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Science for integrative management of a diadromous fish stock: interdependencies of fisheries, flow, and habitat restoration

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Science for integrative management of a diadromous fish stock: interdependencies of fisheries, flow, and habitat restoration

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Fisheries, flow, restoration

Abstract

Fish face many anthropogenic stressors. Authorities in marine, estuarine, and freshwater realms often share interdependent fisheries management goals, but address singular stressors independently. Here, we present a case study suggesting that coordinating stressor relief across management realms may synergize conservation efforts, especially to actualize restoration benefits. Significant efforts are underway to restore juvenile salmon habitat across California's Central Valley landscape but it is unclear how fisheries and flow management will influence juvenile salmon occupancy of restored sites. Leveraging monitoring data, we find that for juvenile salmon (<55mm) to actualize benefits of restored habitats will likely require maintaining spawner abundances and flows at or above intermediate values, especially in less-connected portions of the landscape. Furthermore, restoration efforts may prioritize more connected regions to promote use of restored areas, considering that less connected areas are often uninhabited when water and spawners are scarcer. This ecosystem-based framework that evaluates interdependencies of management decisions may be applied to realize natural productivity and enhance conservation in many systems.

Fisheries, flow, restoration

Introduction

Natural resource managers are often pressed to conserve diadromous fish. Diadromous species, defined by migrations between rivers and oceans, are culturally, ecologically, and economically significant worldwide. For example, they are celebrated by many cultures, foster a sense of place, feed iconic megafauna, fertilize nutrient-poor watersheds, and support hundred million dollar fisheries (Garman 1992, Close et al. 2002, Montgomery 2003, Chasco et al. 2017, NOAA 2019a). Despite this, many diadromous populations face extirpation and chronic depletion of their fisheries. Specifically, 29% of the contiguous U.S.A.'s ≈1400 historical populations of Pacific salmon (*Oncorhynchus* spp.) are extirpated along with 33, 15, and 27% of their ecological, life history, and genetic diversity (Gustafson et al. 2007) and multiple populations are listed under the U.S. Endangered Species Act. This is concerning because the stability, resilience, and availability of diadromous fish to people and other consumers is derived from these sources of biological diversity (Greene et al. 2010, Schindler et al. 2010, Armstrong et al. 2016).

Fisheries and water resource managers must navigate challenges to conserve diadromous fish. Ecologists implicate major drivers of diadromous fish declines that include overharvest, flow regulation, and habitat loss (Nehlsen et al. 1991, Limburg and Waldman 2009). However, these stressors are associated with human activities that benefit society (e.g., fishing, hydropower, agriculture, fundamental water security). Thus, sustainably managing fisheries, water, and land for multiple human uses requires decision-support tools to assess tradeoffs of management actions.

To counter fish declines, regulatory (e.g., DFO, NOAA) and research groups are striving to operationalize ecosystem-based management (Levin et al. 2009). In brief, ecosystem-based management is a holistic perspective that appreciates interactions among managed species, their ecosystems, and people that depend on both to facilitate desirable outcomes across stakeholders (Link 2010). Historically, fisheries management focused on species in isolation and often considered individual drivers or stressors independently. This approach was often less than effective, in particular because species decline when their habitats are degraded and there are myriad interactions within ecosystems, including many that are influenced by people, that determine outcomes for a given species (Pikitch et al. 2004). Thus, a broader perspective stands to enhance management efforts. To enable ecosystem-based approaches, researchers can create tools that explain linkages among ecosystem components and clarify potential tradeoffs of management options.

To relieve cumulative stressors across life cycles of diadromous fish, managers may employ a multifaceted conservation approach. Among practitioners' tools are *fisheries management, flow management, and habitat restoration*.

Fisheries management: Fish populations typically exhibit density dependence, whereby population growth declines as adult abundances approach habitat carrying capacities. These relationships can quantify adult abundances that maximize juvenile production and sustainable yield, allowing harvest of surplus adults with minimal impacts on recruitment.

Flow management: The aquatic environments of watersheds are dynamic, determined by flow pattern and discharge, varying among years and seasons. Complicating matters, some climates receive little precipitation during summers and managers may store water during wet seasons for fundamental (e.g., drinking) and economic (e.g., agriculture) human activities during dry seasons. These decisions impact diadromous fish as annual flow (and associated temperature) conditions can constrain juvenile timing and growth (Munsch et al. 2019) and low flows can increase mortality (Michel et al. 2015), suggesting managers in regulated systems may seek to avoid harmfully low flows.

Habitat restoration: Restoration can improve habitat function (e.g., survival, growth) and capacity in watersheds impacted by people. Restoration of diadromous fish habitat must consider accessibility by rehabilitating habitat within well-connected patches (e.g., migratory routes) and preferable environments (e.g., salinity) (Simenstad and Cordell 2000).

One option to synergize watershed habitat function may therefore be to coordinate fisheries management, flow management, and restoration to increase juvenile production and support juveniles in beneficial habitats. Key to this approach is enabling habitats to support a diversity of life history types by providing appropriate conditions across space (e.g., rivers, deltas, bays) and time (e.g., seasons), which are constricted by habitat and hydrologic modifications (Sturrock et al. 2019). Hypothetically, fisheries management, flow management, and restoration could work in concert: (1) higher spawner abundances could maximize the number of juveniles entering the next generation, (2) environmental flow regimes could enhance juvenile survival, cue juvenile dispersal throughout the watershed (Sturrock et al. 2020), inundate and connect beneficial habitats, and prolong seasonal windows when rearing conditions are viable (Munsch et al. 2019, Sturrock et al. 2020), and (3) restoration could foster habitats that are enhanced by flow (e.g., floodplains, wetlands) and increase the capacity of the watershed to support more juveniles in more places as they disperse in response to flow or to minimize competition when abundances are high (sensu Falcy 2014). Thus, each management realm attempts to enable the success of conservation efforts in other realms.

Naturally spawning Chinook salmon (*O. tshawytscha*) in California’s Central Valley (USA) may benefit from a coordinated framework. Once a productive, expansive habitat mosaic, the Central Valley's watershed and hydrologic regime have been transformed to reduce flooding, store and withdraw water, and irrigate agriculture. Juveniles surviving this watershed migrate to sea and support a valuable fishery. Adult abundances are increasingly supplemented by artificial propagation that masks declines in natural production (Johnson et al. 2012; Willmes et al. 2018), the role of natural spawning in producing juveniles that use extant habitats remains incompletely understood, and its populations are especially vulnerable to climate change (Crozier et al. 2019). Due to this legacy of stressors, the Central Valley's populations continue to decline (Yoshiyama et al. 1998; Johnson and Lindley 2016). Furthermore, decision-makers have recently pressed for increased water supply to human activities (White House 2018) despite incompletely understanding the importance of flow to salmon. At present, largely separate groups of practitioners are tasked with managing fisheries, prescribing flows, and implementing habitat restoration to conserve the Central Valley's salmon.

Here we analyze decades of juvenile surveys, spawner counts, and flow measurements to inform conservation of diadromous fish via three management pathways. These pathways target enhanced natural productivity through fisheries that allow sufficient abundances of spawners to reproduce and increase offspring abundances in the watershed, managed flows that promote favorable rearing and migration conditions, and habitat restoration that considers the influence of landscape on habitat use to prioritize areas frequented by juveniles. We provide quantitative information to inform Central Valley managers deciding fisheries escapement goals, water resource policy, and restoration priorities. More broadly, in California and beyond, the management authorities that enact fisheries, water regulation, and restoration are charged with the interdependent goal of sustaining viable fish populations, yet tools that quantify the potential interdependence of their actions are lacking. Our broader goal was to present a generalizable framework that demonstrates how coordination across management authorities may synergize diadromous fish conservation, and thus provide an important step toward fully implementing ecosystem based fisheries management (Levin et al. 2009).

Methods

Study system

California's Sacramento River is the second largest river on the contiguous U.S. west coast. It meets the San Joaquin River in the Central Valley, forming the Sacramento-San Joaquin River Delta (hereafter: Delta), which flows into San Francisco Bay (hereafter: Bay) and the Pacific Ocean beyond. California experiences cool, wet winters and warm, dry summers. Despite seasonal aridness, dams, reservoirs, and aqueducts supply fresh water to 25.5 million Californians year round and support a multi-billion dollar agricultural economy (USDA 2012). California endured a drought from 2012-2016. Drought challenges decision-makers to provide water for municipal use and agriculture without undermining mandates to protect federally listed species (Mann and Gleick 2015). This challenge to meet the needs of people and fish will escalate as the human population grows and climate change increases drought risk (Diffenbaugh et al. 2015).

Despite their declines, salmon in the Central Valley are remarkably diverse in life history. Three evolutionarily significant units (i.e., population segments recognized by the U.S. Endangered Species Act) of Chinook salmon inhabit the Central Valley, named according to the season that adults re-enter fresh waters: Fall/Late-Fall, Winter, and Spring (NOAA 2019b). The Endangered Species Act lists the Winter and Spring units as endangered and threatened, respectively. The National Marine Fisheries Service designates the Fall/Fate-fall unit as a species of concern. As a stock, these salmon have apparently evolved to exploit the vast, spatially and temporally heterogeneous landscape of the Central Valley. For example, the diversity of return timings translates to adult Chinook salmon being present in the Central Valley year-round (Yoshiyama et al. 1988). Thus, a fundamental objective in countering declines may be to increase across space (habitat landscape) and time (seasonality) the viability of juvenile habitats that enable and contribute to this diversity (sensu Sturrock et al. 2019).

There are many challenges to conserving Central Valley salmon. Its salmon have declined since 1850 (Yoshiyama et al. 1998). The major causes are a legacy of cumulative impacts: overfishing, mining, railroads, logging, water engineering, invasive predators, and agriculture (Yoshiyama et al. 1998). Chinook salmon are now confined to lower, warmer regions by impassible dams that impose artificial flow and salinity regimes in the Delta (Cloern and Jassby 2012). While the life histories of Central Valley salmon have synched juvenile rearing and outmigration with California’s wettest months, water regulation has shifted flows from the wetter months to the drier months. Consequently, juveniles experience flows ≈50% lower than historic levels and juveniles are largely absent when flows peak (Swart 2016). Furthermore, floodplains and estuaries are often salmon nurseries because small prey are abundant and their shallow portions exclude larger, predatory fish (Simenstad et al. 1982, Munsch et al. 2016), and turbid and vegetated conditions reduce predation risk by piscivorous birds (Gregory and Levings 1998). However, the Central Valley’s wetlands and floodplains have largely been replaced by deep, armored channels, filled for agricultural or municipal land, and minimized by hydrologic engineering. Indeed, only 3% of the Delta’s historically vast tidal wetland remains and non-tidal wetlands and floodplains have largely been diked and drained (Whipple et al. 2012). In addition, the fall run is a target of commercial and recreational fisheries that are economically significant and managed annually by the Pacific Fishery Management Council.

Habitat restoration may counter declines. Large-scale efforts are underway across the region to restore habitats by re-establishing wetlands and riparian forests, reconnecting floodplains to their rivers, and breeching or setting back levees (California Eco Restore 2017). These actions may benefit fish by increasing availability of prey, predator refuge, low-velocity holding areas, and cooler, shaded waters. While restoration efforts are likely to improve localized habitat value, we lack a quantitative understanding of how fisheries and water regulation practices will influence juvenile habitat occupancy across the landscape, including on restoration sites.

Analyses (described in detail in Appendix A1)

We asked, how do spawner abundances, flow, and landscape context influence juvenile habitat occupancy? We could then infer how spawning escapement and flow are likely to determine juvenile occupancy across the landscape of current, planned, and potential restoration sites.

To address these questions, we assembled data describing spawner abundances, flow, and juvenile salmon habitat use across the Central Valley (Fig. 1). Spawner abundances were sourced from stream surveys, and included fall, spring, and winter-run (but not late-fall run, whose juveniles have migration timing such that we would not count them) spawners in natural areas throughout the Sacramento basin. Flow was measured on the Sacramento and San Joaquin main stems. We summarized flow as rolling means across 30-day windows and rolling ranges (i.e., maximums - minimums) across 7-day windows to capture effects of long term flow conditions and flow pulses that may trigger fry migrations and enhance survival (Sturrock et al. 2019). We also used the California Department of Water Resources' water year hydrologic classification indexes (http://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST) to describe the total amount of water available to the Sacramento Valley in relation to flow. Juveniles were monitored throughout the system by seining shorelines, which targets the fry life stage of salmon that uses shallow waters. We examined only juveniles <55 mm because we could infer that these were naturally spawned fish (juveniles released by hatcheries were almost exclusively larger), which rely on extant habitat. The watershed included three regions: the Sacramento River, Delta (which includes the lower Sacramento River), and Bay (Fig. 1). We conceptualized the landscape of the Delta according to two axes: *distance downstream* and *distance off-main stem* of the Sacramento River. We conceptualized the landscape of the Bay according to one axis: *distance away* from the Sacramento River mouth. (Metrics defined in Table A1). Then, we used statistical models to relate fry catches to spawners, flow, and the landscape. These models also accounted for effects of seasonality in fry presence and non-independence of repeated sampling at sites and years. We fit separate models for fry presence and catch when present because the data included many zeros (i.e., zero inflation) and in the Bay we only modeled presence because presence there was low, leaving few observations of catch when present. To show how fisheries and water management may influences the use of restoration sites by fry, we used these models to predict fry presence and catches at restoration sites, which varied in their locations within the landscape, across flow levels and spawner abundances.

To enhance the communication of our findings to researchers, managers, and stakeholders, we also analyzed our data by quantifying *annual* descriptors of spawners, flow, and fry and relating them using common stock-recruit functions. Annual indexes of fry were generated using statistical models that quantified the expected catch of fry in the Sacramento River in a given year after accounting for effects of seasonality in fry presence and non-independence of repeated sampling at sites. While an annual time scale was less appropriate for examining habitat occupancy based on real-time flow conditions, it was advantageous because it allowed us to show, using a simple graphic, the influence of spawners on fry densities while accounting for flow.

Results

From 1999-2016, there was considerable variation in spawner abundances, water availability, flow conditions, and fry occupancy across the landscape. In-river spawner counts ranged from 38,705 – 775,732 adults, with a median of 224,310 adults. As per California Department of Water Resources classifications, the Sacramento Valley experienced 3, 5, 4, 3, and 3 years of critical, dry, below normal, above normal, and wet years, respectively. Flow ranged from 123 to 2,599 m^3/s, with a median of 515 m^3/s and considerable variation within and among seasons (Fig. 2). In years when water was scarcer, flow conditions were lower, especially as winters transitioned to springs (Fig. 2). Combining all observations, fry presence decreased from 60% (interannual range: 31-84%) in the Sacramento River (n = 3,940), to 38% (interannual range: 13-66%) in the Delta (n = 8,594), to 4% (interannual range: 0-18%) in the Bay (n = 1,966) and fry catch decreased from medians of 2 fry (interannual range: 0-4) in the Sacramento River, to 0 fry in the Delta (interannual range: 0-4), to 0 fry in the Bay (interannual range: 0-0). Fry presence and catch peaked in February (Fig. 3).

Spawners, flow, and the landscape influenced fry presence and catch (Fig. 3). Fry catches increased with spawners until ≈400,000 adults spawned (Figs. 3, A3). Fry catches also increased when flows were high (Figs. 3, A4) and following flow pulses (Figs. 3, A5). Presence in the Sacramento River and Delta decreased markedly when the mean of 30-day flows fell below ≈500 m^3/s (Figs. 3, A4), a value near median (515 m^3/s) conditions during periods of annual juvenile presence (Dec. – May). Catch given presence in these regions decreased when the mean of 30-day flows fell below ≈750 m^3/s and apparently increased with increasing flow throughout the range of observed flow values (Figs. 3, A4). Importantly, the patterns reported by models and boxplots at means of 30-day flows over ≈1500 m^3/s were informed by a small sample size of observations during uncommonly high flows and should be viewed cautiously. The salient effect of long-term flow in the Sacramento River and Delta, as informed quantitatively by models, was thus marked decreases in catches below flows of ≈500-750 m^3/s, with catches increasing less rapidly with flow thereafter. In the Bay, when flows were higher, fry were more likely to be present and present farther toward sea (Figs. 3, A4). Across critical to wet years, flows exceeded 500 m^3/s (i.e., conditions that largely maximized fry presence) from 19 to 84% of all days Dec - May (Fig. 2). Examining flow pulses, fry presence increased with ranges of 7 day flows until they exceeded ≈ 400 m^3/s (Figs. 3, A5). Catch increased with ranges of 7 day flows until ≈950 m^3/s and declined thereafter, although 7 day ranges of flow exceeding this amount were uncommon (Figs. 3, A5). Landscape connectivity also influenced fry catches (Figs. 3, A6). Catches decreased from the Sacramento River to the Delta to the Bay (i.e., in general, from spawning grounds to the ocean) (Figs. 3, A6). Catches in the Delta decreased off of the main stem and downstream (Figs. 3, A6). Similarly, presence in the Bay decreased with increasing distance toward sea (Figs. 3, A6).

Examining effects of spawners and flow using annual descriptors revealed similar patterns. Fry catches were best and similarly (using AIC) explained by Ricker and Beverton-Holt models that also included flow parameters (Tables A3, A4). Fry catches increased with spawners and flow (Fig. 4). Notably, (1) years with higher flows also included more variable flows (linear model comparing annual log sd flow vs. annual log median flow: $p = 0.0002$; $r^2 = 0.60$); therefore this annual flow metric likely captured effects of both baseline flow and flow pluses and (2) because flow was log-transformed to linearize its relationship with fry, these annual results are consistent with within-season results in that increases in fry occurred most rapidly when flow increased from its lowest to middling values. Annual indexes of fry catches were greatest when spawners exceeded ≈400,000 individuals. Ratios of fry densities in the Sacramento River, Delta, and Bay were directly related (Fig. A7). Hence, it appeared that, on an annual scale, fry density in the Bay was directly related to fry density in the Delta, which was directly related to fry density in the Sacramento River, which was a function of spawners and flow. Overall, fry catches increased with increasing spawners and flow, with catches increasing most rapidly when spawners and flow increased away from lowest observed values.

Spawners and flow influenced predicted presence and catches at current and planned restoration sites. Examining a subset of restoration sites to understand effects across a range of landscape contexts, predicted fry presence and catches in the Sacramento River and Delta fell precipitously when spawner counts and flow levels were low (Fig. 5). In restoration sites in the Bay, fry presence increased linearly with increasing spawner abundances and flow. Especially at sites far from the mainstem and downstream (Delta) or away from the Sacramento River mouth (Bay), fry were unlikely to be present or in large catches unless spawner counts and flows were high.

Discussion

Fisheries, flow, restoration

We investigated effects of density-dependent production, flow, and landscape context on the lower watershed abundance and occupancy of naturally spawned Chinook salmon fry. Habitat occupancy increased rapidly with spawners and flow, particularly until ≈400,000 adults escaped the fishery and flows exceeded ≈500-750 m^3/s. Flows tended to reach these values in wetter years, but were often below them in dry or critical years. In addition, fry occupied habitats more following recent pulses in flow. Across the landscape, habitat occupancy decreased from the Sacramento River to the Delta to the Bay, was highest in the Delta near mainstem waters and upriver, and was highest in the Bay closer to the river mouth. In the Bay, flow expanded habitat occupancy seaward. The distribution of fry across the landscape, including on restoration sites, is therefore determined by spawner abundances, flow, and landscape context. Especially in less-connected portions of the landscape, for fry to inhabit and thus realize benefits of restored habitats will likely require decisions to maintain spawner abundances and flow at or above intermediate values. Furthermore, restoration efforts may prioritize more connected regions to promote use of restored areas, considering that less connected areas are often uninhabited when water and spawners are scarcer.

Fisheries management implications: Fall Run Chinook salmon, which comprised 90% of 2001-2018 natural-area adult spawners in the Sacramento basin, excluding Late-Fall run (PFMC 2019a), are the predominant stock caught commercially and recreationally along California and, often, most of Oregon (Bellinger et al. 2015, Satterthwaite et al. 2015). They also support a recreational freshwater fishery. These fisheries are developed annually by the Pacific Fishery Management Council and California Fish and Game Commission, respectively. The Council uses preseason abundance forecasts to craft fisheries that are designed to achieve optimal yield, while limiting mortality on co-occurring weaker stocks. In years when the fishery is not constrained by the need to protect weaker, co-occurring stocks, it generally targets adult returns of 122,000 Sacramento Fall Run Chinook salmon to hatcheries and natural areas combined and does not distinguish between where these fish return to spawn. Although fisheries managers may be more concerned with maximizing sustainable yield rather than maximizing production, this target is substantially below the 400,000 spawners that we found came close to maximizing fry habitat occupancy in natural areas alone, even when factoring in the presence of spring and winter runs. Therefore, there may be benefits to considering targets for more spawning in natural areas to enhance overall in-river productivity and ultimately to recruitment of the next generation to the fishery. Recommendations to consider revisions to the escapement goal, including specifying the escapement goal in terms of spawners in natural areas, have been made by other scientific advisory bodies as well (Lindley et al. 2009, California HSRG 2012, PFMC 2019). However, pre-fishery abundances (i.e., Sacramento Index, an estimate of potential Sacramento Fall Run Chinook salmon escapement in the absence of fishing) was below 400,000 in 10 out of 36 years 1983-2018 and 9 out of 18 years 2001-2018 (PFMC 2019b), and this number includes adults that would enter hatcheries (i.e., not spawn naturally). This indicates that pre-fishery adult abundance is often low enough that fisheries restrictions alone would likely be insufficient without habitat restoration, flow increases, or other measures to boost productivity.

Flow management implications: Flow levels are tightly managed via California's extensive water storage and delivery infrastructure to meet many objectives, including (1) meeting fundamental human water needs, (2) diversions for agriculture during the growing season, and (3) sufficient flow and cold water to protect egg nests of endangered Sacramento River Winter Run Chinook salmon from dewatering or warming in late summer and fall. Our results suggest that abundance and distribution of Fall, Spring, and Winter Run fry across the landscape is also tied to operational flows in late winter and early spring. Higher flows increased fry counts overall, and the spatial extent of fry rearing in the Delta (by increasing presence in areas otherwise unoccupied) and Bay (by extending accessible habitat seaward). Indeed, the nonlinear effects of flow detected by our models suggest that winter-spring flows above ≈500-700 m^3/s, although constrained by annual variation in water availability, would avoid low flow conditions that appear to be disproportionately deleterious to fry. Our results and those reported in the Stanislaus River (a tributary of the San Joaquin River; Sturrock et al. 2019) suggest that flow pulses, in addition to adequate long-term flows, are beneficial to juvenile salmon. Thus, a flow regime beneficial to fry may be characterized by mid-to-high long-term flows punctuated by intermediate pulses. We provide visualizations of examples of “good” and “bad” flow years for fry in Fig. A8.

There are many plausible reasons that flow promoted fry habitat use. Flow may create and inundate habitat (e.g., Yolo Bypass), deliver cool, oxygen-rich waters, increase turbidity and thus concealment from predators, and move fresh waters seaward in the estuary. Recent studies in the Central Valley found flow increased the survival and annual rearing windows of outmigrating juveniles (Michel et al. 2015, Munsch et al. 2019, Friedman et al. 2019). Notably, adult returns per juvenile rose abruptly when flow exceeded low levels (Michel 2018), similar to our observation of a non-linear flow effect. Thus, it is clear in the Central Valley that flow influences habitat use and that juveniles benefit from higher flows.

Habitat restoration implications: Fry probability of presence was greatest upstream and on main stem waters. As illustrated by our model projections, restoration efforts may consider prioritizing these areas to maximize habitat use. Moreover, it appears that the efficacy of restoration efforts depends on sufficient spawners and flow to promote juvenile abundances and distributions that translate to occupied restored habitats. While restoration projects in the river and Delta (near the mainstem) exhibited probability of presence > 0.5 for a wide range of flow levels and spawner abundances, juveniles were unlikely to be present near and in Bay restoration sites except at very high levels of flow and spawners. These results suggest that restoration projects for Chinook salmon will currently (e.g., while spawner levels are depressed) be most effective in the river and more connected portions of the Delta. Restoration efforts may thus prioritize sites in these areas, especially to ensure habitat use in years when water and spawners are scarcer. Aiming for long-term population resilience, restoration efforts that create large, functional, and connected habitats across the landscape may enable the watershed to capitalize on years when natural conditions and managers facilitate high spawner abundances and flows.

Our work should be interpreted within the greater scope of management in this system. Management would benefit from understanding survival benefits of increased habitat occupancy, as well as environmental and density-dependent constraints during marine life stages (e.g., life cycle modeling: Friedman et al. 2019). For example, if restored watershed habitats enable more, larger juveniles to enter the ocean, it would be important to understand whether density dependence manifests again as salmon compete for prey at sea. Additionally, reservoir releases are used to provide cooler temperatures for adult and embryonic stages in this system, especially during warmer months for endangered Sacramento River Winter Run Chinook salmon (Danner et al. 2012). Decisions to allocate water to promote flow for juveniles must also consider these other runs and life stages. For example, higher flows during adult returns are associated with lower straying rates (i.e., returns to non-natal rivers) (Sturrock et al. 2019). Likewise, other imperiled species in the system (e.g., delta smelt *Hypomesus transpacificus*, green sturgeon *Acipenser medirostris*) are likely to be influenced by flow, and a greater management scope should consider the suite of managed species in the Sacramento-San Joaquin watershed (Zarri et al. 2019). Also, the feasibility of establishing an escapement goal near 400,000 adults to natural areas should be evaluated for the near- and long-term sustainability of the fishery, especially when integrated with flow actions to achieve maximum productivity. Furthermore, restoration is likely to provide habitat for non-native salmon predators that inhabit the Central Valley (Demetras et al., 2017) as well as salmon fry. Accordingly, it will likely be important for restoration efforts to provide protective features, such as shallow areas that attract small, earlier life stages of fish and exclude many aquatic predators (Munsch et al. 2016) or that increase vegetation and turbidity and thus concealment from predatory birds (Gregory and Levings 1998) to more fully actualize benefits of restoration to salmon. Finally, we caution that apparent flow thresholds below which are harmful to fry should not be interpreted as a target, but rather a minimum limit, for conservation efforts. Resilience of salmon stocks is derived in part from populations exploiting variable habitat conditions, plausibly including flooding when flows are greater than median levels.

Complexities and limitations should be considered in the interpretation of our study. First, we examined habitat occupancy in the lower Sacramento River, Delta, and Bay, not total abundances of juveniles in the Central Valley. If, for instance, fry disperse downstream (where sampling occurred) in response to high upstream (where sampling did not occur) fry densities or flows, then responses of total juveniles to spawners, flow, and the landscape will differ from responses of habitat occupancy. Second, our study examined patterns at the scale of the landscape. Recovery planning should account for additional, localized factors specific to current or prospective restoration sites when prioritizing sites for restoration or in maintaining fry presence on them. Third, we examined fry and not later juvenile stages (e.g., smolts). This was a practical decision that allowed us to infer we were assessing habitat occupancy in lower portions of the watershed by naturally spawned fish, although other life stages (e.g., parr, yearlings) also rely on functional habitats, are important in the legacy of the stock, and may experience different constraints on habitat use. Fourth, fry spawned in-river may be the offspring of hatchery-origin fish and/or have significant hatchery-origin ancestry. Hatchery fish in the Central Valley are increasingly raised to ocean-ready smolts, potentially reducing selective pressures on juvenile freshwater stages (Huber and Carlson 2015). Lineages retaining greater adaptation to the freshwater stage may therefore realize greater, more immediate benefits of restoration. Fifth, we incompletely understand how improving habitat experiences in the juvenile freshwater stage will ultimately influence survival at later stages. However, viable freshwater habitats may dampen stress in marine stages, for example by allowing greater growth in the watershed that presumably reduces predation risk at sea (Woodson et al. 2013, Munsch et al. 2019) or allowing juveniles to rear longer and enter the ocean after seasonal prey blooms (Satterthwaite et al. 2014). Additionally, higher flows during adult returns are associated with lower straying rates (i.e., returns to non-natal rivers) (Sturrock et al. 2019). Sixth, our conceptualization of the system did not consider interactions between some factors. For instance, low flows during severe drought may create competition within the juvenile stage, modifying the influence of spawners on habitat occupancy. These complexities were beyond the scope of this paper, but offer further research avenues.

Salmon appear poised to benefit from ecosystem-based approaches. For example, researchers in the Columbia River Basin studied the life history of a depressed salmon population and their interactions with regulated flow. They developed a “Fish-Water-Management-Tool” that minimized egg and juvenile mortality and fisheries managers simultaneously increased escapement goals. In the years that followed, returns of naturally-spawned adults increased considerably (Lichatowich et al. 2018). Similar benefits to more holistically evaluating potential responses of salmon to management decisions are evident in other systems (e.g., Scheuerell et al. 2006, Battin et al. 2007). More broadly, integrating work like ours on ecosystem considerations in the watershed with ecosystem-based fisheries management efforts in the ocean (Wells et al. 2020) and efforts like integrated ecosystem assessments (Levin et al. 2009) may facilitate linkages across marine and freshwater stages. For example, water management may prioritize desirable flow conditions to increase juvenile survival in the watershed and fisheries management may protect marine species that buffer subadult salmon from predation at sea. Ecosystem perspectives also stand to facilitate management of other species: enhancing the natural productivity of salmon may benefit the many species that prey on salmon or assimilate their nutrients (Quinn 2018). Overall, as integrative research and management programs are reaching maturity, there is promise in moving toward coordinated, ecosystem-based decisions that benefit salmon (Hare et al. 2019).

Ecosystem-based approaches may enable managers to address environmental imperatives within broader management scopes. Human dimensions are fundamental to decision-making and ecosystem-based approaches incorporate human dimensions by coordinating across multiple managers and stakeholders (Carwardine et al. 2018, Hare et al. 2019) and appreciating that perceptions of desirable ecosystem states will vary (Ingeman et al. 2019). Addressing a diversity of needs is feasible. Actions that benefit fisheries can benefit people directly or at least not interfere with other human use needs. For example, floodplain restoration can increase fish habitat and protect property from floods and designed flow regimes can protect native species without compromising water security (Chen and Olden 2017). Additionally, many ecological relationships, including those involving salmon, are governed by nonlinearities and thresholds (Munsch et al. in Review). As exemplified by our results, nonlinearities (e.g., fry habitat use vs. flow, fry production vs. escapement) may allow managers to optimize for fish benefits and human use needs of particular systems to achieve more efficient or effective outcomes. More broadly, many management decisions require optimizing across competing goals, but can be made more efficiently by clarifying their underlying cultural, ecological, and economic trade-offs (Mangel and Dowling 2016, Burgess et al. 2018). Decision support tools that integrate across management realms may therefore be conducive to improving real-world decisions that benefit fish and people collectively.

In conclusion, there is potential to realize greater watershed habitat function in the Central Valley by increasing reproduction, enhancing flow conditions, and restoring habitats, especially in areas frequented by juveniles. Ideally, this approach would enable many juveniles to spread across a long juvenile rearing window and a landscape of viable habitats across the watershed, ultimately supporting a more abundant and stable fish population. Fisheries, water, and habitat are managed by separate authorities. Coordinating management realms, as informed quantitatively by our findings, may increase the benefits of their individual efforts. Indeed, many fisheries experience cumulative stressors, and a more integrated approach to relieve multiple stressors at key life stages may enhance recovery efforts (Lichatowich et al. 2018). That spawners and flow appeared to disproportionately increase productivity up to intermediate levels suggests opportunities for “satisficing” (De Lara et al. 2015) fisheries and water managers seeking to improve natural productivity of salmon while meeting other human needs. In many locations, people are struggling to balance conflicting demands (e.g., agriculture, hydropower, land development, fisheries) as they develop watersheds yet remain dependent on fisheries produced by viable watersheds (e.g., Sabo et al. 2017). Research and management in other systems may consider a multifaceted approach similar to the framework we offer to synergize conservation of fish in stressed watersheds worldwide.

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Fisheries, flow, restoration

Figure Legends

Figure 1. Locations of fry sampling and USGS flow gages (Sacramento: 11447650 and San Joaquin: 11303500). Symbols of fry sampling sites reflect delineations into Sacramento River, Delta, and San Francisco Bay regions. The Sacramento River runs along the blue line. Distances downstream in the Bay are measured relative to Middle Ground Island. Map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. Base Map Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community. Hydrography Sources: USGS.

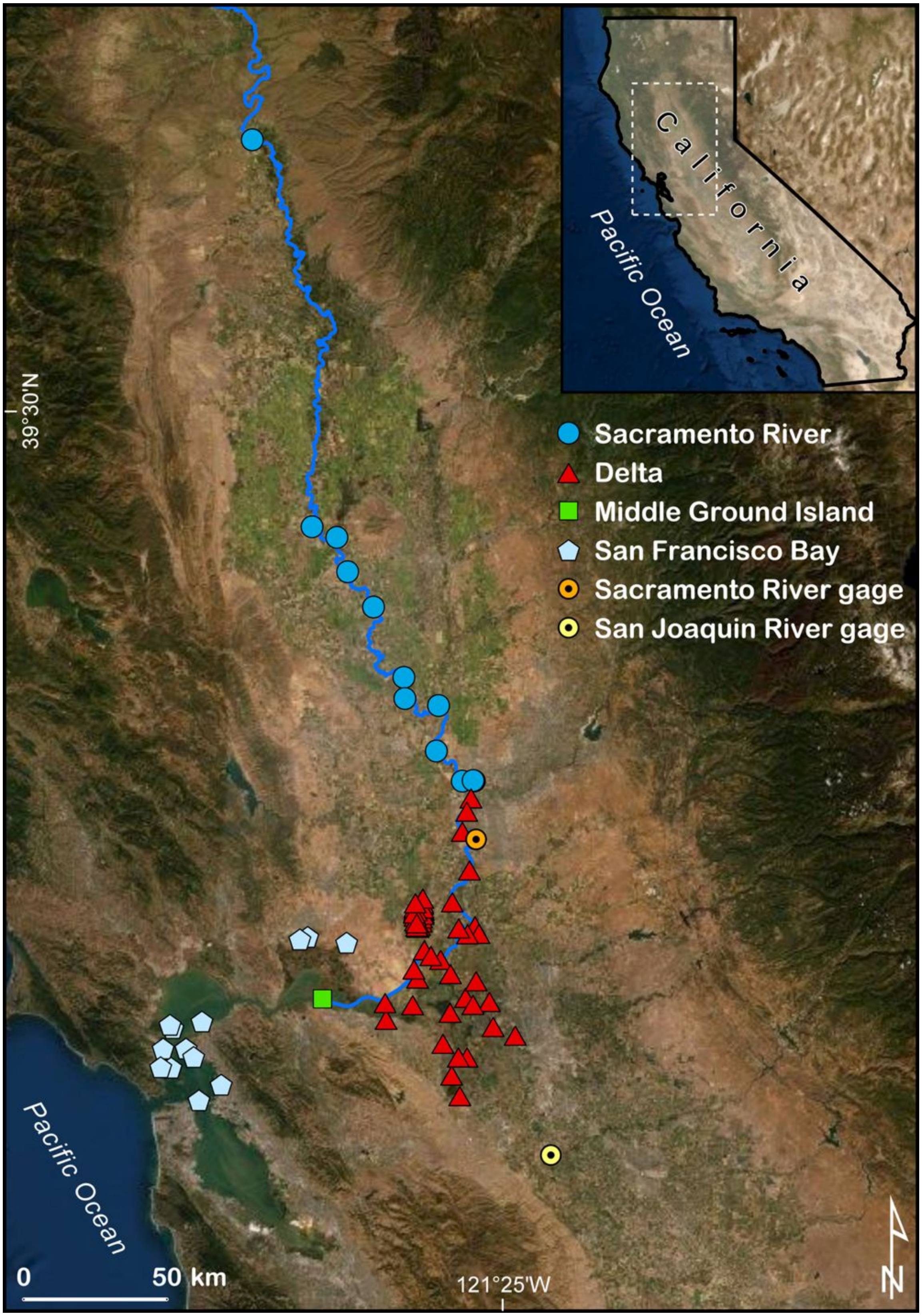
Figure 2. Flow conditions in the Sacramento River Dec. – May, 1999 – 2016. Colors indicate water availability classification. Dashed line indicates median. **Left**: Conditions across individual years. **Center**: Smoothed histogram of all flow values for each water availability classification. **Right:** Percentage of days among water availability classifications when flows exceeded 500 m/s^3, a value below which fry presence fell rapidly.

Figure 3. Model output describing presence (top, blue) and catch when present (bottom, purple) of Chinook salmon fry in the Central Valley. Shading indicates 95% credible intervals.

Figure 4. Annual fry density index compared to spawner abundances and flow overlaid with predictions from model describing relationship among these variables. These models are parameterized by a Beverton-Holt and Ricker stock-recruitment relationships and a linear effect

of log-transformed flow. The thick, solid line indicates the median value of median log-transformed flow across all years. We show predictions from these top two models because AICs indicated they fit the data similarly well.

Figure 5. Probability of fry presence (top two rows) and catches (bottom rows) predicted across different levels of spawners and 30 day flow means in select current and planned restoration sites. We selected these sites to show variation in influence of landscape on fry presence. Models predicted fish responses according to one variable (i.e., spawners, 30 day flow mean, range, or landscape) while holding the other variables at their means, and for January 10, a day of year that corresponded to typical seasonal fish presence (Fig. 3). Map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. Base Map Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community. Hydrography Sources: USGS.



799

800 **Figure 1**

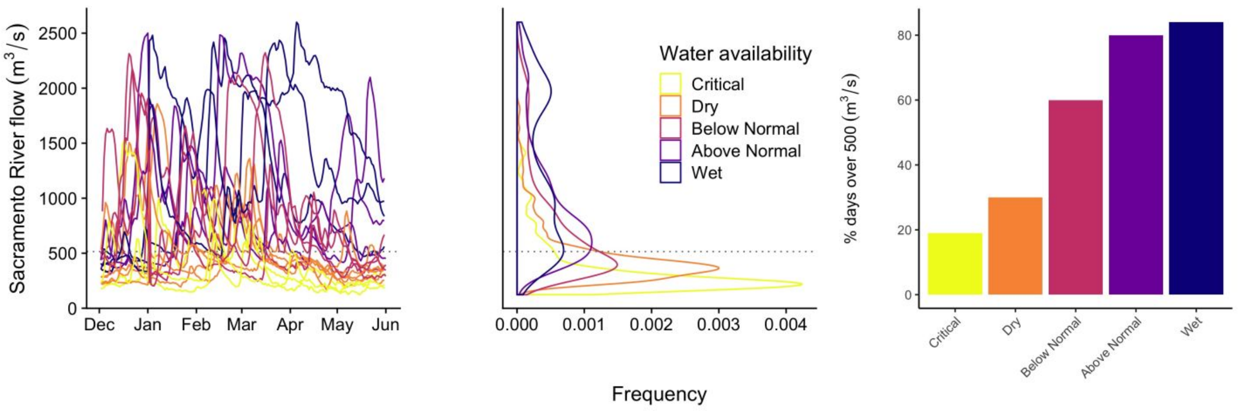

Sacramento River flow (m^3/s)
2500
2000
1500
1000
500
0
Dec
Jan
Feb
Mar
Apr
May
Jun
0.000
0.001
0.002
0.003
0.004
Frequency
Water availability
Critical
Dry
Below Normal
Above Normal
Wet
% days over 500 (m^3/s)
80
60
40
20
0
Critical
Dry
Below Normal
Above Normal
Wet

Figure 2

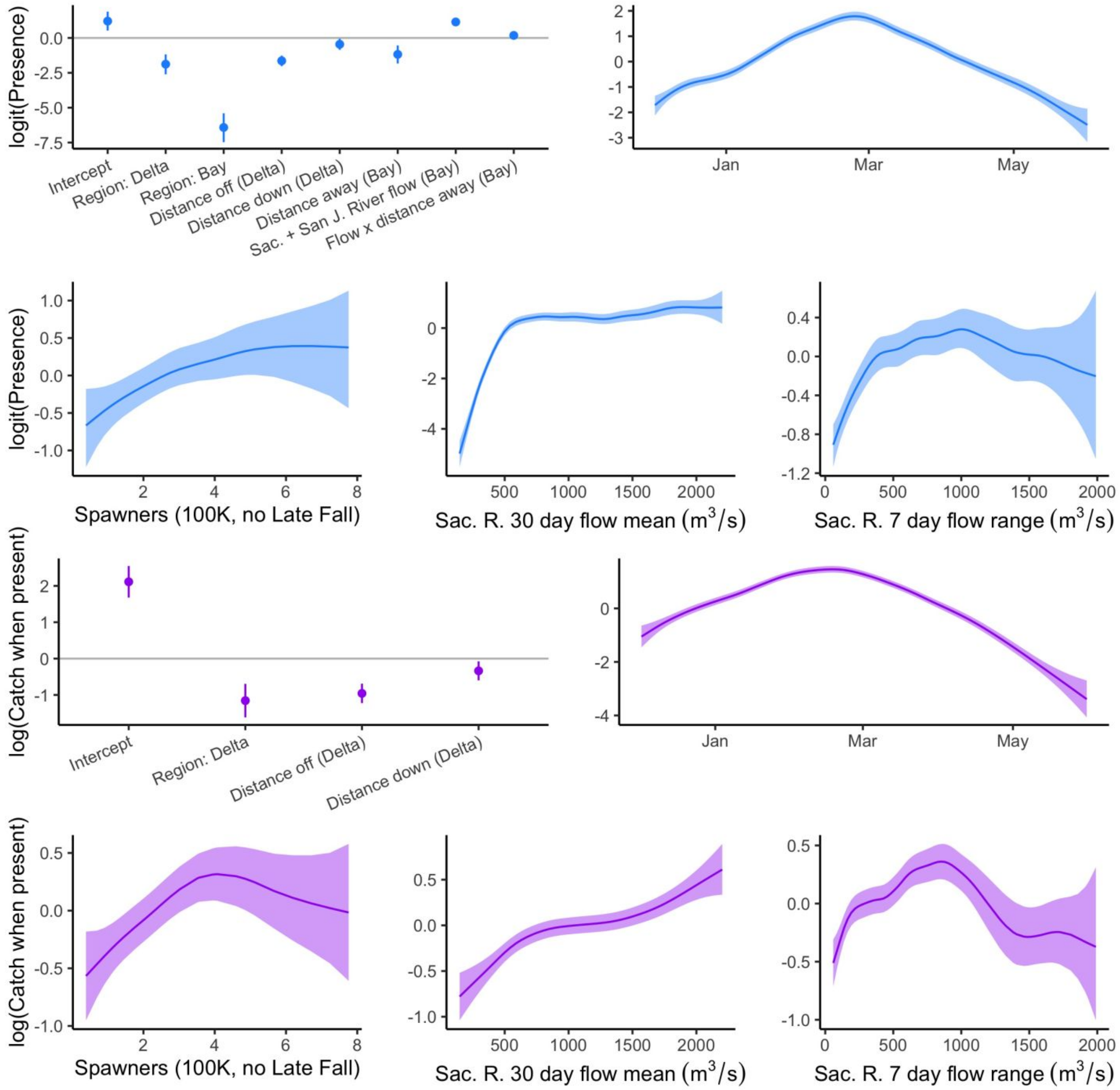
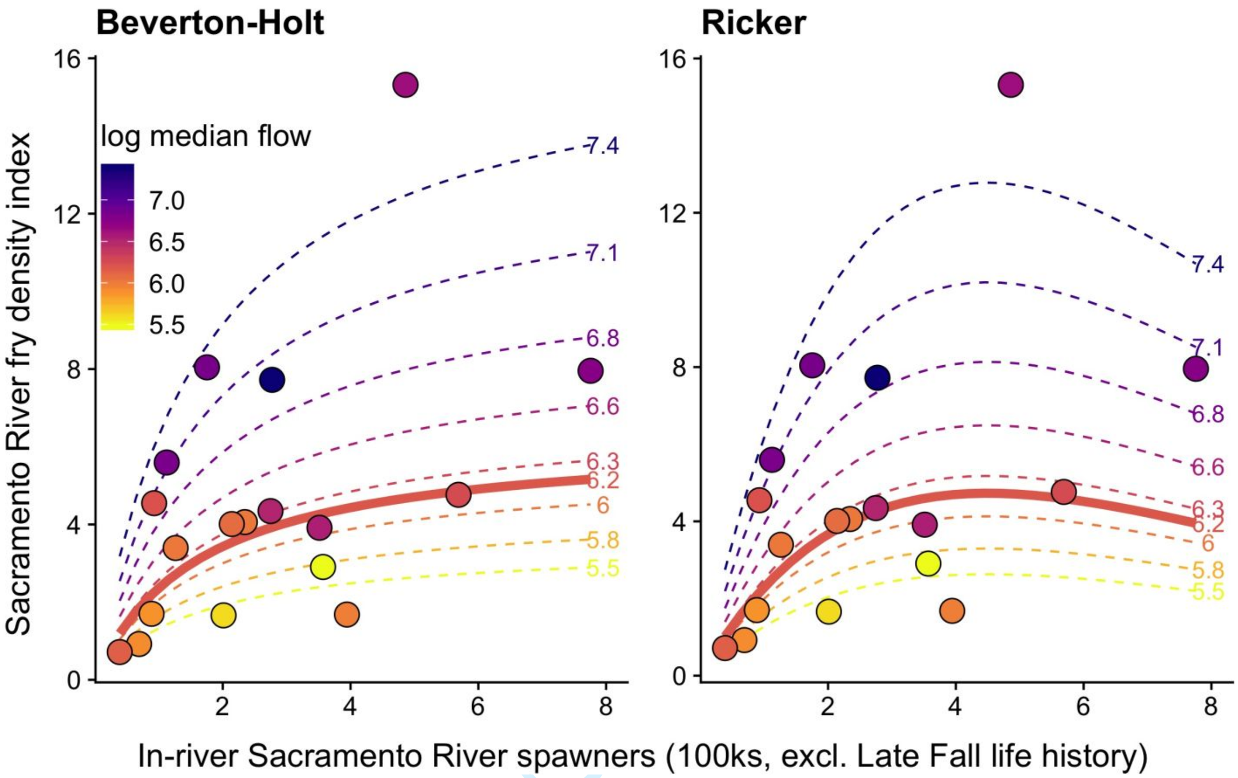

logit(Presence)
0.0
-2.5
-5.0
-7.5
Intercept
Region: Delta
Region: Bay
Distance off (Delta)
Distance down (Delta)
Distance away (Bay)
Sac. + San J. River flow (Bay)
Flow x distance away (Bay)
2
1
0
-1
-2
-3
Jan
Mar
May
1.0
0.5
0.0
-0.5
-1.0
Spawners (100K, no Late Fall)
Sac. R. 30 day flow mean (m³/s)
Sac. R. 7 day flow range (m³/s)
500
1000
1500
2000
0.4
0.0
-0.4
-0.8
-1.2
log(Catch when present)
Intercept
Region: Delta
Distance off (Delta)
Distance down (Delta)
0
-2
-4
2
4
6
8

Figure 3



806

807 **Figure 4**

808

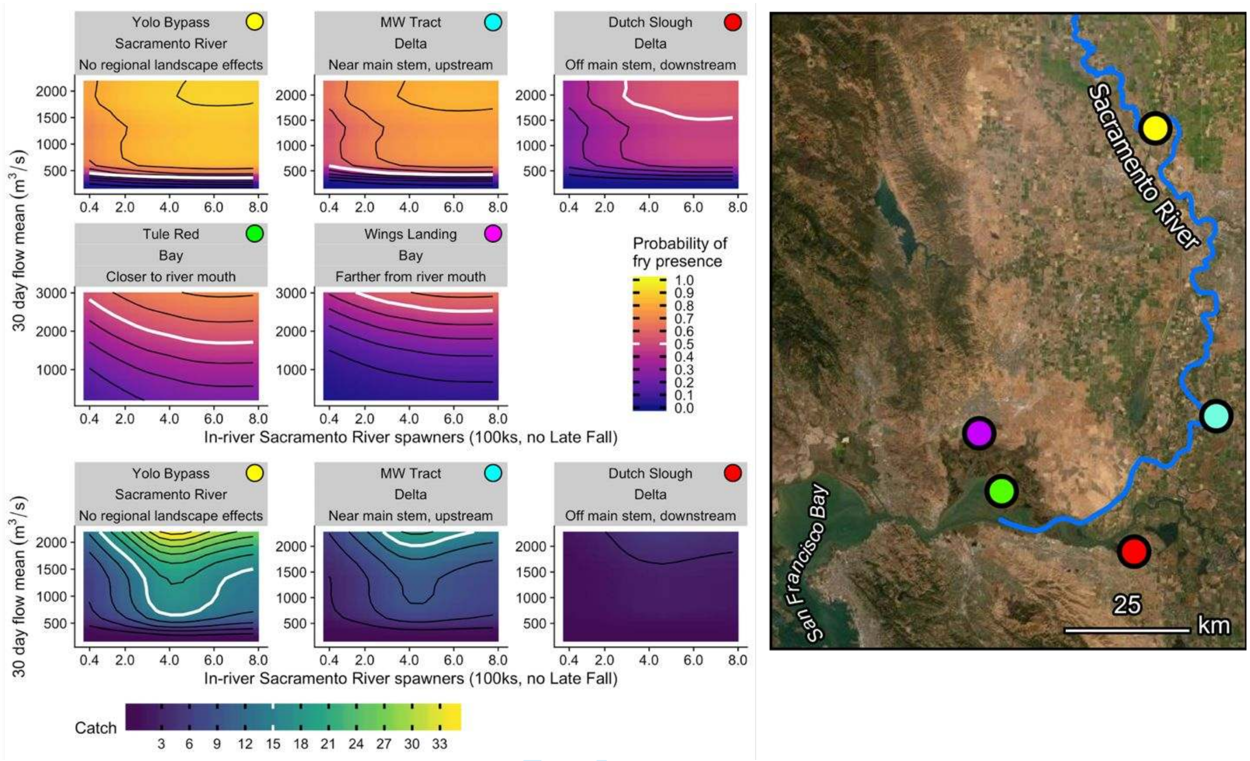

Yolo Bypass
Sacramento River
No regional landscape effects
MW Tract
Delta
Near main stem, upstream
Dutch Slough
Delta
Off main stem, downstream
Tule Red
Bay
Closer to river mouth
Wings Landing
Bay
Farther from river mouth
30 day flow mean (m³/s)
In-river Sacramento River spawners (100ks, no Late Fall)
Probability of fry presence
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Catch
3 6 9 12 15 18 21 24 27 30 33
Sacramento River
San Francisco Bay
25
km

Figure 5

Appendix A1

Assembling data and summarizing metrics

We assembled data describing the abundance and distribution of juvenile salmon, adult salmon, and water quality in the Central Valley. Juvenile salmon abundances and distributions were described by the U.S. Fish and Wildlife Service's (USFWS) Juvenile Fish Monitoring Program (Mahardja et al. 2019). USFWS monitors waters throughout the Central Valley by beach seining for fish. Beach seining involves researchers deploying a net to capture fish in shallows adjacent to shore, and it targets the fry life stage of salmon, which occurs shortly after salmon hatch and emerge from gravel. USFWS conducts several hundred beach seine hauls per year. Abundances of adult salmon were described by the California Department of Fish and Wildlife's GrandTab dataset (https://www.wildlife.ca.gov/Conservation/Fishes/Chinook-Salmon/Anadromous-Assessment). This program estimates annual abundances of spawning fish by compiling abundance estimates and counts from stream surveys. We used in-river population estimates from the Sacramento River system, and excluded fish used in hatchery broodstocks. Finally, water flow was described by U.S. Geological Survey stream gages on the Sacramento and San Joaquin River main stems (gages 11447650 and 11303500, respectively: https://waterdata.usgs.gov/usa/nwis/uv?site_no=11447650; https://waterdata.usgs.gov/nwis/uv?site_no=11303500). Given the Delta's complex network, there are many ways to measure its flow into the Bay. We elected to use a relatively simple measure summing flows from gages on the Sacramento and San Joaquin River main stems because (1) other measures such as the Net Delta Outflow Index (https://water.ca.gov/Programs/Environmental-Services/Compliance-Monitoring-And-Assessment/Dayflow-Data) are highly correlated ($r^2 = 0.92$ during our study's time window) with the gage measurements we presented in the main text, meaning that this choice did not substantially affect our statistical findings or their interpretations and (2) this allowed us to maintain a consistent approach of using direct gage measurements among the three regions (Sacramento River, Delta, Bay). Thus, we could use these data to understand how flow, spawner abundances, and landscape setting govern the presence and abundance of juveniles throughout the Sacramento River, Delta, and Bay.

To prepare data for analyses related to habitat connectivity, we described the locations of observations relative to the landscape. We delineated the watershed into three regions: the Sacramento River (i.e., the river upstream of the Delta), the Delta (which includes a lower portion of the Sacramento River), and Bay (Fig. 1), and analyzed landscape effects in the Delta and Bay. We conceptualized the networked, channelized landscape of the Delta according to two axes: *distance downstream* and *distance off-main stem* of the Sacramento River. Distance off the main stem was described by in-water distances from a site to the Sacramento River main stem using the shortest path. This uses the Sacramento River main stem as a landmark of minimum distance off the main stem. Distance downstream was calculated by the shortest path from the Sacramento River mouth to a site (i.e., a measure of distance *upstream*). Its z score was then multiplied by -1 to calculate a measure of distance *downstream* so that is was a metric describing distances going toward the river mouth. This allowed its representation to be consistent with other landscape metrics that described sites in terms of increasing distances from the upper river reaches of accessible habitat toward the ocean. This effectively uses the Delta site closest to the Bay as a landmark of maximum distance downstream. In reality, the Delta's network of channels and directional flows connecting various shorelines present fish with a more complex route from the upper Sacramento to the Bay at the local scale. However, at our study's focal scale of the landscape, our landscape measurement approach resulted in clear gradients across the Delta consistent with our conceptualization of measuring distance relative to the ocean and off the main stem (Fig. A1), and we refer to "downstream" and "off main stem" in the main text for simplicity. The Delta is also fed by the San Joaquin River, but our preliminary analyses indicated that gradients of fish abundances in the Delta were predominantly driven by the Sacramento River. That is, the juvenile salmon entering the Delta are primarily spawned in the Sacramento River (consistent with current understanding of the system: Carlson and Satterthwaite, 2011), so our conceptualization of the Delta's landscape was georeferenced relative to the Sacramento River. This required us to remove observations from a small number of sites within the Delta along the San Joaquin River main stem because, due to the influence of the San Joaquin River on fish presence, observations at these sites were inconsistent with our conceptual landscape georeferenced by the Sacramento River. In the Bay, which is much less channelized than the Delta, we conceptualized the landscape according to one axis: distance *away* from the Sacramento River mouth (defined at Middle Ground Island) and toward the ocean, also using in-water distances. Thus, we describe the landscape in the Delta as downstream and off of the Sacramento River main stem and the landscape in the Bay as away from the Sacramento River mouth.

We pre-processed the data before analyses so that our comparisons more directly matched our hypotheses about the ecology of the system. First we limited analyses to the period between December and May when juveniles were present (Munsch et al., 2019). Second, we examined only those fish we defined as fry (< 55 mm). This was advantageous because (1) juvenile salmon use nearshore habitats differently as they develop (e.g., Munsch et al., 2016) and examining only the fry life history stage may reduce variations in habitat use not attributable to our focal hypotheses and (2) hatcheries release a substantial number of unmarked juvenile salmon. However, beginning in 1999, hatcheries almost ceased releasing salmon under 55 mm (Fig. A2), allowing us to infer that fish observed beginning in 1999 and less than 55 mm long were naturally spawned. We could then examine relationships between naturally spawning fish and juveniles <55 mm from 1999 - present with confidence that juvenile hatchery production was not substantially confounding our findings. Third, we described annual abundances of adult spawners excluding the Late Fall life history. This was appropriate because Late Fall juveniles rear upstream longer than other life histories and were therefore unlikely to be among our focal fish that were less than 55 mm long (Williams, 2006). We note that because spawner abundances are dominated by the Fall Run, this adjustment was unlikely to drastically affect our statistical findings. Fourth, to describe dynamic flow conditions within seasons, we summarized flow using 30 day running averages to capture long term effects of flow and, following Sturrock et al. (2019), 7 day ranges to capture short term effects of flow pulses. Fifth, we rounded (z-scored) flow variables to the nearest single decimal place so that its nonlinear effect on fry could be described by random walks (that often operate on discrete data), INLA's approach to parameterizing nonlinear functions (R-INLA.org). Parameters input into models are defined in Table A1.

Analysis

Our general approach was to use statistical models to quantify the influence of spawners, flow, and landscape on fry catches. Then, using the location of potential restoration sites within the landscape, we estimated fry catches at restoration sites depending on spawner and flow levels. We define metrics and their representations as variables in models in Tables A1 and A2, respectively.

We modeled the random variable fry catch **Y** and its realization $\mathbf{y_{i,t,s,v,m,w}}$ from observations ***i*** on date ***t*** (with dates for each water year indexed beginning on December 1 and ending May 31) in years with spawner counts ***s***, 30 day flow mean in the Sacramento River ***v*** (for sites in the Sacramento River and Delta regions), 7 day flow range in the Sacramento River ***z***, at site ***m*** in water year ***w*** (water years begin on October 1, which allows the term water year to describe continuous periods of annual fry presence from December to May) using a negative binomial hurdle model with probability of observing at least one fry ***π***, the expected fry counts conditional on seeing at least one fry **μ**, and a parameter defining overdispersion in variance ***k*** as

$$Pr(y_{i,t,s,v,z,m,w} = x)\begin{cases}1-\pi_{i,t,s,v,z,m,w} & \text{if } x=0\\ (\pi_{i,t,s,v,z,m,w})g(y_{i,t,s,v,z,m,w}) & \text{if x} > 0\end{cases}$$

where

$$g(y_{i,t,s,v,z,m,w}) = Pr[\mu_{i,t,s,v,z,m,w},k] = ZeroTruncNegBinom(\mu_{i,t,s,v,z,m,w},k)$$

$$E[y_{i,t,s,v,z,m,w}] = \pi_{i,t,s,v,z,m,n}\,\mu_{i,\,t,\,s,v,z,m,w}$$

$$Var[y_{i,t,s,v,z,m,w}] = \pi_{i,t,s,v,z,m,w}\,\mu_{i,t,s,v,z,m,w}(1+\ \mu_{i,t,s,v,z,m,w}(1-\pi_{i,t,s,v,z,m,w}+k))$$

and

$$logit[\pi_{i,t,s,v,m,w}] = \Upsilon_0+\Upsilon_1X_1+\Upsilon_2X_2+\Upsilon_3X_3+\Upsilon_4X_4+\Upsilon_5X_5+\Upsilon_6X_6+\ \Upsilon_7X_5X_6+f_1(t)+f_2(s)+f_3(v)+f_4(z)+m_a+w_b$$

$$log[\mu_{i,t,s,v,m,w}] = \beta_0+\ \beta_1X_1+\beta_2X_3+\beta_3X_4+\beta_4X_5+f_5(t)+f_6(s)+f_7(v)+\ f_8(z)+m_c+w_d$$

$$m_a\sim N(0,\sigma_a^2);\ w_b\sim N(0,\sigma_b^2);\ m_c\sim N(0,\sigma_c^2);\ w_d\sim N(0,\sigma_d^2)$$

where $\mathbf{X_1}$ and $\mathbf{X_2}$ are binary variables describing whether an observation occurred in the Delta or Bay, respectively (i.e., accounting for the effect of region by contrasting with the global intercepts β_0 and γ_0 such that, when β_1 and β_2 equaled zero, the global intercept represented the effect of occurring in the Sacramento River region), $\mathbf{X_3}$ is the distance off of the main stem (Delta sites only), $\mathbf{X_4}$ is the distance in downstream (Delta sites only), $\mathbf{X_5}$ is the distance away from the Sacramento River mouth (Bay sites only), $\mathbf{X_6}$ is flow (Bay sites only), and **f(.)** are nonlinear functions parameterized in INLA as a second order random walk. That is, following preliminary explorations examining for relationships between flow and fry, we parameterized our model to quantify nonlinear effects of flow in the Sacramento River and Delta (f_3 and f_6) whereas our model quantified a linear effect of flow in the Bay (Y_6) that interacted (Y_7) with distance from the Sacramento River mouth (Y_5). The linear interaction of flow and distance away from the Sacramento River mouth in the Bay represented an effect of flow extending fresh water (that fry appeared to prefer over saltwater) further seaward. The other nonlinear functions represented seasonal rise and fall in fry presence (f_1 and f_5) and potential density-dependent effects of spawners on fry production (f_2 and f_6). We used values of zero (i.e., means because variables were z-scored) to describe landscape and flow variables that were not applicable to an observation because they occurred in a region not described by that parameter. We modeled catch when present only for the Sacramento River and Delta because presence in the Bay was much lower than other regions, resulting in much fewer data points describing catch when present to analyze.

Supplemental to these analyses, we showed the effects of spawners and flow on fry using annual descriptors of spawners, flow, and fry that we related using commonly used stock-recruitment functions. While this approach was not conducive to projecting habitat occupancy at restored sites, it allowed us to encapsulate effects of spawners and flow on juvenile salmon abundances in one visual, thus improving communication of our results to a diverse audience of researchers, mangers, and stakeholders. Our general approach was to collapse many observations per year into annual indexes of fry densities, which we could then compare to spawner abundances and flow. Fry density indexes were generated by fitting models that described abundances in the Sacramento River and the Delta and measures of presence in the Bay among years, while accounting for region-specific landscape variables and phenology associated with individual sampling events. That is, density indexes were the expected number (count data) or probability of presence of fry (presence/absence data) on a typical day of the year and in a typical location within the landscape (Delta and Bay only). For fry in the Bay, we analyzed data only in February to March, when the overwhelming majority of fry were observed, and did not generate density indexes from 2007 or 2015 because, in these years the Bay's shorelines were sampled less than 30 times.

In the Sacramento River, we modeled the random variable fry counts **Y** and its realization $\mathbf{y_{i,t,m}}$ from observations ***i*** on date ***t*** (with dates for each water year indexed beginning on December 1 and ending May 31) at sites **m** with probability of observing at least one fry $\boldsymbol{\pi}$, the expected fry counts conditional on seeing at least one fry $\boldsymbol{\mu}$, and a parameter defining overdispersion in variance ***k*** as

$$Pr(y_{i,t,m} = x)\begin{cases} 1-\pi_{i,t,m} & \text{if } x = 0 \\ (\pi_{i,t,m})g(y_{i,t,m}) & \text{if x} > 0 \end{cases}$$

where

$$g(y_{i,t,m}) = Pr[\mu_{i,t,m},k] = ZeroTruncNegBinom(\mu_{i,t,m}, k)$$

$$E[y_{i,t,m}] = \pi_{i,t,m}\,\mu_{i,t,m}$$

$$Var[y_{i,t,m}] = \pi_{i,t,m}\,\mu_{i,t,m}(1 + \mu_{i,t,m}(1 - \pi_{i,t,m} + k))$$

and

$$logit[\pi_{i,t,m}] = \Upsilon_w X_w + f_1(t) + m_a$$

$$log\left[\mu_{i,t,m}\right] = \beta_w X_w + f_2(t) + m_b$$

$$m_a \sim N\left(0, \sigma_a^2\right); m_b \sim N\left(0, \sigma_b^2\right)$$

where **X_w** is a vector describing the water year **w** as a categorical variable, parameters Υ_w and β_w describe the presence/absence and abundance when present components, respectively, of annual density indexes of juveniles in water year **w**, and **f(.)** are nonlinear functions parameterized in INLA as a second order random walk (these effects accounting for the day of the year were nearly identical to those of the previous models, shown in panels "day of year" of Fig. 3). That is, a negative binomial hurdle model that quantifies (1) probability of fry presence and (2) abundance when fry are present. Parameter estimates for Υ_w and β_w were used to calculate annual fry density index **D** as

$$D = logit^{-1}\left(\Upsilon_w\right) e^{\beta_w},$$

which described the expected fry catch in one sample in a given year **w** after accounting for seasonality and site specific factors. There were no global intercepts included in the models so that differences among years were entirely captured by annual index parameters.

In the Delta, we used the same approach, except we accounted for distances off the main stem $\mathbf{X_1}$ and downstream $\mathbf{X_2}$ so that annual indexes in the Delta also corresponded to catches in typical locations within the Delta's landscape:

$$logit\left[\pi_{i,t,m}\right] = \Upsilon_w X_w + \Upsilon_1 X_1 + \Upsilon_2 X_2 + f_1(t) + m_a$$

$$log\left[\mu_{i,t,m}\right] = \beta_w X_w + \beta_1 X_1 + \beta_2 X_2 + f_2(t) + m_b$$

$$m_a \sim N\left(0, \sigma_a^2\right); m_b \sim N\left(0, \sigma_b^2\right)$$

In the Bay, we modeled fry presence but not abundance when present (because there were fewer observations of abundance when present), did not specify a phenology parameter (because we examined only the peak of presence from February to March), and modeled presence as varying in relation to distance away from the Sacramento River mouth $\mathbf{X_1}$ so that annual indexes in the Bay corresponded to catches in typical locations within the Bay's landscape:

$$logit[\pi_{i,t,s,d}] = \Upsilon_w X_w + \Upsilon_1 X_1 + m_a$$

$$m_a \sim N(0, \sigma_a^2).$$

Using these annual density indexes, we quantified the influence of spawner abundances and flow on fry densities (i.e., a stock-recruitment relationship) and examined patterns in fry densities among regions within years. Detailed below, we considered a range of potential models that did or did not include effects of spawners and flow and did or did not allow for diminishing returns in fry per spawner. To define the stock-recruitment relationship, we used data collected in the Sacramento River because this region was closest to spawning grounds and presumably offered the strongest signal relating juveniles to adults. We examined many candidate models that compared densities of fry to spawner abundances and flow, with flow quantified as the annual median flow values of the Sacramento River between December and May. Median values of flow were log-transformed to reflect diminishing returns of additional flow on increasing fry presence (which we found in the primary analyses described in the Results). Flow values were then standardized as follows. For models with only an effect of flow, we standardized flow to have minimum values of 0.01 by subtracting from each flow value the minimum flow value and adding 0.01. This allowed minimum flow values to correspond to an effect of zero added fish presence, and models using these values therefore did not require an intercept. For models adding a flow parameter to the stock recruitment relationship, we standardized flow by converting it to a z-score. This meant that an average value of flow would correspond to zero effect of flow, allowing model parameters to describe productivity and density-dependent effects under average conditions. Standardizing flow differently did not affect models' AIC values, which we used to evaluate support among models. The models and associated hypotheses relating spawners **S** to fry density **R** are as follows, with the parameter **v** describing effects of flow **F**, with intrinsic population growth rate (i.e., the density independent component of recruitment) described by parameter **a**, and limitations to population growth rates as spawner abundances increase described by density-dependent parameter **b**. We followed protocol by Quinn II and Deriso (1999) and log-transformed both sides of equations to impose a multiplicative error structure to the model. This structure was likely to fit the data better because, in stock-recruit models, variance in errors tends to increase with prediction estimates.

The hypotheses relating fry to flow and spawners (and normally distributed error ε) and their associated equations are as follows:

Fry density is a linear function of spawner abundance:

$$log\ (R)\ =\ log\ (a)\ +log\ (S) + \varepsilon$$

Fry density is a linear function of spawner abundance and flow:

$$log\ (R)\ = log\ (a) + log\ (S)\ +vF + \varepsilon$$

Fry abundance is a linear function of flow:

$$log\ (R)\ =\ vF + \varepsilon$$

Fry density is a function of adult abundances, with diminishing returns of juveniles per spawner as spawner abundances increase (i.e., a Beverton-Holt relationship):

$$log\ (R) = \log\ (a) + \log\ (S) - \log\ (1 + bS) + \varepsilon$$

Fry densities follow the same Beverton-Holt relationship with spawners, but are also influenced by flow:

$$log\ (R) = \log(a) + \log(S) - \log(1 + bS) + vF + \varepsilon$$

Fry densities are a function of adult abundances, with diminishing returns and overcompensation of juveniles per spawner as spawner abundances increase (i.e., a Ricker relationship):

$$log\ (R) = log(a) + log\ (S) - bS + \varepsilon$$

Fry densities follow the same Ricker relationship with spawners, but are also influenced by flow:

$$log(R) = log(a) + log(S) - bS + vF + \varepsilon$$

We implemented analyses in R (R Core Team, 2019) using the packages INLA (Rue et al., 2009) and FSA (Ogle et al., 2018). We used the Bayesian R package INLA for the within-year analyses because it analyzed large datasets efficiently and provided requisite parameter options. We used vague priors so that posteriors were informed predominantly by the data. The exception to this was on random walk parameters defined as a value **μ** along a function at step **t** equaling the value in a previous step **t-1** plus noise **v** that is normally distributed with a standard deviation σ_v, which we constrained by penalized complexity priors stating that the probability **α** of this standard deviation exceeding a value **U** of 1 (for nonlinear effects of day of year and spawners) and 0.1 (for nonlinear effects of flow) was 0.1:

$$\mu_t = \mu_{t-1} + v_t$$

where

$$v_t \sim N(0, \sigma_v^2)$$

and

$$Prob(\sigma_v > U) = \alpha.$$

This constrained the random walks to smoother relationships that were less likely to overfit nonlinear trends to the data (Zuur et al., 2018), a step analogous to limiting the number of knots in generalized additive models. Interannual analyses examining stock-recruit models used the conventional frequentist approach (Ogle et al., 2018) because these datasets were much smaller and their model parameterizations simpler.

Appendix Figures

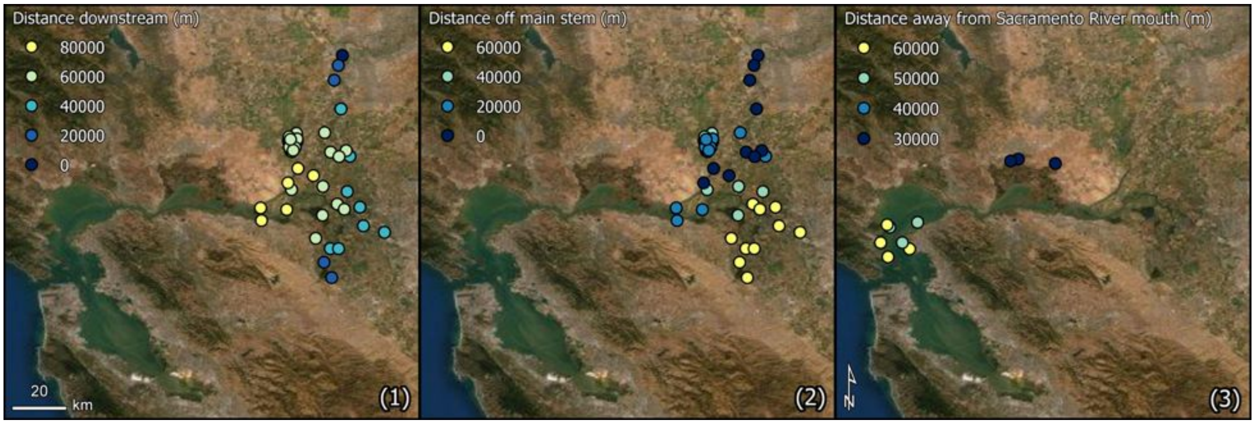


Figure A1. Maps of the Delta and Bay showing realizations of landscape metrics. Map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. Base Map Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community. Hydrography Sources: USGS.

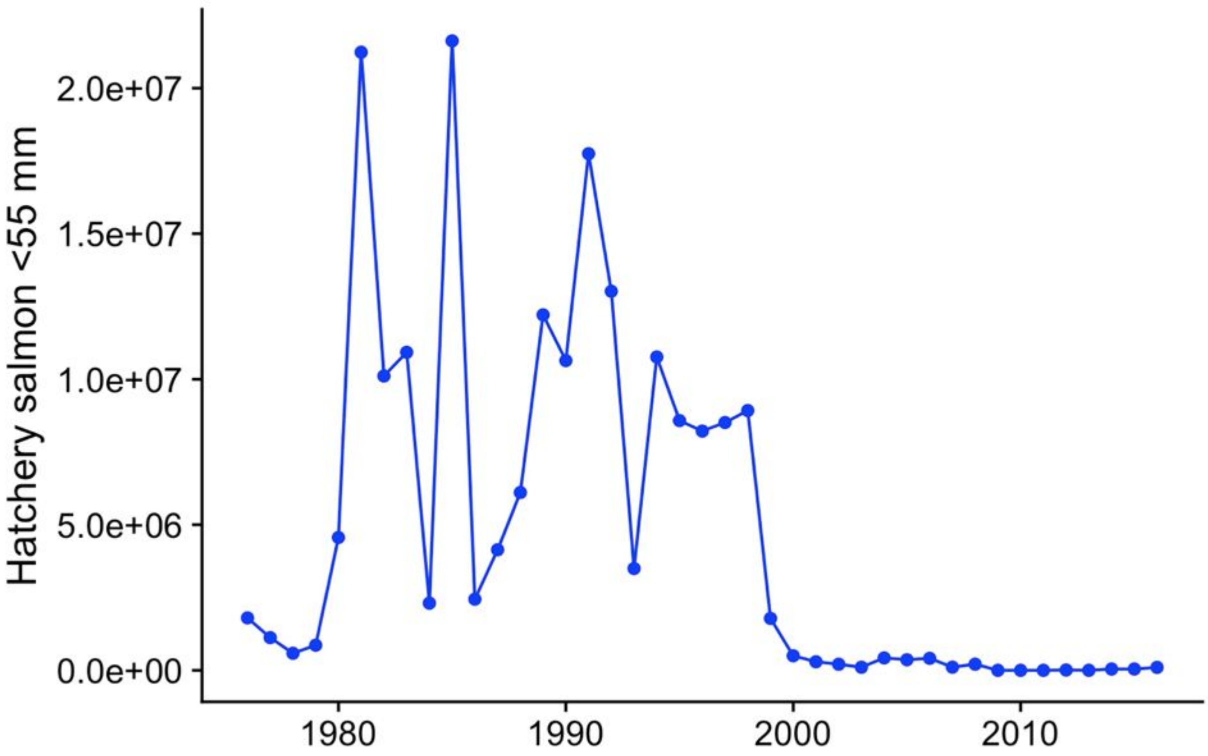


Figure A2. Abundances of hatchery fry released into the Sacramento River. Our stock-recruit analyses examined fry <55 mm in the Sacramento River beginning in 1999 to examine a time period with minimal hatchery influence on the abundance of these smaller fish.

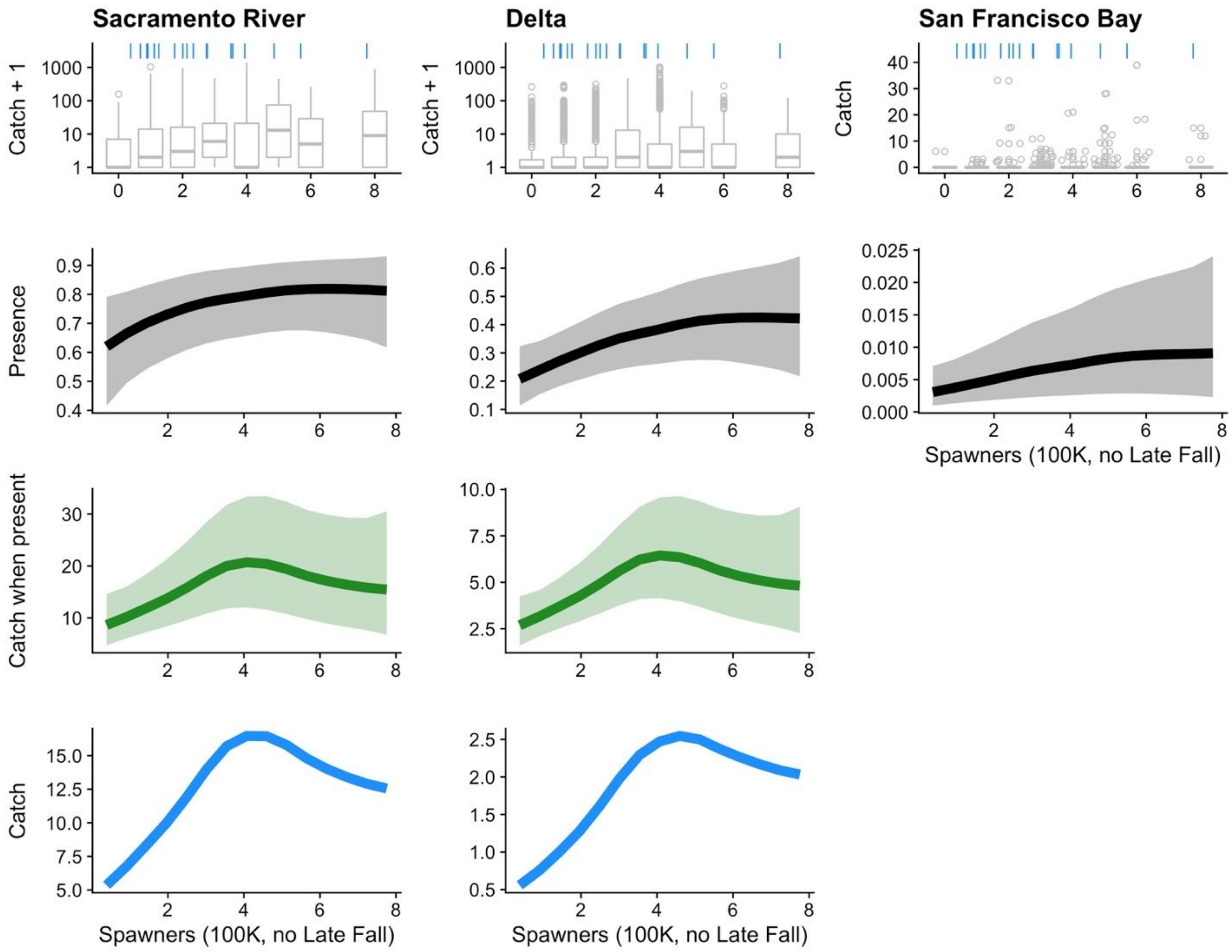


Figure A3. Influence of spawners on fry catches. **Top:** Raw data of fry catches compared to counts of spawners contributing to annual cohorts. For this and subsequent figures, the independent variable (spawners here) is binned to allow for boxplots that show distribution of fry catches. Blue vertical lines indicate individual annual spawner counts. **Middle:** Model predictions and 95% credible intervals of the probability of presence and catch when present of fry as a function of spawner counts. **Bottom:** Expected catch, estimated by the product of the probability of presence and catch when present (i.e., the two middle rows). For this and subsequent figures, models predicted fish responses according to one variable (i.e., spawners, 30 day flow mean, 7 day flow range, or landscape) while holding the other variables at their means, and for January 10, a day of year that corresponded to typical seasonal fish presence (Fig. 3).

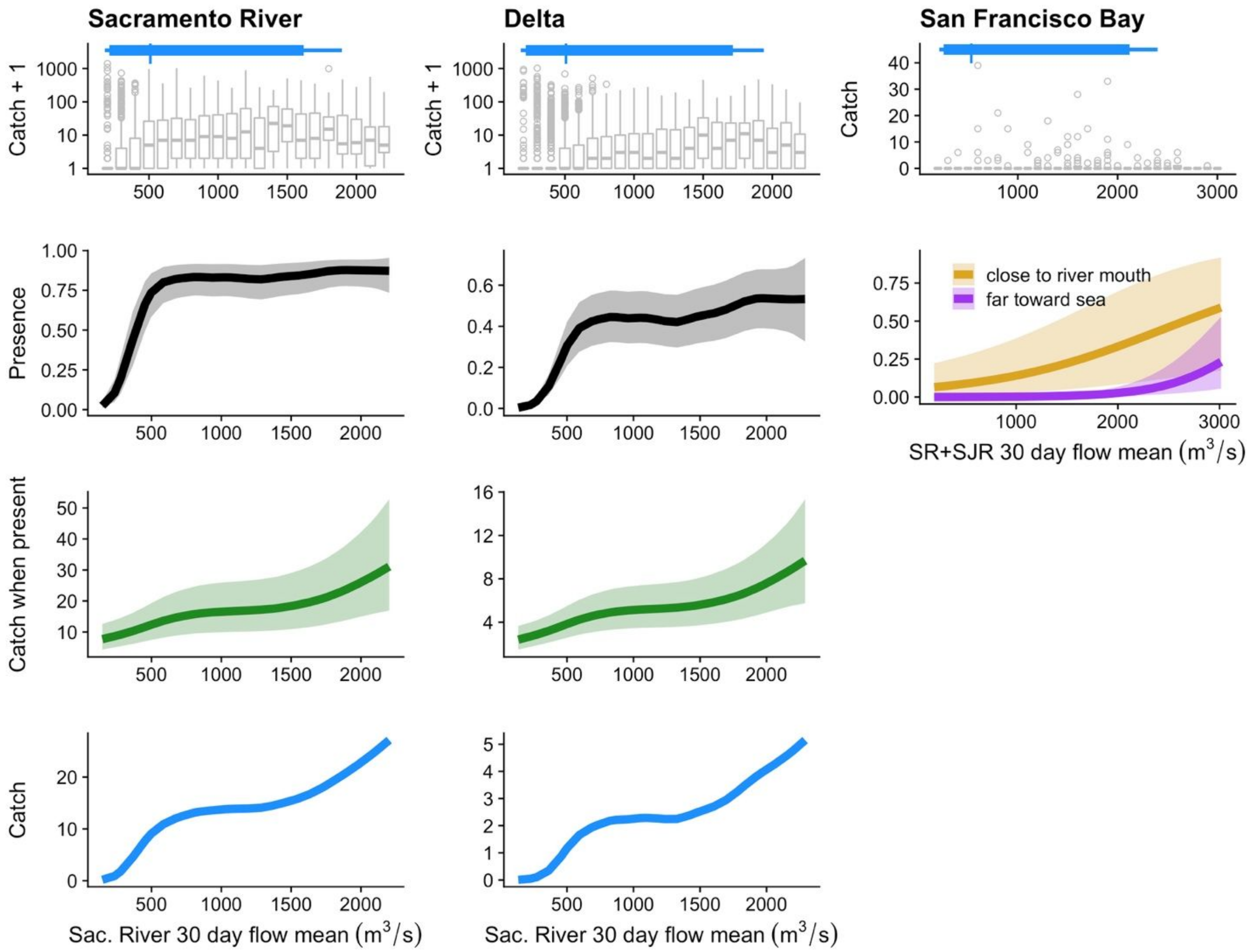


Figure A4. Influence of 30 day flow means on fry catches. **Top:** Raw data of fry catches compared to 30 day flow means. Blue horizontal lines indicate the middle 90 (thick) and 95 (thin) percent of flow observations. Blue vertical line indicates median flow. **Middle**: Model predictions and 95% credible intervals of the probability of presence and catch when present of fry as a function of flow. In the Bay, predictions are shown for the sites least and most away from the Sacramento River mouth to illustrate the interactive effect of the landscape with flow. SR: Sacramento River. SJR: San Joaquin River. **Bottom:** Expected catch, estimated by the product of the probability of presence and catch when present (i.e., the two middle rows).

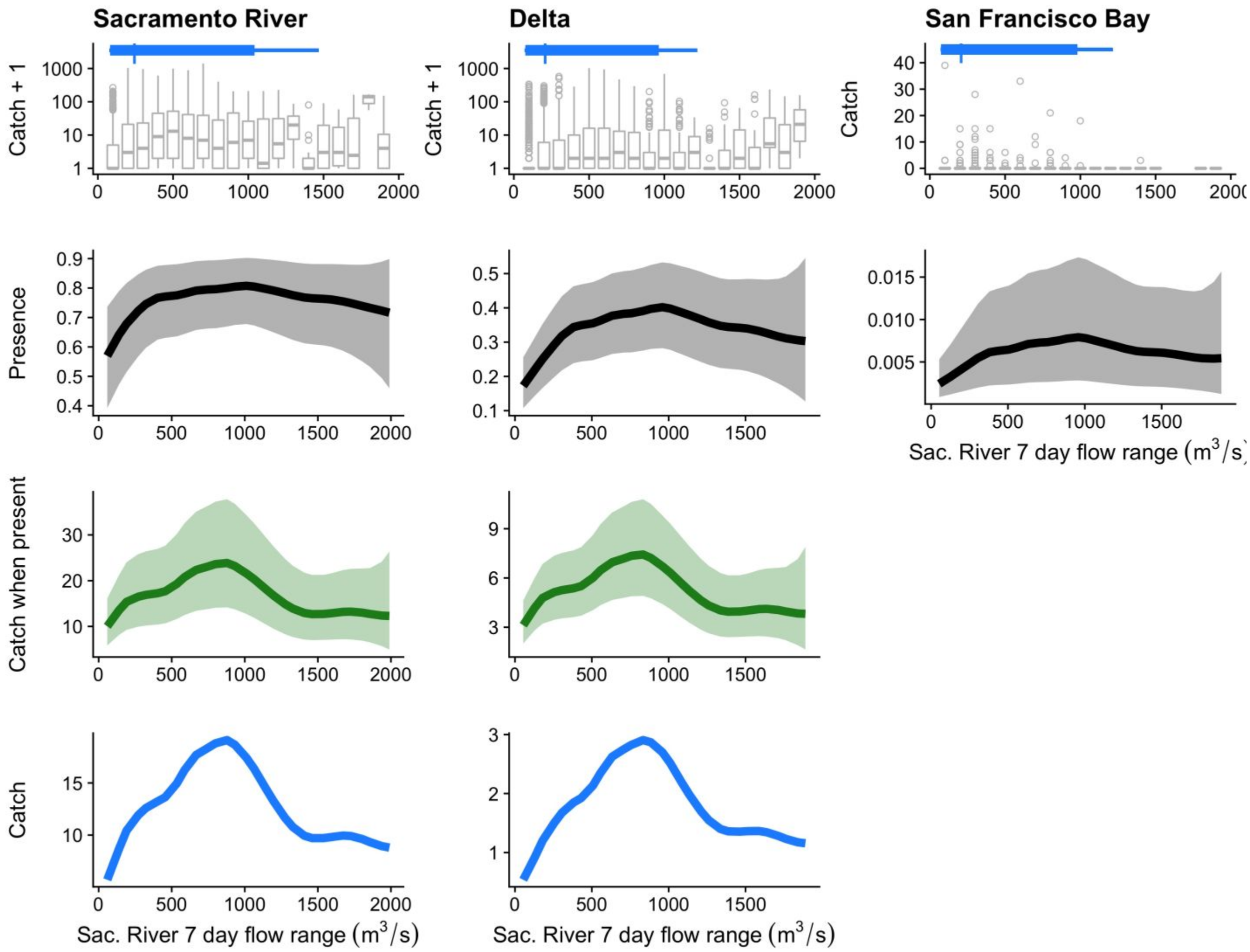


Figure A5. Influence of 7 day flow range on fry catches. **Top:** Raw data of fry catches compared to 7-day flow ranges. Blue horizontal lines indicate the middle 90 (thick) and 95 (thin) percent of flow observations. Blue vertical line indicates median flow. **Middle**: Model predictions and 95% credible intervals of the probability of presence and catch when present of fry as a function of flow. **Bottom:** Expected catch, estimated by the product of the probability of presence and catch when present (i.e., the two middle rows).

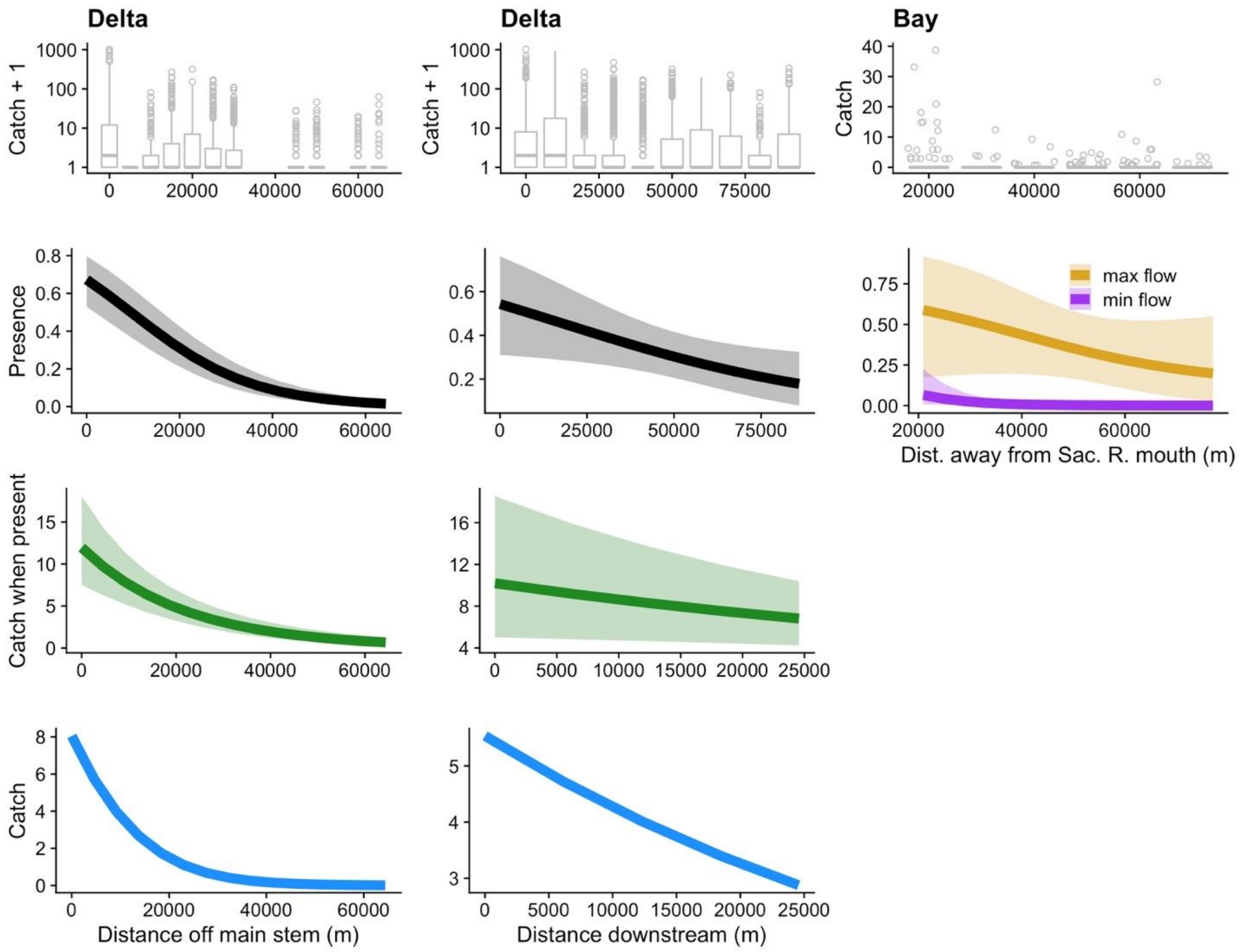


Figure A6. Influence of the landscape on fry catches. **Top:** Raw data of fry catches compared to locations with the landscape. Locations within the landscape are binned to allow for boxplots to show the distribution of fry catches. **Middle:** Model predictions and 95% credible intervals of the probability of presence and catch when present of fry as a function of landscape metrics. In the Bay, predictions are shown for the highest and lowest flows observed to illustrate the interactive effect of flow with the landscape. **Bottom row:** expected catch, estimated by the product of the probability of presence and catch when present (i.e., the two middle rows).

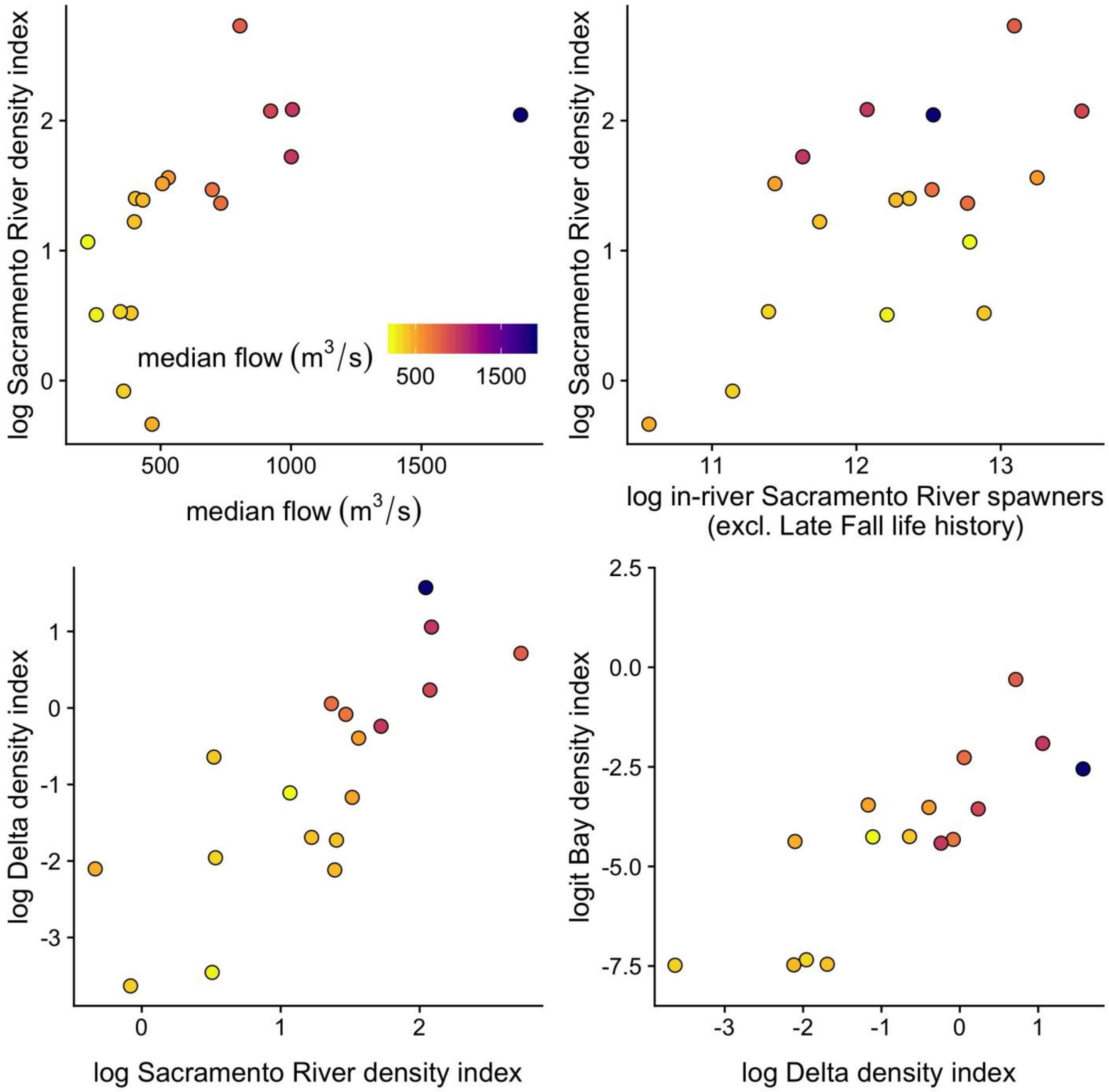


Figure A7. Annual indexes of fry density compared to flow, spawner abundances, and across regions. Points are colored in all panels by flow.

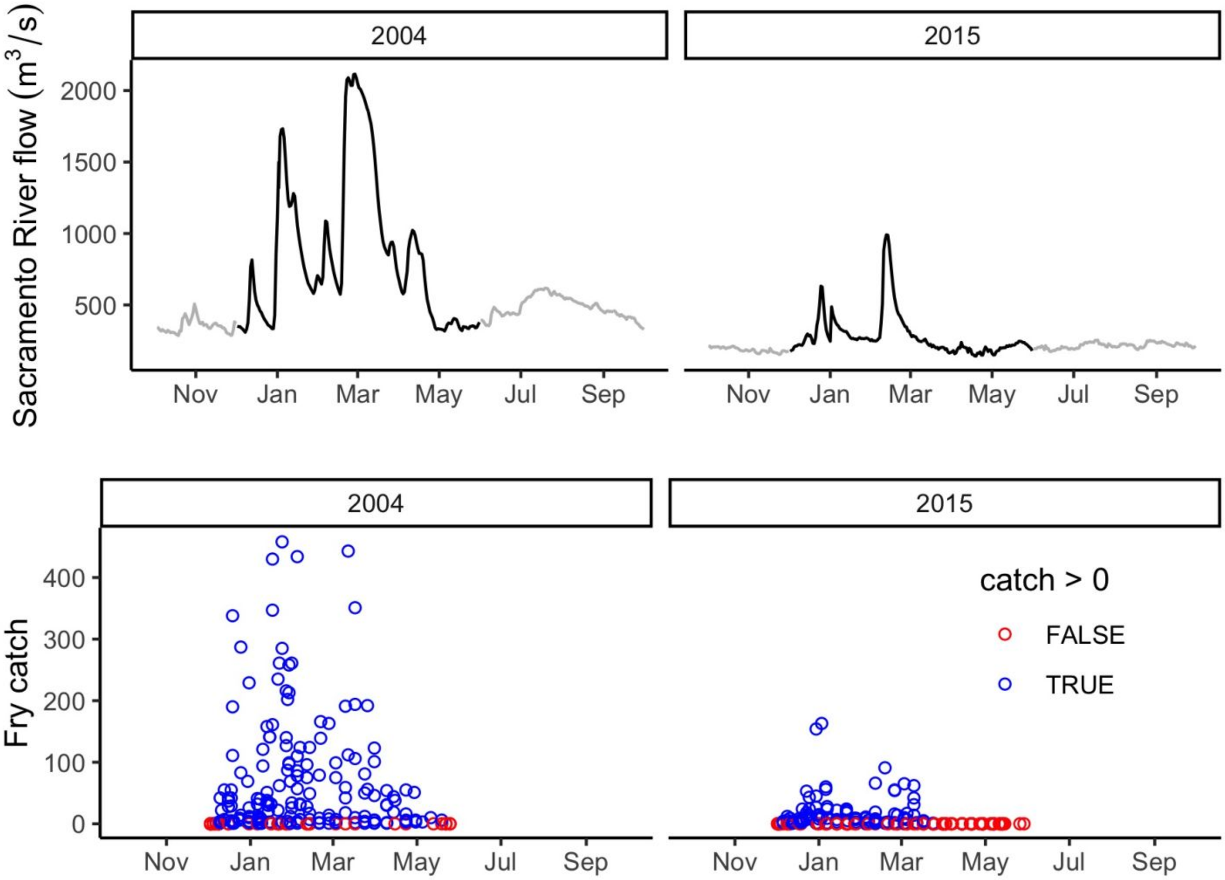


Figure A8. Flow and fry catches compared between two select years of "good" (2004) and "bad" (2015) flow conditions. A "good" flow regime maintains flow above ≈500 m^3/s and is punctuated by pulses. Fry catches are shown for December – May (i.e., the time window examined in this study) and flows during the same time period are shown in black rather than grey.

Appendix Tables

Table A1. Definitions of metrics used in models describing the distribution and density of salmon fry.

Region	Metric	Definition
All	Spawners	Abundance of spawning adults in the Sacramento River during the most recent reproductive season, excluding the Late Fall life history type (source: GrandTab)
Sacramento River	Annual median flow	Median flow on Sacramento River main stem between December and May (source: USGS gage 11447650)
Sacramento River and Delta	30 day flow mean	30 day moving average (i.e., previous 30 days) of flow on Sacramento River main stem (source: USGS gage 11447650)
Bay	30 day flow mean	30 day moving average (i.e., previous 30 days) of the sum of flow on Sacramento and San Joaquin River main stems (sources: USGS gages 11447650 and 11303500)
All	7 day flow range	7 day moving range (i.e., previous 7 days) of the difference between the highest and lowest flow values
Delta	Dist down	Distance downstream, georeferenced by the most seaward Delta site
Delta	Dist off	Distance off of the Sacramento River main stem
Bay	Dist away	Distance away from the Sacramento River mouth, as moving toward the Pacific Ocean, georeferenced by Middle Ground Island
All	Density index	Annual index of fry density. This is the expected number (Sacramento River and Delta) or presence (Bay) of fry per net after controlling for seasonality and landscape (Delta and Bay) effects.

Table A2. Definitions of variables used in analyses.

Variable	Definition
Y	Fry count
$\boldsymbol{\pi}$	Fry presence
μ	Fry counts conditional on presence
i	Observation
t	Date (Beginning Dec. 1 and running continuously to May 31)
s	Spawner count
v	30 day flow mean
z	7 day flow range
m	Site
w	Water year (Period of Oct. 1 - Sep. 31 indexed by calendar year on which the period ends)
R	Annual fry density index (Expected counts of fry after removing effects of phenology, repeated measures at sites, and the landscape)
S	Spawner count
F	Flow (median from Dec – May for each water year)
a	Density independent population growth parameter
b	Density dependent population growth parameter

Table A3. Candidate models examining effects of spawners and flow on fry densities in the Sacramento River. Models are ranked by ΔAIC.

Model	AIC	ΔAIC
Beverton-Holt and flow	26.83	0
Ricker and flow	27.25	0.42
Flow	36.71	9.88
Linear spawners and flow	37.5	10.67
Beverton-Holt	37.96	11.13
Ricker	38.29	11.46
Linear spawners	40.74	13.91

Table A4. Summary statistics of the top ranked models predicting fry density as a product of spawner abundances and flow. The a parameter describes productivity, the b parameter describes density dependence, and the F parameter describes flow.

model	parameter	estimate	se	p
Beverton Holt and flow	a	4.16	1.49	0.01389
	b	0.608	0.379	0.129
	F	0.446	0.111	0.001147
Ricker and flow	a	3.13	0.592	0.0000916
	b	0.222	0.0581	0.00166
	F	0.451	0.113	0.00117

References

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