Floodplain trophic subsidies in a modified river network: managed foodscapes of the future?

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Abstract

Context Cross-boundary subsidies create important growth opportunities for a range of taxa. In modified river systems, remnant patches of floodplain and flood bypasses become ephemeral hotspots of zooplankton production, however, the extent to which these prey items are (or could be) transported downstream is unclear.

Objectives We investigated the diet of juvenile salmon under varying hydroclimatic conditions to assess the importance of floodplain-produced prey subsidies in an otherwise food-scarce region.

Methods Juvenile salmon (n = 3033) and zooplankton were sampled across the California Central Valley Sacramento-San Joaquin River Delta in 2014–2018, incorporating a range of climatic conditions including drought and flood. Salmon stomach fullness and diet composition, and ambient zooplankton densities were used to assess spatiotemporal patterns in prey production and consumption.

Results Floodplain-produced cladocerans provided ephemeral food pulses to juvenile salmon in downstream riverine habitats. Salmon had the fullest stomachs in wetter years (2016–2017) and the emptiest stomachs in the final year of a multi-year drought (2015). Cladoceran abundances in the water column and salmon diets were highest during wet periods and below floodplains, and decreased with increasing distance downstream, consistent with flow-mediated trophic subsidies.

Conclusions These data emphasize the importance of maintaining diverse, interconnected habitats to support resilient fish populations and the potential for managing floodplains to boost prey production and delivery. Here, the inundation of a flood bypass (or lack of) played a pivotal role shaping the juvenile salmon foodscape. As freshwater ecosystems are increasingly transformed by large-scale engineering, it is important to coordinate infrastructure, habitat and flow modifications to maximize climate resilience and trophic benefits to target species.

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Introduction

Subsidies—defined in ecology as the flux of energy or materials across space—shape food web dynamics and support key ecosystem services. These cross-boundary resource flows create critical linkages between ecosystems and taxa, driving population productivity, stability, and food web structure (Polis et al. 1997; Richardson and Sato 2015). Understanding the spatiotemporal dynamics of subsidies, their sensitivity to environmental change, and the degree to which species or communities utilize them, is an important consideration in ecosystem management and conservation biology (Wipfli 2005; Richardson and Sato 2015). In river systems, economically important and imperiled fishes are often heavily supported by terrestrial subsidies, either directly via terrestrial invertebrates or indirectly via terrestrially sourced nutrients (Kawaguchi et al. 2003; Richardson and Sato 2015). Yet, there are limited examples where such trophic subsidies have been empirically quantified and formally incorporated into management decisions or conservation plans.

The exchange of trophic resources between floodplains and adjacent river channels provides an oft-cited example of dynamic cross-system subsidies. As the primary interface between aquatic and terrestrial ecosystems, river floodplains are characterized by significant physical and biological exchange (Junk et al. 1989; Polis et al. 1997). Nutrients and labile terrestrial organic material mobilized in flooded soils are used for in situ production on the floodplain and exported back to the river during drainage periods and high flows (Thorp and Delong 1994; Schemel et al. 2004; Winemiller 2004; Ahearn et al. 2006). Terrestrial plants in flooded areas also break down into detritus, fueling primary production and feeding zooplankton (Bayley 1995; Jeffres et al. 2020). The 'flood pulse concept' describes the river-floodplain as an interconnected system, where the inundation of floodplains by flood pulses exports nutrients, organic matter and organisms into the river, driving riverine productivity (Junk et al. 1989; Tockner et al. 2000).

Incorporating the dynamic and ephemeral nature of riverscapes into infrastructure design and landscape management is challenging, but spatially contextualizing the interactions between food production, food transport, and consumer foraging behavior using a 'foodscape' framework could guide management efforts to maximize benefits to fish of economic and conservation value. The term 'foodscape' (often used interchangeably with 'food environment') describes landscape scale variation in food availability, and has most commonly been applied to investigate the organization and utilization of food delivery systems in human societies (Vonthron et al. 2020). Rossi (2020) first used the term in an aquatic setting, building on the 'resource shed' concept to describe the shifting mosaic of habitats supplying food to juvenile salmonids (*Onchorynchus* spp.) across river networks (Power and Rainey 2000; Wipfli and Baxter 2010). The location, abundance and phenology of invertebrate prey along the migratory corridor create variable growth opportunities for salmonids and underpin the diverse life history tactics displayed within species and even within populations (Rossi 2020; Cordoleani et al. 2022). Foodscapes rely on connectivity between the consumer and their food, and are thus highly dynamic, shaped by variation in resource abundance in time and space, as well as the abundance and foraging behavior of the consumer (Searle et al. 2007; Dwinnell et al. 2019). Historically, large-scale landscape alterations have had major impacts on the diversity, connectivity and productivity of riverine foodscapes (Opperman et al. 2010). Today, there is growing interest in mitigating these impacts by using or modifying existing infrastructure to increase the growth potential of target consumer species. For example, weirs and levees could be lowered to increase among-habitat connectivity and allow consumers to access additional prey fields, or—in subsidy-driven foodscapes—actions might be taken to increase the strength or frequency of fluxes into recipient areas. Designing effective management actions requires a comprehensive understanding of the mechanisms driving foodscape dynamics, yet managers often lack key information regarding the spatial extent and timing of subsidies, the conditions that control them, and their utilization by consumer species.

This study focuses on the diets of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) inhabiting the

highly altered California Central Valley Sacramento-San Joaquin River Delta (hereon 'Delta'), and the role of floodplain subsidies in this otherwise food-scarce region. Central Valley Chinook salmon are at the southern edge of their native range and populations have declined significantly due to multiple interacting stressors, including habitat loss and degradation, water extraction, introduced predators, and extreme multi-year droughts (Katz et al. 2013; Nobriga et al. 2021). Historically, the Central Valley boasted a rich mosaic of floodplain, riparian and wetland habitats that provided critical feeding opportunities to a variety of resident and migratory fishes (Whipple et al. 2012). Today, like many river systems in North America and Europe, the region has lost most of its floodplains to land use change, dams, levees and water diversions, impairing important ecosystem services such as contaminant removal, groundwater recharge and nutrient cycling (Tockner and Stanford 2002; Whipple et al. 2012). Habitat modification has been particularly dramatic in the freshwater Delta, which is now dominated by agricultural and urban developments. Its waterways have been simplified and channelized to improve water conveyance, and the water quality is often impaired by elevated contaminant loads and high temperatures (Whipple et al. 2012; Stewart et al. 2020). Furthermore, the base and top of the food web has been transformed by introduced clams (e.g., *Corbicula fluminea*) and piscivorous predators (e.g., Centrarchids) (Sommer et al. 2007; Greene et al. 2011). Survival rates of salmon smolts through the Delta in mid to late spring are often low (Buchanan et al. 2018; Michel et al. 2015), but relatively little is known about the fate of the millions of fry that enter the Delta each year in winter and early spring (Williams 2012; Johnson et al. 2017; Sturrock et al. 2020). Given that smoltification timing and ocean survival rates can be strongly influenced by size and growth rate (Sogard 1997; Thorpe et al. 1998; Woodson et al. 2013), the fate of these early migrants is heavily dependent on habitat and food availability in the Delta during this critical period. Many assume that early migrants experience negligible survival, however, juvenile catch data and otolith (earstone) reconstructions show that large numbers of fry can successfully rear in the Delta, suggesting areas and/or periods of suitable habitat quality (Miller et al. 2010; del Rosario et al. 2013; Sturrock et al.

2015; Phillis et al. 2018; Munsch et al. 2020; Sturrock et al. 2020).

Two major floodplains drain directly into the Delta: the Yolo Bypass and Cosumnes River floodplain (Fig. 1). Both floodplains are highly productive, producing zooplankton densities orders of magnitude higher than the adjacent river channels (Ahearn et al. 2006; Grosholz and Gallo 2006; Corline et al. 2017; Katz et al. 2017). The Yolo Bypass is a flood control structure that allows water to enter during high flow events, typically inundating only in average to wet years, but not during dry years. During the non-flooding season the Yolo Bypass is managed for agriculture and wetland habitats. Conversely, the Cosumnes River floodplain is situated on the lower reaches of an unregulated river and inundates almost every year. Invertebrate communities on these floodplains tend to be dominated by cladocerans, particularly large-bodied species such as *Daphnia pulex* that thrive in their relatively warm, slow-moving waters (Davidson et al. 2000; Corline et al. 2021). Both of these floodplains support exceptionally high growth rates in juvenile salmon that are experimentally reared on them (Sommer et al. 2001; Jeffres et al. 2008; Katz et al. 2017), resulting in considerable interest in enhancing fish passage opportunities to enable more frequent volitional access to them. However, the extent to which these floodplains subsidize the downstream food web is unknown. Even without direct access to them, these productive habitats could still supplement the diet of fishes in the Delta via water-to-water subsidies (i.e., floodplain water carrying invertebrate prey downstream during drainage periods) (Polis et al. 1997; Farly et al. 2019). Here, we analyzed spatiotemporal patterns in zooplankton densities, juvenile salmon stomach fullness, and salmon diet composition across the Delta landscape from 2014 to 2018 (Fig. 1). Samples were collected across a wide range of hydrologic conditions to explore the following hypotheses:

1. Zooplankton densities: In wetter years, increased invertebrate production on floodplains and increased advection downstream will result in elevated cladoceran densities below floodplain drainage points, extending further downstream during high flows.
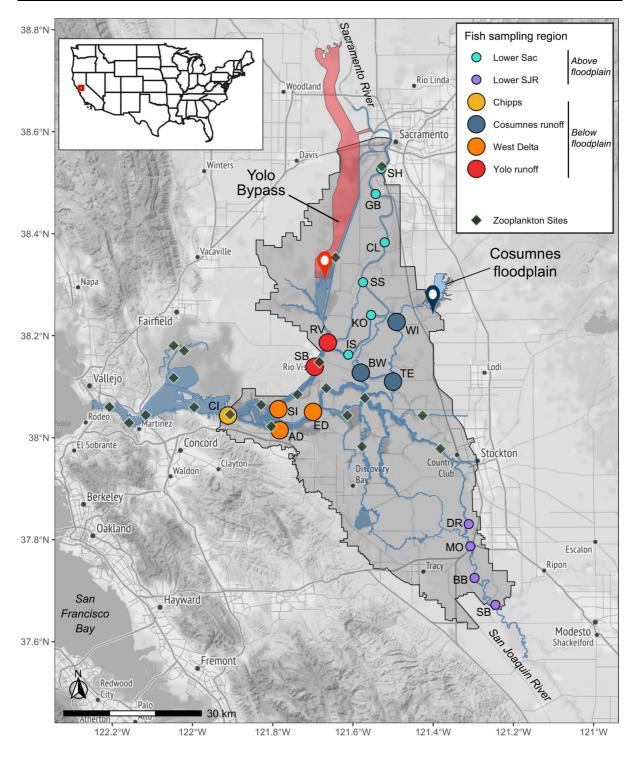2. Salmon stomach fullness: The increased flooding of off-channel habitats during years of high flows

Fig. 1 Juvenile salmon (circles) and zooplankton (diamonds) collection sites in the Sacramento-San Joaquin River Delta. The legal Delta region is shaded darker grey. Salmon collection sites are grouped into above (small circles) and below (large circles) the Cosumnes River floodplain and Yolo Bypass and separated into six regions: lower Sacramento River ('Sac', turquoise), San Joaquin River ('SJR', purple), Yolo runoff (red), Cosumnes runoff (blue), west Delta (orange) and Chipps Island (yellow). The main drainage point of each floodplain is indicated by an inverted teardrop marker. Site details provided in Table S1

will be associated with increased invertebrate prey production and salmon stomach fullness.

3. Trophic subsidies: If advection of cladocerans from floodplains to downstream habitats provides an important food source to juvenile salmon, (a) the dietary importance of cladocerans to salmon sampled in the Delta will be highest in wet years and in areas below floodplain drainage points, (b) the cladocerans consumed in these areas will be dominated by large-bodied, floodplain-associated species, and (c) the dietary contribution of cladoceran prey will decrease with increasing distance downstream.

Ultimately, understanding the drivers of zooplankton production and transport in managed river networks creates exciting opportunities to use habitat, infrastructure, and flow management to enhance key ecosystem services and curate foodscapes for the benefit of native fish species.

Methods

Zooplankton sampling

Mesoplankton were sampled at 18 sites in the Sacramento-San Joaquin River Delta ('Delta') and San Francisco estuary by the California Department of Fish and Wildlife (CDFW) Interagency Ecological Program (IEP) Zooplankton Study (Fig. 1). Samples were generally collected monthly using a modified Clarke-Bumpus net (data source: https://portal.edire pository.org/nis/mapbrowse?scope=edi&identifier= 522&revision=7. Background information: https:// www.wildlife.ca.gov/Conservation/Delta/Zooplankton-Study). In addition, zooplankton (filtered using 150 μm mesh size) were sampled at Sherwood Harbor in the Sacramento River and the drainage canal on the east side of the Yolo Bypass (Fig. 1) at roughly two-week intervals by the Department of Water Resources (DWR) Yolo Bypass Fish Monitoring Survey (data source: https://portal.edirepository.org/nis/mapbr owse?packageid=edi.494.1). Samples were fixed in formalin then identified and enumerated. Taxonomic resolution varied among datasets, sometimes going down to species level in the DWR data, but typically to order, occasionally genus level, in the CDFW data. We combined all individuals within the Cladocera

order, given that this reflects the taxonomic resolution used for most stomach contents analyses (see below). However, we repeated the analysis for all *Daphnia* spp. and *Bosmina* spp. (cladocerans consistently identified to genus level) to investigate whether patterns were consistent among taxa. Catch per unit effort (CPUE) was calculated as the number of individuals in a particular taxonomic grouping per cubic meter of filtered water. To map spatiotemporal patterns in cladoceran densities during the salmon emigration and floodplain inundation/drainage period (Jan-June), we summed the CPUE for all cladoceran species combined for a given sampling date and site, and calculated a mean average monthly CPUE value, then averaged these into two-monthly bins (Jan-Feb, Mar-Apr, May-Jun).
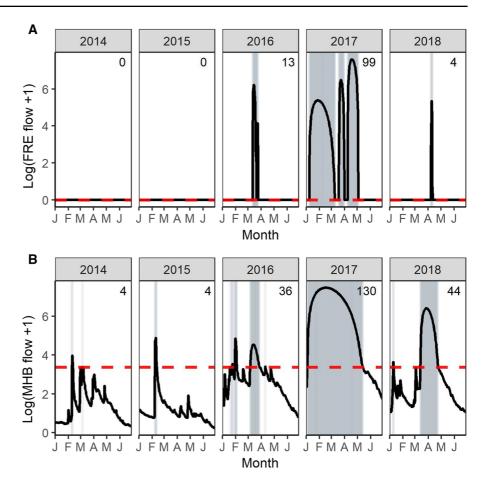
Fish sampling

Unmarked juvenile fall-run Chinook salmon were collected from by the Delta Juvenile Fish Monitoring Program from January to June of 2014–2018, encompassing a range of flow conditions that inundated the two focus floodplains for varying lengths of time (Fig. 2). A total of 3033 juvenile salmon were sampled by beach seine, Kodiak trawl and Midwater trawl as they entered the Delta from the Sacramento and San Joaquin Rivers, as they exited the Delta at Chipps Island, and from sites within the Delta situated downstream of Yolo Bypass and Cosumnes River floodplain drainage points (Fig. 1; Tables S1, S2). Sites were grouped into regions based on primary river flow direction and floodplain outlet location and sampled at approximately 7–14 day intervals. Each sampling day, up to five individuals were lethally sampled, their fork length (FL) measured immediately, then they were stored at − 20 °C.

Stomach contents analysis

In the laboratory, juvenile salmon were weighed to the nearest 0.01 g. The prey items in their foregut were enumerated and identified to life stage and the lowest taxonomic level possible; usually to family or order level (Table S3). To estimate a mean dry weight for each prey item based on its taxon-life stage grouping, intact prey were sampled from stomach contents, dried in groups of typically 5–30 individuals, then weighed to the nearest 0.1 mg to produce

Fig. 2 Mean daily flow (log transformed, in m^3s^{-1}) at **A** Fremont Weir (FRE; main input to the Yolo Bypass) and **B** Michigan Bar (MHB) in the Cosumnes River during the January-June 2014–2018 study period. The red dashed line represents the approximate minimum flow needed to inundate each floodplain, the vertical shading shows the inundation periods, and the inset text indicates the cumulative number of days each Jan-June period that the floodplain was flooded

a mean dry weight value per taxon-life stage combination (Table S3). Where we could not obtain sufficient numbers of intact specimens to obtain a reliable weight measurement, we used dry weight values from the literature and from Cramer Fish Sciences (Table S3). In total, 92,186 prey items were identified. Of these, seven individuals (<0.001%) were excluded due to insufficient taxonomic resolution (Table S3).

The number of prey consumed was multiplied by the mean dry weight for that taxon and life stage, and used to estimate (1) an index of fullness for each fish (IF = total dry weight of stomach contents / fish FL) (Merz 2002), (2) a year- and region-specific percent index of relative importance (%IRI = % frequency of occurrence x (% dry weight + % number)) (after Hyslop 1980), and (3) a year- and site-specific %IRI. Because salmon numbers were low in drought years 2014–2015 and floodplain inundation periods were the same in both years (Fig. 2), we aggregated these two years for IRI calculations.

Fish with empty stomachs were included in the IF calculations, but excluded from IRI calculations.

To track prey items transported off floodplain habitats, we would ideally focus on specific species known to be highly associated with off-channel habitats. Given the dominance of large-bodied cladocerans *D. pulex* and *D. mendotae* on floodplains, but limited abundance in fast-moving river channels (Corline et al. 2021), we hypothesized that these species would dominate the diets of fish caught from areas below floodplain drainage points during wet years. However, identifying partially-digested stomach contents to species level is often not possible so we only performed high resolution taxonomic analysis on a small subset of samples (three fish from each region during wet year 2017 and three from the west Delta during drought year 2014; n = 18 total). To improve the likelihood of obtaining sufficient numbers of zooplankton with identifiable species characteristics, we selected the fish that

had consumed the highest numbers of cladocerans within each region/year combination.

Environmental data

Flow data for Fremont Weir (Station ID 'FRE'), Cosumnes River at Michigan Bar (Station ID 'MHB') and Delta outflow (Station ID 'DTO') were obtained from CDEC (https://cdec.water.ca.gov; accessed Jan 29th 2020). Daily average FRE and MHB flows were used to infer the cumulative inundation periods for Yolo Bypass and Cosumnes River floodplain during the January-June salmon rearing period during each of the study years, based on the assumption that Yolo Bypass inundation occurs at FRE flows > 0 m^3 s^{-1} and Cosumnes floodplain inundation occurs at MHB flows > 28 m^3 s^{-1}. To explore differences in flow across the two floodplains and their relative contribution to total Delta outflows, daily computed flows for Yolo ("YOL"), Cosumnes ("CSMR") and total Delta outflow ("TOT") were summed in monthly bins using the CA Department of Water Resources Dayflow dataset (https://data.ca.gov/dataset/dayflow; accessed 22nd July 2022). The monthly ratio of floodplain flow to total outflow and Cosumnes to Yolo flow was calculated for the study period (Jan-June of 2014–2018).

Statistical analyses

All analyses were performed in R software v.4.1.0 (R Core Team 2021). To investigate interannual differences in food supply, we compared the index of fullness (IF) among years. We rescaled IF to ensure that empty stomachs (IF = 0) were included in the analysis, using the equation x.IF = (IF * $(n-1)$ + 0.5)/n where n is the sample size (Smithson and Verkuilen 2006). Log-transformation of x.IF improved homogeneity of variance, but the data still did not meet the assumptions of a parametric test, so log(x.IF) was compared among years using a Kruskal–Wallis chi-squared test and among each pair of years using the Dunn Test with adjusted p-values for multiple comparisons. Finally, loess smoothers were fitted to daily log(x.IF) values to explore within-season changes in feeding activity.

To test whether cladocera consumption rates were associated with floodplain proximity and/or inundation period, we fitted a linear model using site- and year-specific cladocera %IRI estimates as the dependent variable, and (1) upstream floodplain, (2) river distance from floodplain outlet to the collection site, and (3) seasonal cumulative inundation period as predictor variables. Only sites along primary river channels from each floodplain were included, and the river distance measured from each site to its 'hydrologically linked' floodplain (Table S1). The cumulative inundation periods were also specific to the upstream floodplain and varied by sampling year. The model was weighted by the log-transformed number of fish per site and year (summing the two years' sample sizes for '2014–2015').
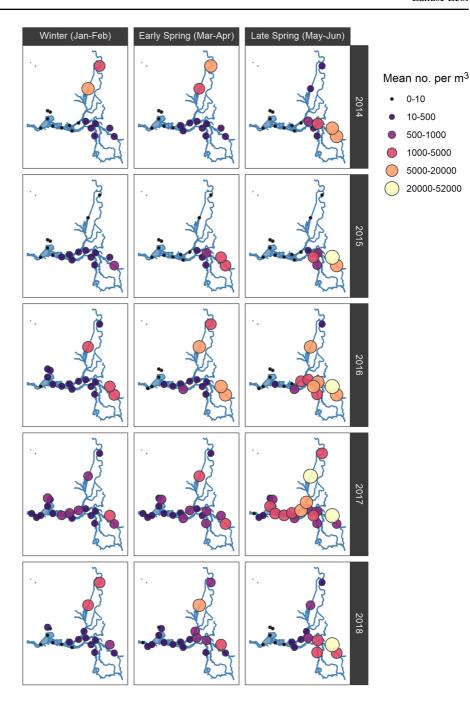
Results

Zooplankton densities

Across the study system, densities of cladocerans were on average highest in wetter years 2016 and 2017 (mean ± SD for Jan-June = 1904 ± 5831 individuals m^{-3} and 2297 ± 10,597 individuals m^{-3}, respectively) and lowest in dry years 2014 and 2015 (mean ± SD in Jan-June = 1147 ± 4799 individuals m^{-3} and 900 ± 4649 individuals m^{-3}, respectively). However, there was large variation in cladoceran abundance among sites, months, and years (Fig. 3). Cladoceran 'hotspots' tended to be concentrated around the northern (Yolo Bypass and occasionally also the Sacramento River at Sherwood Harbor) and southeastern (NZM10 "Disappointment Slough near Bishop Cut" and NZ092 "San Joaquin River at Buckley Cove") parts of the Delta. In every year, average monthly cladoceran abundances were highest in June and lowest in January to March. In 2016 and 2017, cladoceran densities were elevated in and beyond the west Delta, particularly in late spring 2017 when high numbers were observed downstream as far as Carquinez Strait (Fig. 3). Spatiotemporal patterns were similar for all cladocerans combined (Fig. 3) and for the two most common genera within it: *Bosmina* spp. and *Daphnia* spp. (Fig. S1), which represent 68% and 15% of all cladocerans in the entire CDFW Zooplankton dataset, respectively.

Salmon stomach fullness

While there was considerable variability among individuals, salmon stomach fullness differed

Fig. 3 Mean bimonthly Cladocera densities (all species combined) at 16 sites across the study region in winter (Jan-Feb), early spring (Mar-Apr) and late spring (May–June) 2014 to 2018. Data provided by CDFW and DWR (see methods)

significantly among years (Kruskal–Wallis test, $\chi^2 = 170$, df = 4, p < 0.001) (Fig. 4). Despite some fish caught in the lower San Joaquin River in April to May 2014 exhibiting extremely full stomachs (Fig. 5A), fish caught in drought years 2014, and particularly 2015, had significantly emptier stomachs compared with wetter years 2016–2018

(Fig. 4). Within years, the index of fullness (IF, untransformed) was weakly related to mean daily Delta outflow (r = 0.14, p < 0.001), with fish generally exhibiting the fullest stomachs in early to mid-spring, and the emptiest stomachs at the end of the emigration season, coincident with decreasing flows (Fig. 5).
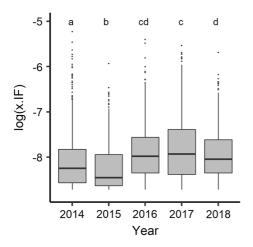
Fig. 4 Among-year differences in juvenile salmon stomach fullness (IF), rescaled to include zeros (x.IF) and log transformed to improve homogeneity of variance. Years with the same letter are not significantly different to each other (Dunn Test, p-values adjusted for multiple comparisons)

Trophic subsidies

(a) Spatiotemporal patterns in salmon diets

Overall, zooplankton and dipterans represented the most important prey types for juvenile salmon in this study (Fig. 6; Table S3). Within the zooplankton fraction, cladocerans dominated numerically and gravimetrically, and copepods and ostracods to a lesser extent. Malacostracans (particularly corophiids, cumaceans and mysids, Table S3) featured heavily in the diets of fish caught at Chipps Island in all years except for 2017 when freshwater outflows were particularly high (Fig. 6). Cladocerans were the most important prey item for fish sampled below Cosumnes and Yolo floodplains, and also for fish sampled in the west Delta in 2017, the year characterized by the highest outflows and longest floodplain inundation periods (Figs. 2, 5).
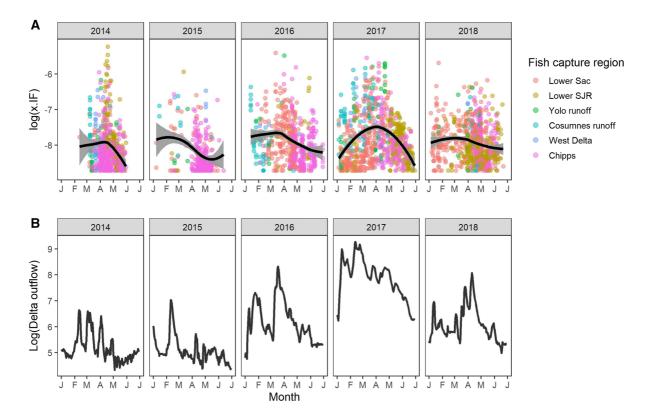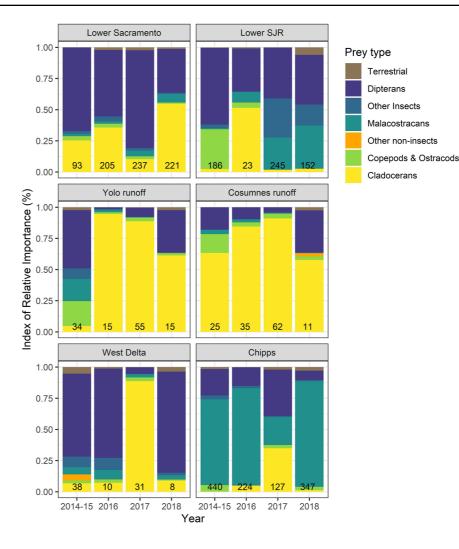

Fig. 5 Within-year patterns in **A** juvenile salmon stomach fullness (IF; log transformed and rescaled to include empty stomachs) and **B** logged daily Delta outflow in $m^3 s^{-1}$. In A, each point represents a single fish colored by capture region colored by capture region, while each line represents a loess smoother (±95% CI)

Fig. 6 Bar plots show-
ing regional patterns in
juvenile Chinook salmon
diets during drought
(2014–2015 pooled given
low sample sizes), above
average (2016), wet (2017)
and below average (2018)
hydrologic regimes.
Zooplankton (copepods,
ostracods and cladocer-
ans) appear at the bottom
of each bar. The number
at the bottom of each bar
indicates the sample sizes
of fish stomachs dissected
(excluding those with
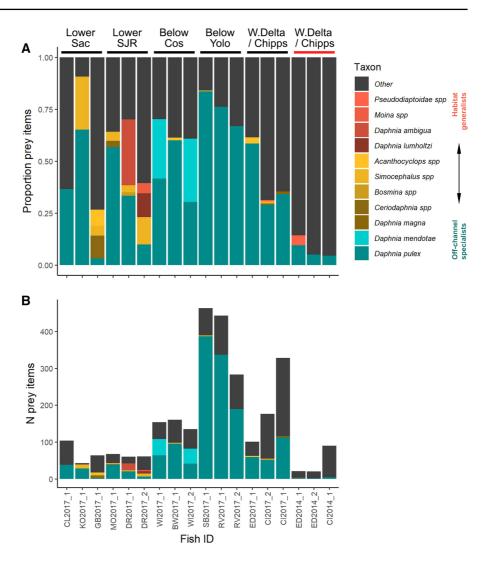empty stomachs). Finer-
scale taxonomic resolution
provided in Table S3

(b) Species composition of salmon diet

For the subset of stomach contents where zooplankton
were identified down to species level, *Daphnia pulex*
represented a key prey species for juvenile salmon
caught throughout the Sacramento-San Joaquin River
Delta, but their importance (both relative and in abso-
lute numbers) varied considerably between regions
and years. Overall, *D. pulex* was the most commonly
observed species, comprising 90% of all identifiable
zooplankton (within fish range = 11–100%, Fig. 7). In
all fish except those caught in the lower Sacramento
and San Joaquin Rivers, *D. pulex* represented at least
half of all identifiable zooplankton, and were highest,
proportionally and gravimetrically, in the stomachs of
salmon caught below Yolo Bypass in 2017 (Fig. 7). In
fish caught below the Cosumnes River floodplain, *D.*

mendotae, another floodplain associated species, also
featured heavily in the fish's diets. In fish caught in
the lower San Joaquin and Sacramento Rivers, zoo-
plankton prey diversity was higher, featuring greater
contributions of generalists such as *Simocephalus*
spp. (cladoceran) and *Acanthocyclops* spp. (copepod).
Fish caught in the lower San Joaquin River also fea-
tured higher contributions of small-bodied generalists
such as *D. ambigua* and *D. lumholtzi*. The diets of
fish caught in the west Delta tended to feature higher
contributions of non-zooplankton species, however
in wet year 2017, *D. pulex* represented at least (some
cladocerans could not be identified to species level)
37% of all prey items consumed, contrasting to 5% in
dry year 2014 (Fig. 7).

Fig. 7 The species composition of zooplankton prey in fish caught from the different Delta regions (Fig. 1), shown proportionally (**A**) and numerically (**B**). Zooplankton taxa considered to be habitat generalists *vs.* off-channel specialists are colored from red to turquoise, respectively (Corline et al. 2021). The fish capture site code (Fig. 1) and year was used to generate the individual Fish IDs. The capture region and year is indicated above the plot (black bar = wet year 2017; red bar = drought year 2014). All zooplankton taxa shown are cladocerans, except for *Acanthocyclops* spp. and *Pseudodiaptoidae* spp., which are copepods

(c) Factors associated with increased cladoceran consumption

We fitted a linear model to predict cladoceran %IRI based on the floodplain upstream of the fish capture site, its cumulative inundation period during the season of capture, and the river distance between floodplain drainage point and fish capture site. The model explained about two thirds of the variation in cladoceran %IRI ($F_{3,27} = 63.4$, $p < 0.0001$, adj. $r^2 = 0.67$, Table 1). The importance of cladoceran prey decreased with increasing distance downstream of both floodplains in all years examined (Fig. 8A; Table 1). The cumulative floodplain inundation period was positively associated with cladoceran %IRI, with salmon consuming relatively fewer cladocerans in drier years, particularly by individuals caught below the Yolo Bypass in 2014 and 2015, when Fremont Weir never overtopped (Fig. 2). Conversely, in wet year 2017, fish collected at the sites furthest from each floodplain, Chipps Island and Antioch Dunes (~ 60–80 rkm downstream) featured relatively high abundances of cladocerans in their stomachs, averaging 40% IRI (*cf.* 0.5–10% other years).

Discussion

This study supports the mounting body of evidence that floodplains support hotspots of zooplankton production and represent a critical food supply for migratory and resident fishes. It also reveals some of the

Table 1 Linear model examining the factors influencing the relative contribution of cladocerans to the diets of juvenile salmon in the Sacramento-San Joaquin River Delta based on the %IRI by year[a] and collection site (Figs. 1, 8)

Model term	Coefficient estimate	Std. Error	t-value	p-value
Intercept	0.7889	0.1184	6.663	< 0.00001
Floodplain: Yolo	− 0.1526	0.07535	− 2.025	0.05280
River distance between floodplain drainage point and fish capture site	− 0.0095	0.00186	− 5.092	0.00002
Annual[a] inundation period during the Jan-June sampling period	0.00363	0.00077	4.708	0.00007

The model was weighted by the log-transformed number of fish available for each site-year combination

[a]Given identical floodplain inundation periods and low sample sizes in 2014 and 2015, they were combined into a single 'year' for this analysis
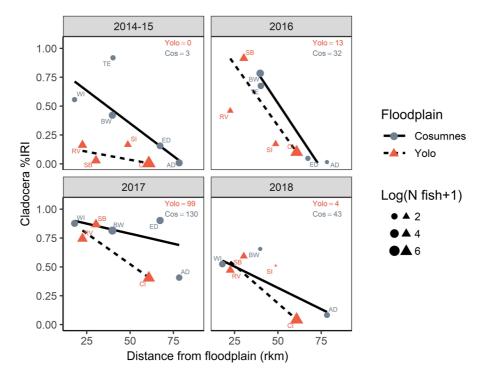

Fig. 8 The importance of cladocerans (inferred by % Index of Relative Importance [IRI] by year and capture site) to juvenile salmon diets as a function of how far downstream the capture site was from the Yolo Bypass (triangles, dashed lines) or the Cosumnes River floodplain ('Cos', circles, solid lines) measured in river kilometers (rkm). Inset text shows the upstream floodplain's cumulative inundation period (in days) for Jan-June of the capture year. Given identical floodplain inundation periods and low sample sizes in 2014 and 2015, they were combined for this analysis. Lines were fitted by year and floodplain, weighted by the log-transformed number of fish (indicated by symbol size). Note that these fits are not the predicted lines generated by the global model (Table 1). Capture site codes are shown in Fig. 1

landscape-level processes shaping foodscape dynamics in a managed system, which is an essential first step towards incorporating the foodscape concept into management and conservation. While management actions in altered lowland rivers often focus

on reconnecting floodplains and improving opportunities for fish to access them (i.e., increased lateral connectivity), longitudinal connectivity can also result in significant export of invertebrates, subsidizing distant food webs and providing trophic benefits

to consumers lacking direct access to them. Juvenile salmon exhibited fuller stomachs and diets dominated by floodplain-associated zooplankton in wetter years, particularly below floodplain drainage points. Cladocera abundances (both in the water column and salmon stomachs) were also higher in wetter years, exhibiting 'zooplankton plumes' that extended furthest downstream in wet year 2017. Here, we discuss the results, mechanisms, outstanding questions and the potential to use strategic management actions to enhance food production and delivery in altered river and estuarine systems.

Trophic subsidies and foodscapes

Floodplain connection and hydrodynamics can drive local zooplankton production (Grosholz and Gallo 2006; Górski et al. 2013), but few studies have contextualized these resource subsidies to consumer fish in a foodscape framework nor assessed their impact on recipient food webs. In this study, the extent of the foodscape for juvenile salmon was strongly influenced by floodplain inundation dynamics, with *D. pulex* dominating the water column and salmon stomach contents in wet years, and concentrated in areas below floodplain drainage points. Large bodied cladocerans such as *D. pulex* thrive in off-channel habitats, but perform poorly in turbulent riverine environments (Pace et al. 1992; Sluss et al. 2008; Górski et al. 2013; Corline et al. 2021), suggesting that the large numbers observed downstream during high flow periods were ephemeral events and the direct result of floodplain subsidies. We are confident that the non-random distribution of *D. pulex* was not an artifact of differential digestibility, as the chitinous structure of the *D. pulex* exoskeleton is similar to the other species of cladocerans and copepods found in the same samples. The results support our hypotheses regarding the importance of floodplain-to-river trophic subsidies for juvenile salmon, and reinforce previous studies that suggest that flow-mediated pulses of zooplankton from off-channel habitats represent a critical component of riverine foodscapes. For example, Boucek and Rehage (2013) and Saunders and Lewis (1988) both showed that peaks in zooplankton abundances in the mainstem river channel were highly correlated with the timing of pulse flows and drainage of upstream floodplains and marsh habitats. Such prey pulses have been associated with increased

immigration of consumer fishes into the recipient habitat (Boucek and Rehage 2013), but relatively few studies have directly quantified their relative contribution to the consumer diet. A study on the Cosumnes River showed significant predation on cladocerans by native splittail that peaked following floodplain inundation (Grosholz and Gallo 2006). Elsewhere, tissue stable isotope analyses suggested that floodplain-produced invertebrates typically contribute 30–40%, and sometimes > 70% of consumer fish diets, albeit with important variation among species and time periods (Farly et al. 2019). Although the frequency of zooplankton and salmon sampling in this study was not sufficient to describe short-term changes in zooplankton abundance and consumption, the stochastic variability of river flows and floodplain connectivity suggest that trophic subsidies from floodplain habitats would be equally variable through time.

Mediterranean climates are known for their inter-annual variability in precipitation, however, large-scale infrastructure can intensify the variability in foodscape dynamics among years. In the Central Valley, a significant fraction of the water entering the system is captured and diverted upstream of the Delta, and the Yolo Bypass only floods during high water events via an upstream weir. In historic wet year 2017, the bypass was inundated for almost the entire study period, and cladoceran densities were elevated in habitats more than 60 river kilometers downstream that are usually (given careful balancing of water storage *vs.* diversions in all but very wet years) too brackish for them to survive and reproduce in. Conversely, during the 2014–2015 drought years, the Yolo Bypass did not flood once, and cladoceran densities were exceptionally low, particularly in the west Delta. Overall, wet years were associated with abundant trophic resources to native fish due to the activation and connection of floodplains that generated prey for direct foraging by resident fishes and for export into the greater Delta system. Conversely, dry years were associated with scarce trophic resources as a result of the contraction or total disconnection of off-channel foraging areas, and the reduction or absence of flow-mediated subsidies.

Interestingly, ambient zooplankton densities were sometimes elevated in areas not obviously influenced by any off-channel habitats. The high cladoceran densities sometimes observed at the northernmost entrance to the Delta were likely explained

by advection from the Sutter Bypass (Cordoleani et al. 2022), a large floodplain that drains into the Sacramento River approximately 40rkm upstream of Sherwood Harbor (SH on Fig. 1). The hotspots in the southeastern Delta tended to increase in intensity towards the summer (i.e., outside of the floodplain inundation period) and are less easy to explain, but are consistent with the results of Orsi and Mecum (1986), and likely relate to agricultural runoff fueling the local food web. These areas are also typically associated with low numbers of juvenile salmon to graze the zooplankton down (Brandes and McLain 2001), and this area may also receive additional zooplankton subsidies from the Cosumnes and Sacramento Rivers as water is routed south to large export facilities (Orsi and Mecum 1986). We lacked the taxonomic resolution to ascertain whether these hotspots were dominated by off-channel specialists (e.g., *D. pulex* and *D. mendotae*), but the more diverse species composition observed in the stomachs of fish caught in the area suggest that these larger-bodied species are rarer there, requiring salmon to feed more diversely across the zooplankton community. Overall, these data emphasize the importance of maintaining a mosaic of habitats (even novel cultivated habitats) for creating a resilient foodscape (Katz et al. 2017; Holmes et al. 2021). Indeed, in a series of caging studies carried out north of the Delta, agricultural fields typically exhibited invertebrate densities and juvenile salmon growth rates closer to those exhibited on productive wetlands than those exhibited in the mainstem river channels (Cordoleani et al. 2022). Managing floodplains and agricultural lands to grow and export invertebrate prey to feed target species requires an understanding of the relationships between local hydrology, prey production, and the longevity and survivorship of prey in the recipient habitats, and could prove to be a valuable conservation tool in modified river systems (Katz et al. 2017; Frantzich et al. 2018; Holmes et al. 2021).

Foodscape management in a changing climate

Floodplains are inherently ephemeral in nature (Junk et al. 1989), creating unique challenges when trying to incorporate them into management plans. This is particularly true for the Central Valley, which exhibits a dynamic Mediterranean climate and significant variation in temperature, precipitation and flooding patterns within and among years (Cloern et al. 2011; Dettinger 2011). Across the full study period (Jan–June 2014–2018), flows from the Yolo Bypass and Cosumnes River represented, on average, 5.1% and 1.1% of monthly Delta outflow respectively, however there were considerable variations within and among years, with Yolo Bypass flows representing 54% of total outflows in February 2017 (Fig. S2A), coincident with the large plumes of zooplankton extending into the San Francisco Estuary (Fig. 3). Importantly, while Yolo Bypass flows typically exceeded those down the Cosumnes River, the system is dynamic and asynchronous, with multiple periods when the Cosumnes was inundated for longer (Fig. 2) and experienced higher flows (Fig. S2B). The resulting 'shifting habitat mosaic' (sensu Stanford et al. 2005) generates a complex foodscape of local and subsidized production, which parallels the diverse movements and life history patterns of salmon and other native fishes (Rossi 2020; Coleman et al. 2022; Cordoleani et al. 2022). Today, the productivity and resilience of riverine foodscapes are threatened by climate change (Larsen et al. 2016; Tockner and Stanford 2002), particularly in systems already stressed by land use change, flow alteration and invasive species (SFEI-ASC 2014). Yet the importance of bottom-up controls (i.e., food availability) on the resilience of cold-adapted fishes has never been greater, particularly at lower latitudes, given that increased prey consumption can at least partially offset the increased metabolic demands created by rising temperatures (Nobriga and Feyrer 2007; Lusardi et al. 2019). Data, such as those presented here, can be used to identify habitats and flow conditions that support salmon rearing, to help to parameterize life cycle and bioenergetic models, and to prioritize restoration projects aiming to improve the quality and quantity of critical habitats. In such analyses, it is important to quantify the phenology, strength and directions of resource flows. Particularly in degraded and food-scarce systems such as the Delta (Feyrer et al. 2003; Montgomery et al. 2015), cross-boundary trophic subsidies could be a major determinant of salmon rearing success.

In systems with regulated river flows, using water transfers or reservoir releases to inundate floodplains and trigger advection events could boost growth opportunities for commercially important or endangered fishes inhabiting or migrating through

downstream habitats. Globally, more than half of all large rivers are impounded, and adjacent terrestrial habitats are increasingly transformed by urbanization and agricultural reclamation (Opperman et al. 2010; Lehner et al. 2011). While these changes have led to widespread degradation or cessation of ecosystem processes important for the life history of river biota, novel management of water and floodplain infrastructure could also provide unique opportunities to influence and—under extreme drought scenarios—potentially enhance key ecological processes to benefit native species. Our study provides strong evidence that the inundation of a managed floodplain (or lack of) plays a pivotal role in shaping the Central Valley foodscape for juvenile Chinook salmon. Engineered systems such as the Sacramento-San Joaquin River Delta represent exciting opportunities to actively manage foodscapes at a landscape scale. Indeed, results from an experiment re-routing agricultural drainage water through Yolo Bypass instead of the Sacramento River during the fall showed promising results for creating a food pulse to support the critically endangered Delta smelt (*Hypomesus transpacificus*) (Frantzich et al. 2018). Also, a number of interagency projects are underway to improve juvenile and adult fish passage onto the Yolo Bypass and connectivity within the bypass (https://www.usbr.gov/mp/bdo/yolo-bypass.html, accessed 3rd July 2022). Such modifications should also create co-benefits to fish downstream by increasing inundation frequency and prey export events. By taking a systemwide and strategic approach to habitat and flow management (e.g., changing the timing or routing of water transfers and reservoir releases) there are exciting opportunities to create inundation and drainage events to benefit a suite of target species during critical phases of their life cycles.

Droughts are typically characterized by low zooplankton production alongside increased metabolic demands and food requirements of consumer species. Droughts in California are projected to increase in frequency and severity (Cloern et al. 2011), and are typically accompanied by major water overallocation and shortages, creating tradeoffs and controversy around the concept of using reservoir releases as an environmental management tool (Grantham and Viers 2014). In this study, the unmanaged floodplain inundated even in drought years, and was associated with detectable increases in zooplankton consumption by

fish sampled immediately downstream. Conversely, the managed flood bypass did not flood in either drought year. Using a combination of approaches such as modified infrastructure (e.g., lowering of the weir), timed reservoir releases or water transfers (Yarnell et al. 2015; Frantzich et al. 2018), and novel use of agricultural lands (Corline et al. 2017; Katz et al. 2017; Holmes et al. 2021), there is potential to create food pulses in water-efficient ways, even during drought years.

Future studies should focus on better resolving the mechanisms underpinning foodscape structure and extent. Understanding the relationships between abiotic factors and zooplankton production, transport and survival will allow managers to react to the hydroclimatic conditions in a given year and perform actions that maximize trophic benefits to target species, periods and/or areas. It is also important to quantify the relative importance of prey subsidies *vs.* consumer foraging behavior, as the management actions required to increase fish access to floodplains *vs.* prey transport from floodplains are very different. While the observed patterns in stomach contents data could be partially explained by sampling fish that had recently foraged on the floodplain during flood periods, fish access points are limited in this system, digestion times are short (~ 1 day), and the plumes of cladocerans observed in the water column exhibited the same distance-decay relationship as the salmon stomach contents, suggesting a dominance of flow-mediated subsidies. To help disentangle the various mechanisms, sampling fish and zooplankton at finer temporal scales (e.g., Grosholz and Gallo 2006) would have improved our ability to track flow-mediated resource pulses, as would using finer-scale taxonomic resolution and focusing on species more tightly associated with the putative source habitats (Davidson et al. 2000; Corline et al. 2021). Importantly however, while California floodplains are highly associated with large-bodied cladocerans such as *Daphnia pulex*, *D. pulex* thrive in almost any slow-moving freshwater habitat (Corline et al. 2021). As such, the importance of system-wide off-channel flooding and downstream tidal marshes and sloughs for zooplankton production should not be underestimated, as these habitats almost certainly contributed to some of the patterns observed in this study (Montgomery et al. 2015; Young et al. 2021). Ultimately, to effectively monitor foodscape

dynamics and the impact of management actions aimed at specific geographic areas, we need to embrace state-of-the-art tools capable of achieving higher spatiotemporal resolution, such as tracking fish habitat use via telemetry (e.g., Perry et al. 2013) and isotopic records in incrementally grown tissues (e.g., Bell-Tilcock et al. 2021; Phillis et al. 2018), and fingerprinting and tracking the origin of prey items using genomic sequencing (Peek et al., unpublished).

Overall, migratory fishes require a variety of habitats to complete their life cycle, and their needs vary at multiple temporal and spatial scales. We found that ephemeral flooding events exported food resources from floodplains in the lower Central Valley into downstream food webs, which were utilized by emigrating juvenile Chinook salmon in the recipient habitats. Understanding the processes driving the phenology, duration and strength of these trophic subsidies is critical to designing multifaceted management actions (e.g., habitat restoration, infrastructure modification, reservoir releases) that benefit target species during critical periods. Integrating management approaches to conserve, restore or even create novel habitat mosaics and foodscapes is a key step towards ensuring the reliability of ecosystem services and increasing the resilience of imperiled species occupying an engineered system in a rapidly changing climate.

Declarations

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