, agreement number: F19AC00062. In addition, we would like to acknowledge the California Department of Water Resources for funding a concurrent project that enhanced the work that could be done on this project. We would like to thank Sutter Mutual Water Company, US Fish and Wildlife Service, California Waterfowl Association, Motna Farms, and Lundberg Family Farms for site access and project support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.108681>.

References

- Ahearn, D.S., Viers, J.H., Mount, J.F., Dahlgren, R.A., 2006. Priming the productivity pump: flood pulse driven trends in suspended algal biomass distribution across a restored floodplain. *Freshw. Biol.* 51 (8), 1417–1433. <https://doi.org/10.1111/j.1365-2427.2006.01580.x>.
- Akaike, H. (Ed.), 1973. *2nd International Symposium on Information Theory*. Akadémiai Kiadó, Budapest, Hungary.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bellmore, J.R., Baxter, C.V., Martens, K., Connolly, P.J., 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. *Ecol. Appl.* 23 (1), 189–207. <https://doi.org/10.1890/12-0806.1>.
- Brett, J.R., Shelbourn, J.E., Shoop, C.T., 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *J. Fish. Board Canada* 26 (9), 2363–2394. <https://doi.org/10.1139/f69-230>.
- Buer, K., Forwalter, D., Kissel, M., Stohler, B., 1989. The middle Sacramento River: human impacts on physical and ecological processes along a meandering river. USDA Forest Service Gen. Tech. Rep. PSW-110. 11.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer-Verlag, New York.
- Cordoleani, F., Satterthwaite, W., Daniels, M., Johnson, M., 2020. Using life cycle models to identify monitoring gaps for central valley spring-run chinook salmon. *SFEWS* 18 (4). <https://doi.org/10.15447/sfeWS>.
- Corline, N.J., Sommer, T., Jeffres, C.A., Katz, J., 2017. Zooplankton ecology and trophic resources for rearing native fish on an agricultural floodplain in the Yolo Bypass California. *Wetlands Ecol. Manage.* 25 (5), 533–545. <https://doi.org/10.1007/s11273-017-9534-2>.
- Corline, N.J., Peek, R.A., Montgomery, J., Katz, J.V.E., Jeffres, C.A., 2021. Understanding community assembly rules in managed floodplain food webs. *Ecosphere* 12 (2). <https://doi.org/10.1002/ecs2.3330>.
- Correa, S.B., Winemiller, K., 2018. Terrestrial–aquatic trophic linkages support fish production in a tropical oligotrophic river. *Oecologia* 186 (4), 1069–1078. <https://doi.org/10.1007/s00442-018-4093-7>.
- Craddock, D.R., Blahm, T.H., Parente, W.D., 1976. Occurrence and utilization of zooplankton by juvenile chinook salmon in the lower Columbia River. *Trans. Am. Fish. Soc.* 105 (1), 72–76.
- [CVFMPP] Central Valley Flood Management Planning Program, 2010. State Plan of Flood Control Descriptive Document.
- Dudgeon, D., 2019. Multiple threats imperil freshwater biodiversity in the Anthropocene. *Curr. Biol.* 29 (19), R960–R967. <https://doi.org/10.1016/j.cub.2019.08.002>.
- Feyrer, F., Sommer, T., Harrell, W., 2006. Managing floodplain inundation for native fish: production dynamics of age-0 splittail (*Pogonichthys macrolepidotus*) in California's Yolo Bypass. *Hydrobiologia* 573 (1), 213–226. <https://doi.org/10.1007/s10750-006-0273-2>.
- Friberg, N., Angelopoulos, N.V., Buijse, A.D., Cowx, I.G., Kail, J., Moe, T.F., Moir, H., O'Hare, M.T., Verdonschot, P.F.M., Wolter, C., 2016. Chapter Eleven - Effective River Restoration in the 21st Century: From Trial and Error to Novel Evidence-Based Approaches. In: Dumbrell, A.J., Kordas, R.L., Woodward, G. (Eds.), *Advances in Ecological Research, Large-Scale Ecology: Model Systems to Global Perspectives*. Academic Press, pp. 535–611. <https://doi.org/10.1016/bs.aecr.2016.08.010>.
- Furst, D., Aldridge, K., Shiel, R., Ganf, G., Mills, S., Brookes, J., 2014. Floodplain connectivity facilitates significant export of zooplankton to the main River Murray channel during a flood event. *Inland Waters* 4 (4), 413–424. <https://doi.org/10.5268/IW-4.4.696>.
- Goertler, P., Jones, K., Cordell, J., Schreier, B., Sommer, T., 2018. Effects of extreme hydrologic regimes on juvenile Chinook salmon prey resources and diet composition in a large river floodplain. *Trans. Am. Fish. Soc.* 147 (2), 287–299. <https://doi.org/10.1002/tafs.10028>.
- Górski, K., Collier, K.J., Duggan, I.C., Taylor, C.M., Hamilton, D.P., 2013. Connectivity and complexity of floodplain habitats govern zooplankton dynamics in a large temperate river system. *Freshw. Biol.* 58 (7), 1458–1470. <https://doi.org/10.1111/fwb.12144>.
- Górski, K., De Leeuw, J.J., Winter, H.V., Vekhov, D.A., Minin, A.E., Buijse, A.D., Nagelkerke, L., a. J., 2011. Fish recruitment in a large, temperate floodplain: the importance of annual flooding, temperature and habitat complexity. *Freshw. Biol.* 56, 2210–2225. <https://doi.org/10.1111/j.1365-2427.2011.02647.x>.
- Grosholz, E., Gallo, E., 2006. The influence of flood cycle and fish predation on invertebrate production on a restored California floodplain. *Hydrobiologia* 568 (1), 91–109. <https://doi.org/10.1007/s10750-006-0029-z>.
- Healey, M.C., 1991. *Life History of Chinook Salmon (Oncorhynchus tshawytscha)*. In: Groot, C., Margolis, L. (Eds.), *Pacific Salmon Life Histories*. UBC Press, Vancouver, pp. 311–395.
- Hendrix, A.N., Jennings E., Criss A., Danner E., Sridharan V., Greene C.M., Imaki H., Lindley S.T., 2017. Model description for the Sacramento River winter-run Chinook Salmon Life Cycle Model. Appendix H of California WaterFix Biological Opinion prepared by NOAA Fisheries.
- Holmes, E.J., Jeffres, C.A., 2021. Juvenile chinook salmon weight prediction using image-based morphometrics. *North Am. J. Fish. Manag.* 41 (2), 446–454. <https://doi.org/10.1002/nafm.10533>.
- Holmes, E.J., Saffarinia, P., Rypel, A.L., Bell-Tilcock, M.N., Katz, J.V., Jeffres, C.A., Kimirei, I.A., 2021. Reconciling fish and farms: methods for managing California rice fields as salmon habitat. *PLoS One* 16 (2), e0237686. <https://doi.org/10.1371/journal.pone.0237686>.
- Humphries, P., King, A.J., Koehn, J.D., 1999. Fish, flows and flood plains: links between freshwater fishes and their environment in the murray-darling river system, Australia. *Environ. Biol. Fishes* 56 (1–2), 129–151. <https://doi.org/10.1023/A:1007536009916>.
- Jeffres, C.A., Holmes, E.J., Sommer, T.R., Katz, J.V.E., Hovel, R.A., 2020. Detrital food web contributes to aquatic ecosystem productivity and rapid salmon growth in a managed floodplain. *PLoS One* 15 (9), e0216019. <https://doi.org/10.1371/journal.pone.0216019>.

- Jeffres, C.A., Opperman, J.J., Moyle, P.B., 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. *Environ Biol Fish* 83 (4), 449–458. <https://doi.org/10.1007/s10641-008-9367-1>.
- Jodun, W.A., Millard, M.J., Mohler, J., 2002. The effect of rearing density on growth, survival, and feed conversion of juvenile Atlantic sturgeon. *North Am. J. Aquaculture* 64 (1), 10–15.
- Johnson, R.C., Lindley, S.T., 2016. Central Valley Recovery Domain. Pages 48 – 63 in T. H. Williams, B.C. Spence, D.A. Boughton, R.C. Johnson, L. Crozier, N. Mantua, M. O'Farrell, and S.T. Lindley. 2016. Viability assessment for Pacific salmon and steelhead listed under the Endangered Species Act: Southwest. 2 February 2016 Report to National Marine Fisheries Service – West Coast Region from Southwest Fisheries Science Center, Fisheries Ecology Division 110 Shaffer Road, Santa Cruz, California 95060.
- Jonsson, B., Forseth, T., Jensen, A.J., Naeije, T.F., 2001. Thermal performance of juvenile Atlantic Salmon, *Salmo salar* L. *Funct. Ecol.* 15, 701–711. <https://doi.org/10.1046/j.0269-8463.2001.00572.x>.
- Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain system. *Can. Special Publ. Fish. Aquat. Sci.* 106, 110–127.
- Kail, J., Brabec, K., Poppe, M., Januschke, K., 2015. The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: a meta-analysis. *Ecol. Ind.* 58, 311–321. <https://doi.org/10.1016/j.ecolind.2015.06.011>.
- Karanovic, I. (Ed.), 2012. *Recent Freshwater Ostracods of the World*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- Katz, J.V.E., Jeffres, C., Conrad, J.L., Sommer, T.R., Martinez, J., Brumbaugh, S., Corline, N., Moyle, P.B., Dias, J.M., 2017. Floodplain farm fields provide novel rearing habitat for Chinook salmon. *PLoS One* 12 (6), e0177409. <https://doi.org/10.1371/journal.pone.0177409>.
- Kawaguchi, Y., Nakano, S., 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream: Riparian prey contribution to salmonids. *Freshw. Biol.* 46 (3), 303–316. <https://doi.org/10.1046/j.1365-2427.2001.00667.x>.
- Kelley, R., 1989. *Battling the Inland Sea: American Political Culture, Public Policy, and the Sacramento Valley, 1850–1986*, 1st edition. University of California Press, Berkeley.
- Kjelson, M.A., Raquel, P.F., Fisher, F.W., 1982. Life history of fall-run juvenile Chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin Estuary, California. In: *Estuarine comparisons*. Academic Press, New York, pp. 393–411.
- Koehler, M.E., Fresh, K.L., Beauchamp, D.A., Cordell, J.R., Simenstad, C.A., Seiler, D.E., 2006. Diet and bioenergetics of lake-rearing juvenile chinook salmon in Lake Washington. *Trans. Am. Fish. Soc.* 135 (6), 1580–1591. <https://doi.org/10.1577/T05-178.1>.
- Kruskal, J.B., 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29 (1), 1–27. <https://doi.org/10.1007/BF02289565>.
- Kruskal, J.B., 1964b. Nonmetric multidimensional scaling: A numerical method. *Psychometrika* 29 (2), 115–129. <https://doi.org/10.1007/BF02289694>.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129 (2), 271–280. <https://doi.org/10.1007/s004420100716>.
- Lusardi, R.A., Hammock, B.G., Jeffres, C.A., Dahlgren, R.A., Kiernan, J.D., 2020. Oversummer growth and survival of juvenile coho salmon (*Oncorhynchus kisutch*) across a natural gradient of stream water temperature and prey availability: an in situ enclosure experiment. *Can. J. Fish. Aquat. Sci.* 77 (2), 413–424. <https://doi.org/10.1139/cjfas-2018-0484>.
- McInerney, P.J., Stoffels, R.J., Shackleton, M.E., Davey, C.D., 2017. Flooding drives a macroinvertebrate biomass boom in ephemeral floodplain wetlands. *Freshw. Sci.* 36 (4), 726–738. <https://doi.org/10.1086/694905>.
- McReynolds, T.R., Garman, C.E., Ward, P.D., Plemons, S.L., 2006. Butte and Big Chico creeks spring-run Chinook salmon, *Oncorhynchus tshawytscha* life history investigation 2004–2005. Administrative Report No. 2006-4.
- Merritt, R.W., Cummins, K.W., Berg, M.B. (Eds.), 2008. *Introduction to Aquatic Insects in North America*, 4th, edition. ed. Kendall Hunt Publishing Company, Dubuque, Iowa.
- Morrison, B.R.S., 1983. Observations on the food of juvenile Atlantic salmon, *Salmo salar* L, reared in a Scottish hill loch. *J. Fish Biol.* 23 (3), 305–313. <https://doi.org/10.1111/j.1095-8649.1983.tb02909.x>.
- Myrick, C.A., Cech, J.J., 2001. Temperature Effects on Chinook Salmon and Steelhead. Bay-Delta Modeling Forum Technical Publication 01-1.
- Ndehedehe, C.E., Onojeghuo, A.O., Stewart-Koster, B., Bunn, S.E., Ferreira, V.G., 2021. Upstream flows drive the productivity of floodplain ecosystems in tropical Queensland. *Ecol. Ind.* 125, 107546. <https://doi.org/10.1016/j.ecolind.2021.107546>.
- Opperman, J.J., Moyle, P.B., Larsen, E.W., Florsheim, J.L., Manfree, A.D., 2017. *Floodplains: Processes and Management for Ecosystem Services*, 1st ed. University of California Press.
- Pander, J., Mueller, M., Geist, J., 2018. Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. *Biol. Conserv.* 217, 1–10. <https://doi.org/10.1016/j.biocon.2017.10.024>.
- Pereira, L.C., Lansac-Tóha, F.A., Martens, K., Híguti, J., 2017. Biodiversity of ostracod communities (Crustacea, Ostracoda) in a tropical floodplain. *Inland Waters* 7 (3), 323–332. <https://doi.org/10.1080/20442041.2017.1329913>.
- Peterson, J.T., Duarte, A., 2020. Decision analysis for greater insights into the development and evaluation of Chinook salmon restoration strategies in California's Central Valley. *Restor. Ecol.* 28 (6), 1596–1609. <https://doi.org/10.1111/rec.13244>.
- Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28 (1), 289–316. <https://doi.org/10.1146/annurev.ecolsys.28.1.289>.
- R Core Team, 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Sabater, S., Bregoli, F., Acuña, V., Barceló, D., Elosegi, A., Ginebreda, A., Marcé, R., Muñoz, I., Sabater-Liesla, L., Ferreira, V., 2018. Effects of human-driven water stress on river ecosystems: a meta-analysis. *Sci. Rep.* 8, 11462. <https://doi.org/10.1038/s41598-018-29807-7>.
- Scharbert, A., Borcherding, J., 2013. Relationships of hydrology and life-history strategies on the spatio-temporal habitat utilisation of fish in European temperate river floodplains. *Ecol. Ind.* 29, 348–360. <https://doi.org/10.1016/j.ecolind.2013.01.009>.
- Sommer, T., Baxter, R., Herbold, B., 1997. Resilience of Splittail in the Sacramento-San Joaquin Estuary. *Trans. Am. Fish. Soc.* 126 (6), 961–976.
- Sommer, T.R., Nobriga, M.L., Harrell, W.C., Batham, W., Kimmerer, W.J., 2001. Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. *Can. J. Fish. Aquat. Sci.* 58 (2), 325–333. <https://doi.org/10.1139/f00-245>.
- Staggs, M.D., Otis, K.J., 1996. Factors affecting first-year growth of fishes in Lake Winnebago, Wisconsin. *North Am. J. Fish. Manag.* 16 (3), 608–618.
- Szlauer-Lukaszewska, A., Pesić, V., 2020. Habitat factors differentiating the occurrence of Ostracoda (Crustacea) in the floodplain of a small lowland River Krapiel (N-W Poland). *Knowl. Manag. Aquat. Ecosyst.* (421), 23. <https://doi.org/10.1051/kmae/2020012>.
- Thorp, J., Covich, A., 2009. *Ecology and Classification of North American Freshwater Invertebrates*, 3rd Edition. Academic Press.
- Van den Brink, F.W.B., De Leeuw, J.P.H.M., Van Der Velde, G., Verheggen, G.M., 1992. Impact of hydrology on the chemistry and phytoplankton development in floodplain lakes along the Lower Rhine and Meuse. *Biogeochemistry* 19 (2), 103–128. <https://doi.org/10.1007/BF00000798>.
- Ward, J.V., Tockner, K., Schiemer, F., 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Res. Manage.* 15, 125–139. [https://doi.org/10.1002/\(SICI\)1099-1646\(199901/06\)15:1/3<125::AID-RRR523>3.0.CO;2-E](https://doi.org/10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E).
- Whipple, A., Grossinger, R., Rankin, D., Stanford, B., Askevold, R., 2012. Sacramento-San Joaquin Delta Historical Ecology Investigation: Exploring Pattern and Process. Prepared for the California Department of Fish and Game and Ecosystem Restoration Program. A report of SFEI-ASC's Historical Ecology Program, Publication #672, San Francisco Estuary Institute-Aquatic Science Center, Richmond, CA.
- Williams, J.G., 2006. Central valley salmon: a perspective on chinook and steelhead in the Central Valley of California. *San Francisco Estuary and Watershed. Science* 4 (3). <https://doi.org/10.15447/sfews>.
- Winemiller, K.O., 2004. Floodplain river food webs: generalizations and implications for fisheries management, in: *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries*. Presented at the Phnom Penh: Mekong River Commission, Welcomme, R. L., and T. Petr, Eds., pp. 285–309.
- Yoshiyama, R.M., Fisher, F.W., Moyle, P.B., 1998. Historical abundance and decline of chinook salmon in the Central Valley Region of California. *North Am. J. Fish. Manag.* 18 (3), 487–521.
- Yoshiyama, R.M., Gerstung, E.R., Fisher, F.W., Moyle, P.B., 2001. Historical and present distribution of Chinook salmon in the Central Valley of California, in Brown, R. L. 2001. *Contributions to the Biology of Central Valley Salmonids*. Volumes 1 & 2. California Department of Fish and Game Fish Bulletin 179. 1, 699.