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Migratory phenology and spatial distributions of a recovering Chinook salmon run in a flow regulated creek, considerations for management

By

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Abstract

Salmon populations are declining globally, and there are few examples of successful conservation science culminating in partial or fully-recovered runs. We report on the status of a recovering run of anadromous Chinook salmon (*Oncorhynchus tshawytscha*) in Lower Putah Creek, California. Following environmental litigation in 2000, changes to flow management, in addition to restoration initiatives, habitat conditions became suitable again for Central Valley fall-run Chinook salmon. Suitability was confirmed in this study based on annual return of spawning adults and juvenile production in Lower Putah Creek over a six-year period. Yet despite initial optimism, we identify several factors impeding a more full recovery of salmon in the watershed. Bottlenecks include fish passage barriers that influence timing of adult up-river migrations and juvenile smolt outmigration survival. Additionally, a mass mortality event (fish kill), including pre-spawn adult salmon during fall 2021 demonstrated critical water quality issues that will be increasingly amplified under projected climate change conditions. Thus, while carcass surveys and downstream migrant trapping suggest past restoration actions have generally improved habitat for native fishes including salmon, additional management is still needed. Similar to other long-term studies of restoration, this work also demonstrates that ecological recovery in freshwater ecosystems is frequently slow, non-linear and incomplete. A more robust recovery of salmon in Putah Creek, and similarly reconciled ecosystems, will require science, long-term data collection and broad collaborations. Nevertheless, Putah Creek remains an ecological bright spot, and thus an example of native salmon recovery potential, especially in California and the Pacific Coast.

Introduction

The Central Valley region of California once supported abundant and diverse salmon populations in terms of both richness and intraspecific run-timing phenotypes (e.g., spring-, fall-, late-fall, winter-run Chinook salmon *Oncorhynchus tshawytscha*) (Yoshiyama et al. 1998). This diversity evolved, in part, as an adaptation to variable environmental regimes (e.g., water temperatures) to support multiple migratory behaviors (Quinn et al. 1997; Waples et al. 2008). Populations of Chinook salmon found in Central Valley rivers occur at the southern edge of the species geographic range and are adapted to Mediterranean climates. Such ecosystems are characterized by high spatiotemporal heterogeneity in water availability (e.g., high flows during winter followed by low flows during summer) (Moyle 2002; Grantham et al. 2010; Kiernan et al. 2012). As such, salmonids, including Chinook salmon, have historically used these environments to support a rich diversity of run types that vary primarily in timing of reproduction and juvenile development.

Through a combination of habitat loss and degradation (McClure et al. 2008; Zeug et al. 2011), hatchery influences (Goodman 2005; Araki et al. 2008; Chilcote et al. 2011) and genetic homogenization (Williamson and May 2005), salmon are broadly declining throughout the Central Valley and elsewhere (Yoshiyama et al. 1998; Moyle et al. 2017). Within the Central Valley, water storage, extraction and conveyance systems have compressed stream flow variability and are linked to loss of life-stage specific habitats for anadromous fishes (Lindley et al. 2006; Murchie et al. 2008). As a result, two of four recognized Central Valley runs of Chinook salmon (spring- and winter-run) are now listed under the United States Endangered Species Act (NMFS 1999, 2005). Fall-run Chinook salmon remain the most abundant run of Chinook salmon in the Central Valley (Yoshiyama et al. 1998), yet anthropogenic landscape changes (e.g., farming land use) and water management structures (e.g., dams and weirs) have altered habitats and hydrology such that they are unlike the historical regimes to which native California salmon are adapted (Waples et al. 2009; Moyle 2014).

Reductions in natural streamflow variability affect the physical and biological processes of rivers (Poff et al. 1997, 2006; Allan and Castillo 2007) and the species that depend on them (Marchetti and Moyle 2001; Jager and Rose 2003; Naiman et al. 2008; Moyle 2014). Yet, hydrologic regimes varying in streamflow frequency, duration, magnitude, rate of change, and predictability (Poff et al. 1997; Lytle and Poff 2004; Arthington et al. 2006; Waples et al. 2009) are especially critical to the maintenance of Chinook salmon life-history diversity (Bunn and Arthington 2002; Zeug et al. 2011, 2014; Beechie et al. 2013). As such, changes to the natural flow regimes associated with anthropogenic disturbance are broadly known to negatively impact Chinook salmon (Lytle and Poff 2004).

Major rivers across the Central Valley (e.g., Sacramento and San Joaquin Rivers) have been extensively modified for water management in order to supply reliable water sources for communities and agricultural uses (Beechie et al. 2006; Grantham and Moyle 2014; Moyle 2014). However, under current conditions, low flows typical of summers in Mediterranean climates often coincide with increased water demand and extraction for human uses, particularly crop irrigation (Grantham et al. 2010). Disjointed timing of environmental water availability and urban/agricultural water demand is present throughout the Central Valley of California. Subsequently, water managers have designed and applied regulated flow regimes that attempt to restore river functionality and benefit ecosystem processes and species, particularly anadromous salmon (Healey 1991; Poff et al. 1997; Lytle and Poff 2004; Williams 2012; Sturrock et al. 2015; Yarnell et al. 2015, 2020).

Lower Putah Creek, located in the Sacramento River watershed, has been managed to produce a flow regime aimed at recovery of native fishes, with a particular focus on fall-run Chinook salmon (Kiernan et al. 2012). Historical flows in Putah Creek ranged widely prior to dam construction (43.2 to $1.7\text{B m}^{-3} \text{y}^{-1}$) depending on water year (Smith 1991). During high flow periods, riparian flooding was common. Conversely, during droughts, segments of the creek became intermittent, and fishes were often restricted to large pools (Shapovalov 1947; Smith 1991; Kiernan et al. 2012). However, years in

which the creek remained connected to the Sacramento River, anadromous fishes, such as Pacific salmonids and lamprey, were able to successfully access Putah Creek and reproduce (Shapovalov 1947; Smith 1991).

Numerous anthropogenically-induced disturbances have greatly affected Putah Creek and its natural flow regime. In 1948, Putah Creek was permanently diverted around the city of Davis and directed into a US Army Corps of Engineers man-made channel (Smith 1991). Later, two dams were constructed to provide water for municipal and agricultural needs across Solano County (e.g., Monticello Dam and the Putah Diversion Dam). Construction of dams immediately affected the spatial distribution of fishes (Moyle et al. 1998; Kiernan et al. 2012) and precipitated the decline of salmon in the watershed (Moyle et al. 1998; Moyle 2014). Although regular water releases from the Putah Creek Diversion Dam (hereafter PDD) began in 1970, providing patchwork refugia for native fishes, permanent streamflow remained restricted to only those areas directly below the PDD in Lower Putah Creek for several decades (Moyle et al. 1998; Kiernan et al. 2012).

Civic action in response to observed fish kills during summer 1989 led to a final legal settlement in 2000 known as “The Putah Creek Accord” (the Accord, hereafter) (Putah Creek Council vs. Solano Irrigation district and Solano County Water Agency, Sacramento Superior Court Number 515 766; Moyle et al. 1998; Kiernan et al. 2012). The Accord settlement dictated immediate implementation of components of a natural flow regime in Lower Putah Creek such that “continuous surface water” be supplied from the PDD to the western boundary of the Yolo Bypass. Notably, the Accord outlined, among other flow directives, spawning and rearing flows for native fishes as well as supplemental pulse flows that, when possible, would attract anadromous fishes to Putah Creek. To date, this implemented flow regime has provided cool, flowing water during biologically relevant periods for native fauna (Rosenzweig 2003).

Subsequent to these changes, there has been a resurgence in native fishes in Lower Putah Creek, including Chinook salmon (Marchetti and Moyle 2001; Kiernan et al. 2012; Jacinto 2020). Small numbers of spawning adult Chinook salmon have been observed since 2003; however, consistent monitoring of this recovering Chinook salmon run began in 2016, coincident with larger numbers of returning adults (Table 1). Early investigations into the re-emerging population indicated pioneering Chinook salmon were primarily of hatchery-origin and of a young age-distribution (Willmes et al 2021a). While robust production has been observed in the juvenile Chinook salmon population (e.g., >33,000 sampled juveniles in 2018, Table 1), we know little about their outmigration success and habitat use.

Here, we examined six years (2016-2021) of data on fall-run Chinook salmon escapement, juvenile production, and one year of juvenile out-migration dynamics in Lower Putah Creek. Ultimately, we were interested in generating improved understanding of factors limiting Chinook salmon recovery. Adult carcass surveys and downstream juvenile migrant trapping were used to describe the migration phenology of returning adults and outmigrating juveniles, and to characterize patterns of habitat use and distribution within the creek to better aid conservation efforts and restoration actions broadly. Results from this research will be used to inform adaptive conservation management of water and anadromous salmonids in Putah Creek, and potentially other reconciled streams where habitats are impacted by dams and flow regulation.

Field Methods & Sample Collection

Study Area

The headwaters of Putah Creek are located in the Coast Range of California and flow east until impounded by multiple dams. As a part of the US Bureau of Reclamation's Solano Project, the Monticello Dam and PDD were constructed in 1957, forming Lake Berryessa and Lake Solano, respectively. At the PDD, water is either diverted to the Putah South Canal, a conveyance system for agricultural purposes in Solano County, or released into Lower Putah Creek, the focal site of this study.

Below the PDD, Lower Putah Creek continues to flow east ~42 river kilometers (rkm) until reaching its terminus with the Sacramento River at the Yolo Bypass (a managed floodplain), where it meets and drains through the Cache-Linsey slough complex. In addition to the two larger dams in the upstream tributary reaches of Putah Creek, the system is also constrained by an earthen road crossing and a privately operated check dam located two rkm upstream of the creek's terminus with the Yolo Bypass. The check dam does not permit environmental flows downstream of its location until flashboards are removed for fish passage in late October through early spring.

Carcass Surveys

Beginning in 2016, weekly (early November through mid-January) adult salmon carcass collections were performed each year with the primary objectives of (1) describing phenology of returning Chinook salmon, (2) assessing spawning distributions, and (3) measuring the proportion of hatchery-origin Chinook salmon that strayed into Lower Putah Creek using Coded Wire Tags (CWTs). Surveys consisted of visual observation and collection of carcasses throughout 21 rkm of Lower Putah Creek beginning immediately downstream of the PDD. Initial surveys established that upstream reaches of Lower Putah Creek represented the greatest potential for recovery of carcasses, as these sites were characterized by habitat features suitable for spawning (i.e., optimal water temperatures and improved channel complexity associated with recent restoration activities). Therefore, between 2016 and 2019, Lower Putah Creek was divided into four sampling sections (A-D; Figure 1) representing a range of habitat conditions along the longitudinal profile of the creek. During subsequent years (i.e., 2020 and 2021) various impediments to fish passage arose that required surveys to be shifted downstream after repeatedly identifying carcasses in distinct downstream locations. For instance, an unusually large beaver dam was identified during fall of 2020 that truncated upstream movements by adult Chinook salmon as water levels receded (Figure 1), and an unseasonable collapse of dissolved oxygen following a large storm in the fall of 2021 resulted in the recovery of Chinook salmon carcasses in a limited area

(approximately 1.5 rkm) immediately downstream of the check dam. Accordingly, additional surveys were conducted downstream with two additional survey sections during 2020 (E-F), and a third additional reach during 2021 (G).

All carcasses recovered during surveys were spatially referenced using a hand-held GPS device (Garmin GPSmap 78sc) and measured for fork length (mm). Presence or absence of an adipose fin was documented for each carcass recovered and it was assumed that salmon exhibiting an adipose fin clip originated from a hatchery (Nandor et al. 2010). If a carcass had a clipped adipose fin, or if the mark was unclear, the snout was sampled for a Coded Wire Tag (CWT). As part of the California Department of Fish and Wildlife (CDFW) Constant Fraction Marking/Tagging Program, beginning in 2007, approximately 25% of all hatchery released salmon are tagged (Nandor et al. 2010). Chinook salmon snouts were delivered to the CDFW Coded Wire Tag Laboratory in Sacramento, California where CWTs were removed, if present, and analyzed (see below). Final determination of origin was therefore made for a subsample of fish based on CWT recovery results. Further, to better understand whole-system phenology, daily capture events of adult Chinook salmon in the Toe Drain, located downstream of Putah Creek in the slough complex, were aggregated from 1999 to 2017 using data provided by the California Department of Water Resources Yolo Bypass Fish Monitoring Program (<https://portal.edirepository.org/nis/mapbrowse?packageid=edi.233.2>).

Downstream Migrant Trapping

A rotary screw trap was used to estimate the potential for juvenile salmon production in Lower Putah Creek. The rotary screw trap (RST) was also used to sample fish for acoustic telemetry in order to characterize juvenile Chinook salmon outmigration dynamics. During water years 2017, 2018, 2019 and 2021, a 1.5m diameter RST was deployed 9 rkm downstream of the PDD. The location of RST operation was selected as the furthest downstream location with sufficient depth and flow velocity to operate the trap.

Due to sustained high flow events in spring of 2017 and 2019, the RST was not deployed for safety and logistical reasons until later in the season; as a result, the number of salmon captured in the trap varied across years (Table 1). Additionally, in 2020, due to logistical constraints imposed by the COVID-19 pandemic that impacted access within private property, a fyke net was operated 12 rkm downstream of the PDD at a site without sufficient depth and velocity for the RST. Therefore, excluding years for which winter flows precluded safe sampling for extended windows, the RST was deployed in early spring and operated consistently throughout summer until water temperature increased to 21°C, at which time the RST was removed.

During deployment, the RST was fished 24 hours a day, seven days a week - excluding periods of overbank flow when the RST cone was raised for safety concerns - and checked daily. The frequency of sampling at the RST increased based on debris load, flow, and capture rates. The trap was checked a minimum of twice within the same 24-hour period during pulse flow events to reduce mortality of juvenile Chinook salmon. Areas of fish refuge were created for salmon within the live box to minimize predation events by larger native and nonnative predators. Each day, contents of the live box were removed, identified, and enumerated; 100 Chinook salmon and 25 of every other species encountered were haphazardly sampled for length and weight measurements.

Acoustic Telemetry

Fall-run Chinook salmon smolts captured using the RST during spring 2021 were subsampled for use in an acoustic telemetry study to identify and evaluate patterns of downstream migration and to approximate residence time in the creek. Tagging Chinook salmon using acoustic transmitters (tags) started on 12 April 2021 and concluded on 25 May 2021. Tagging events occurred whenever five or more fish of appropriate size were captured in the RST and tagging continued until a total of 170 individuals were tagged and released.

The selection of individuals to be tagged was determined by weight on the day of tagging. Juvenile Salmon Acoustic Telemetry System (JSATS transmitters, Model SS400; Advanced Telemetry Systems, St. Paul, Minnesota) were surgically implanted intraperitoneally using methods outlined by Singer et al. (2013), but are briefly outlined here. Only smolts >4.5g wet mass were tagged with acoustic transmitters to keep tag burden below 5% of total body mass. Smaller fish might be unable to compensate for the greater tag burden, and higher tag burden is noted to negatively impact post-surgery survival (Brown et al. 2010; Singer et al. 2019). Smolts ranging in size between 72-98mm were individually anesthetized using a 90mg/L dose of tricaine methanesulfonate (MS-222) in accordance with UC Davis Animal Care Protocol #20970. During surgery, a continual supply of a 30g/L concentration anesthetic was flushed over the gills to maintain sedation. An incision, 5-7mm in length, was made parallel to the mid-ventral line anterior to the pelvic girdle. The SS400 JSATS tag was placed in the incision with the transducer in an anterior direction. The incision was sutured closed with a single 2X2 surgeon's knot.

Following surgery, tagged fish were held for a minimum of 24h to allow full recovery and ensure live release. There was a total of eight release groups. The first release occurred during mid-April and the last release occurred during late May. All releases were performed during morning, between 07:00 and 09:00, and all fish in all release groups were tagged by the same surgeon to help mitigate for surgeon effects between individuals. An additional 20 unused tags were used to monitor battery life using identical handling procedures. The manufacturer estimated a 100-day battery life, all test tags remained active throughout the 100-day test period, and no tag life corrections were necessary.

The spatial pattern of acoustic detections was analyzed using an array of 11 stationary, autonomous JSATS receivers deployed at a total of 8 sites (Figure 2). All receivers were deployed downstream of the field tagging site (i.e., the RST) and upstream of Putah Creek's confluence with the slough complex. The array consisted of Advanced Telemetry Systems and Lotek (Seattle, Washington)

receivers. The creek was separated into seven telemetry segments based on ecologically distinct units that provided reliable access and reference points. Receivers were placed upstream and downstream of possible passage barriers where fish may experience greater mortality because of delayed or impaired migration. We evaluated three possible Chinook salmon passage barriers including (beginning in the upstream direction): (1) a large beaver dam, (2) a road culvert, and (3) the agricultural check dam.

Data Analyses

Phenology & Distributions of Salmon Carcasses

Chinook salmon spawn timing and distribution in Lower Putah Creek were determined using a combination of recovery date and carcass location. The reach in which a carcass was recovered (i.e., A-G) was assumed to be the reach where spawning occurred. Provided the limited spawning habitat in Lower Putah Creek, spawning distribution was assessed at the reach scale. Data collected from individual carcasses were used to describe characteristics of the spawning population using a combination of CWT results, morphometric data, and visual assessments. Mean fork lengths (mm) were calculated for each year and within each categorical reach surveyed. The natal origin, release strategy, and age of hatchery strays in Lower Putah Creek was retrieved using recovered CWTs.

Growth, Survival, and Movement Patterns of Juvenile Salmon

Daily salmon catch at the RST was evaluated in tandem with daily discharge data from the PDD to provide an indication of response by juvenile Chinook salmon to discharge conditions. The condition and growth rates of juvenile salmon sampled at the RST were also calculated to allow comparisons between and among years. Juvenile salmon in the RST were preliminarily assessed using Fulton's Condition Factor ($K = W(100,000)/L^3$) (e.g., Neumann et al. 2012). Used as an indicator for fish health, populations with high K values (>1.0) reflect conditions suitable for somatic and gonadal growth (Moyle and Cech 2002). K was calculated for individual juvenile salmon sampled in each year by comparing the measured length and weight of a fish to its expected weight at that length, providing an indication of

relative condition between individual fish (Moyle and Cech 2002). To evaluate differences in fish condition and to account for unequal variance, Welch's Analyses of Variance (ANOVAs) were performed for all sampling years using the *rstatix* R package, a post hoc analysis using the Games-Howell multiple comparisons method was performed to determine differences between years.

To evaluate growth, fork length data (mm) were aggregated by week to understand salmon size structure throughout the sampling period in each year. These data were also used to evaluate differences in juvenile growth between sampling events and water years. Analyses of Covariance (ANCOVAs) were used to compare juvenile growth differences between 2018 and 2021, the two most complete years of juvenile morphometric data. Sample sizes were sufficiently large to meet assumptions; therefore, we tested for differences in fork length as a function of sampling year and Julian Date of capture. We used fork length (FL) as the dependent variable, age or time as the independent variable, and water year as a blocking factor. Differences in growth rate were assessed using the significance of the FL x water year interaction term. A post hoc test using Tukey's method was applied to identify statistically significant differences between the mean fork lengths in each sampling season.

Acoustic detection data from individual receivers were processed using a filtering algorithm adapted from the University of Washington Columbia Basin Research Group to remove false and inaccurate detection data. Further information regarding filtering criteria is available at www.cbr.washington.edu/analysis/apps/fast. Post-filtering, detection histories were individually and manually assessed using a behavior-based filter designed to capture obligate anadromy demonstrated by juvenile Chinook salmon (Healey 1991). As such, these data were checked for movement irregularities (e.g., upstream movement indicative of predatory behavior (Zeug et al. 2020)), but all detection histories met expectations and therefore did not require truncation. Additionally, if an individual fish was detected at one upstream location, but never again detected at a downstream location, we assumed fish mortality somewhere in between.

Residence times and average ground speed were calculated for all tagged fish using filtered detection histories for each reach (A-G). Residence time in each reach was determined by calculating the difference in time between the first detection at the upper bound of a segment and the first detection at the upper bound of the next downstream segment without further upstream movement thereafter. Time spent in each creek segment was divided by the segment length to approximate average ground speed for each segment.

All data were analyzed in R (version R-4.1.2). All data are represented as means \pm SD where appropriate, and differences were considered significant if $\alpha < 0.05$.

Results

Phenology & Distributions of Salmon Carcasses

Overall, numbers of carcasses recovered in each of the five survey years varied widely, ranging from 211 in 2018 to just a single carcass in 2019 (Table 1). Despite variation in removal timing of upstream passage barriers, mean date of carcass recovery for the first several years of collections remained relatively unchanged, falling within the same two-week time frame in December between 2016 and 2020 (e.g., 12/16/2016, 12/17/2017, 12/9/2018, 12/10/2019, and 12/24/2020), with small deviations in peak carcass recovery (Figure 3). Unlike previous years, in 2021, more than half (57%) of all carcasses were recovered early in the season on a single day, 5 November 2021. During years when flashboards were removed earlier in the season (2017 and 2018), the greatest number of carcasses were recovered (Table 1, Figure 3). When flashboards remained in place at the check dam until mid- to late-November (2019 and 2020), fewer carcasses were recovered. Further, data collected by the Yolo Bypass Fish Monitoring Program illustrated the presence of up migrating Chinook salmon downstream of Putah Creek, in the slough complex, as early as September during most years (Figure 4).

Contrary to the relative spatial uniformity observed early in this study, spatial recovery of carcasses in Lower Putah Creek diverged greatly in 2020 and 2021, likely caused by disruptions in

upstream movements. In 2016, 2017, and 2018, carcasses were predominately recovered within the most upstream reach (A); 62.0%, 62.5%, and 70.1%, respectively (Table 2, Figure 5). However, only one carcass was recovered in 2019, likely caused by a delay in removal of flashboards towards the end of November. Yet in 2020 and 2021, most carcasses were found within the lowest 2 rkm of Lower Putah Creek (primarily reaches E and G). In 2020, after the initial recovery of several carcasses from within upstream reaches during November, a greater proportion of carcasses were recovered lower in the system after the formation of a natural passage barrier (e.g., a large beaver dam approximately 2m in height, that, when flow was adequate, permitted upstream passage but became impassable as flows receded. More than half of the carcasses recovered in 2020 were discovered downstream of this natural passage barrier, whereas few carcasses were identified in habitats more typical of spawning grounds higher in the system (Table 2). In 2021, all recovered carcasses were found in the lowest reaches of Lower Putah Creek after poor water quality conditions resulted in the pre-spawn mortality of most of adult Chinook salmon. While surveys continued for two months following the identified fish kill, no additional carcasses were recovered after the initial discovery of numerous carcasses downstream of the check dam following the collapse of water quality. The distribution and timing of carcass recovery in 2021 was unusual, likely because poor water quality precipitate low dissolved oxygen that when coupled with an early attraction flow elicited by an unseasonably large rain event caused

Mean fork length of recovered carcasses beginning in 2016 were 713, 717, 776, 807, and 712 cm, respectively, with the exclusion of 2019 for which there was only one measurement available (Table 2). All carcasses recovered in Lower Putah Creek were mature adults, including many age-two fish in all sampled years, and several age-4 fish during 2016 and 2020 (2016: n=7 ;2020: n= 6). While age distributions shifted between years, hatchery strays in the creek were composed of two- and three-year-olds, as indicated by CWT results (Figure 6C). An overwhelming majority (79%) of CWTs recovered originated from the Mokelumne River Fish Hatchery (MOK), located on the Mokelumne River, a

tributary of the San Joaquin River, and were released from a Net Pen near Sherman Island, also in the San Joaquin River (Figure 6 B & C).

Growth, Survival, and Movement Patterns of Juvenile Salmon

Using daily trap data from the RST, a seasonal pattern was apparent with a peak migration of juvenile salmon occurring in late March or early April with a second smaller peak emerging in mid-May during most years. Catches gradually declined through May and virtually ceased by mid-June (Figure 7). Trap deployment dates influenced our ability to capture earlier outmigration pulses by fry. Nevertheless, high capture rates at the initiation of sampling during years of delayed deployment indicate salmon had already commenced outmigration (Figure 7A). During periods of extended trap operation that permitted earlier sampling however, a discernible increase in juvenile Chinook salmon capture rates followed or coincided with pulse flows (Figure 7B).

Condition factors were similar between juvenile cohorts (Figure 8). Calculated condition factors between years were closely aligned. Mean values from 2017 to 2021 were 1.22 ± 0.10 SD, 1.06 ± 0.15 SD, 1.11 ± 0.11 SD, 1.12 ± 0.14 SD, and 1.07 ± 0.11 SD respectively. However, condition between years varied significantly (ANOVA, model df = 4, $F = 129.25$, $p < 0.001$). Statistically significant differences in condition factor were detected between all years except between 2018 and 2019, 2019 and 2020, and 2019 and 2021 (Games-Howell multiple comparisons post hoc analyses, $p < 0.001$).

Although similar trends in juvenile growth were evident between sampling years with similar patterns of discharge (Figure 9A), observed growth in young-of-year salmon captured in the RST also differed significantly (ANCOVA, model df = 1, 8,479, $F = 66.29$, $p < 0.001$). Mean fork length was significantly greater in 2021 (73.15 ± 0.13) than 2018 (64.00 ± 0.11) (A post hoc Tukey's HSD test showed that fork length differed significantly between sampling seasons at $p < 0.001$, Figure 9). Aided by the large size of the dataset, data sufficiently met assumptions of normality, linearity, and homogeneity.

Statistical support for these differences in condition and growth is clear in both transformed and untransformed data, therefore data remained untransformed for clarity.

Median travel time within identified segments varied widely downstream of the RST; observed residence times were longest in the most upstream segment, located immediately downstream of the tagging location (Figure 10). Fish then moved downstream more consistently, spending the least amount of time in the lower segments of the creek (D and E). Ground speeds were consistent throughout the study area except for one reach (segment D), therefore any differences in residence time between reaches can likely be explained by the length of the reach. In segment D, average ground speeds tripled, from approximately 0.2km per hour to nearly 0.6km per hour. Median travel time from the location of tagging (nine rkm downstream of the PDD) to the last receiver location, positioned downstream of the check dam ranged between seven and eight days (for those fish detected at the release site and the final detection site below the check dam). Juvenile fish passage proportions were high at the culvert and beaver dam, but strongly declined at the check dam (Table 3). Most tagged fish (80%) were unable to pass the check dam, with only six individuals successfully passing.

Discussion

Through long-term monitoring and select studies, we identified several limiting factors depressing the recovery of Chinook salmon in Putah Creek, principally barriers to salmon ingress and egress. Results of these studies clearly illustrate the fragility of recovering salmon runs constrained by natural and artificial bottlenecks while also highlighting the need for innovative and adaptive management strategies. Additionally, there are a number of important lessons that can be applied to other highly modified and regulated creeks seeking to improve conditions for anadromous salmon.

Phenology & Distributions of Salmon Carcasses

CWT data recovered from adult Chinook salmon carcasses show a mixed age distribution of returning hatchery salmon. Further, age data retrieved from CWTs in 2016 aligned proportionally with

results of Willmes et al. (2021b) who used otolith microchemistry to determine age and origin. Also, similar to Willmes et al (2021), data reflected age patterns of CWT recovery rates analogous to those observed for other Central Valley salmon populations (Letvin et al. 2020, 2021b, 2021a; Palmer-Zwahlen and Kormos 2020). While hatchery-origin fish may be a coarse proxy for natural-origin analyses, Satterthwaite et al. (2014) demonstrated concordance between natural-origin stocks and hatchery proxies using genetic techniques. Therefore, we posit that age distribution of salmon returning to Lower Putah Creek is composed primarily of age-2 and -3 salmon and occasionally age-4 fish. Satterthwaite et al (2017) also demonstrated that across all run-types, age-3 spawners were predominant. Analyses by Satterthwaite et al (2017) also revealed that, while still common throughout the Central Valley, age-2 spawners were most prevalent among Mokelumne River and other San Joaquin River salmon populations. The staggered age structure of returning salmon to Putah Creek is evolutionarily important for risk spreading in populations because it reduces the likelihood that all individuals of a cohort will experience the same maladaptive environmental conditions (Schindler et al. 2010; Satterthwaite et al. 2017), like those illustrated by the collapse of dissolved oxygen that precipitated the fall fish kill in 2021. Thus, mixed age structures may promote phenotypic plasticity and support population buffering (Greene et al. 2009).

Interestingly, CWT results also demonstrated that known hatchery-strays recovered in Lower Putah Creek largely originated from the Mokelumne River Fish Hatchery and were released in a Net Pen proximal to the Delta (the Sherman Island Net pen), perhaps explaining the predominance of age-2 Mokelumne River-origin spawners. ‘Straying’ is a commonly observed phenomenon in Pacific salmonids, particularly in the Central Valley as trucking efforts that deliver juvenile hatchery salmon to proximal ocean locations have increased in the face of warming river temperatures and diminished flows (Keefer et al. 2008; Huber and Carlson 2015; Sturrock et al. 2019), particularly during dry years or drought. Nonsequential imprinting, which occurs when the emigration of juvenile fish is disrupted, as is the case

during Delta releases, can reduce homing accuracy upon return to freshwater and may lead to increased straying (Bett et al. 2017), as we speculate is the case for hatchery strays in Lower Putah Creek.

There are benefits and consequences to straying behavior within salmon populations. For instance, straying has been noted to disadvantage recipient populations by reducing population fitness as a result of inappropriate selective pressures introduced by straying salmon (i.e., “the donor”) (Quinn 1984). However, evolution of straying behavior in salmon also permits colonization of new habitats following glacial recession, dam removal, or water quality improvements to create newly accessible habitats (Anderson et al. 2015; Quinn et al. 2021). These same pioneering behaviors may be useful in recovering extirpated runs of salmon following ecosystem restoration. Indeed, following the removal of an impassible dam after nearly a century of isolation, straying salmon from diverse sources have been observed spawning in newly accessible habitats in the Elwha River, Washington, USA (Quinn et al. 2021). Therefore, in the early stages of Chinook salmon recovery, high stray rates are likely beneficial because they represent a mechanism for recolonization, and thus also recovery.

Anthropogenic passage barriers, namely a seasonally-manipulated earthen road and check dam, influenced run timing and distribution of Chinook salmon in Lower Putah Creek by constraining or preventing salmon from entering the system volitionally during each year. Despite the shifted location of spawning in 2020 and 2021, caused by various impediments, the consistent recovery of carcasses in upstream habitats in previous years indicates preferential habitat selection in those locations. Indeed, previous research (Jacinto et al., *In revision*) also reports a greater positive shift in other native fish assemblages in upstream sections of Lower Putah Creek and to a lesser degree downstream in response to natural flow management. Furthermore, the effects of dams on salmonids, particularly with respect to movement and migration, has been well-documented (Marchetti and Moyle 2001; Bunn and Arthington 2002; Moyle 2002; Graf 2006; Lindley et al. 2006; Moyle et al. 2011, 2017; Lusardi and Moyle 2017). Spatial or temporal restrictions of spawning migrations may have implications for the

establishment of salmon in Putah Creek. For example, migratory delay can negatively influence the condition, and ultimately the spawning success of adult salmon by depleting energy reserves and delaying arrival at spawning grounds (Quinn et al. 1997; Mann et al. 2009; Babin et al. 2021). As described earlier, except for the Chinook salmon carcasses recovered immediately following the water quality collapse in 2021, no other salmon were observed in the system despite several consecutive weeks of monitoring. Therefore, if varied migratory timings were present or if upstream passage barriers had been removed earlier, this could have encouraged adult salmon returns throughout the fall and allowed for higher likelihood of spawning success.

Time-dependent barriers (i.e., those that are dependent on anthropogenic or precipitation factors) that prevent passage by salmon also have the potential to bias genotypes contributing to juvenile production and truncate the evolutionary timing of spawning migrations. Fortunately, increasing phenological diversity in Lower Putah Creek is possible if barriers to passage can be ameliorated, as evidenced by the presence of Chinook salmon downstream of the check dam between late September and December. Providing adult migration access throughout this period ensures a greater diversity of run timing genotypes contributing to juvenile production.

However, dams and other impediments augment ecosystem dynamics independent of fish passage. Selective conditions naturally occur, and passage barriers arise frequently in nature (Sergeant et al. 2017; Till et al. 2019), but anthropogenic changes to landscapes, such as increased nutrient loads from agricultural practices, warming water temperatures, and low flow conditions ultimately contribute to a spatially and temporally restricted run of returning adult Chinook salmon in Lower Putah Creek. Indeed, during fall 2021 carcass surveys, we documented development of dangerous water quality conditions at the point-of-entry to Putah Creek following an atmospheric river event. This unusual early fall event inundated the region with 25-30% of its total annual rainfall typically. The storm peaked, in advance of scheduled fall attraction flows, and prior to removal of the check dam by managers. The

event, in conjunction with removal of several flashboards at the check dam to handle increased flows, resulted in a minor attraction flow queuing adult Chinook salmon downstream of Putah Creek to begin upstream movements. Chinook salmon were observed downstream of the check dam shortly after the initial removal of flashboards, but without the complete removal of flashboards, passage beyond the check dam was not possible. Significant agricultural runoff and high concentrations of dissolved organic matter promoted a reduction in dissolved oxygen that persisted in the lower system for several weeks that resulted in a widespread fish kill that impacted the fall 2021 Chinook salmon run in Lower Putah Creek and other native and nonnative fishes in the Yolo Bypass. Dissolved oxygen levels following the storm were the lowest reported levels in the last several years (Figure 11). Therefore, when conditions outside the bounds of expected environmental variability occur like those observed in 2021, management actions are required to be more nimble in response. As large storms, such as the one that occurred during October 2021 become more common in California because of climate change (Dettinger 2016), managers will need to consider planning for additional adaptive scenarios.

Growth, Survival, and Movement Patterns of Juvenile Salmon

Condition factors, while influenced by seasonality and the changing shape of fish throughout ontogenetic shifts, (Neumann et al. 2012) can be useful in describing food availability and overall body energy composition in diverse fish populations (Blackwell et al. 2010; Trudel et al. 2011; Rypel et al. 2011). Indeed, condition factors suggested physicochemical conditions suitable for positive growth and survival, indicating that biotic and abiotic conditions in Lower Putah Creek may be more or less amenable to rigorous somatic growth of salmon despite observed differences in growth rates in 2018 and 2021.

Several factors may explain interannual differences in juvenile salmon growth in Lower Putah Creek. Surprisingly, interannual growth variations were not linked to timing of adult salmon migration and suspected spawning activity; passage barriers were removed earlier in the fall of 2017 than in 2020,

which we would expect to positively influence juvenile growth in 2018. However, juvenile salmon in 2018 were smaller and grew more slowly. Since both years exhibited similar patterns of discharge, and there was no clear link between adult migration timing and juvenile growth, there are likely myriad other factors influencing juvenile growth, such as interannual thermal regimes, density-dependence, intraspecific competition, and/or food web composition and abundance (Achord et al. 2003; Grant and Imre 2005; Walters et al. 2013; Lusardi et al. 2020). In the Snake River watershed of Central Idaho, Walters et al. (2013) found that all populations of juvenile Chinook salmon exhibited density dependence across a wide range of conditions despite abundances of spawning adults that were significantly below their historical capacity. The ubiquity of density dependence in juvenile salmon populations is often hypothesized to be the result of a shortage of nutrients that would otherwise be derived from decomposing salmon carcasses at historical levels (Achord et al. 2003). Nevertheless, density dependence in juvenile salmonids may encourage population recovery in variable environments by reducing intraspecific competition and thus increasing the growth rate of remaining individuals, thus affecting demographic metrics such as survival and fecundity (Vincenzi et al. 2008).

Differences in growth may also be attributed to thermal variation and prey availability (Marine and Cech 2011; Myers et al. 2018; Lusardi et al. 2020; Willis et al. 2021). According to the California Department of Water Resources, based on water year hydrologic classification indices (California Data Exchange Center), on average, water temperatures were greater, and conditions drier in 2021 than in 2018 during juvenile rearing. Although we see little evidence for the effect of discharge patterns on juvenile growth, we posit that juvenile Chinook salmon in Lower Putah Creek respond to flow pulses as a cue for outmigration, but perhaps not immediately. Salmon may also hold in upstream habitats closer to spawning grounds, but we are unable to detect downstream transitions until fish are captured much farther downstream in the RST. The initiation of migratory behavior in response to increased flow is well-documented (Poff et al. 1997; Bunn and Arthington 2002), and high capture rates at outset of

sampling during years of delayed deployment indicate young salmon had already commenced out-migration. Therefore, we hypothesize that juvenile Chinook salmon outmigrate in a minimum of two life stage waves in Lower Putah Creek: the first and ostensibly larger wave, occurring early in the spring (February-March) as fry; the second occurring later in spring (late April-May) as smolts.

Outmigration of multiple phenotypes at separate times has been reported elsewhere and is proposed to have developed in response to varying environmental conditions that promote population variability and resilience overall (Miller et al. 2010; Sturrock et al. 2020). Considerable research also suggests that juveniles outmigrating at larger sizes (i.e., parr and smolt) disproportionately contribute to adult populations, likely because of improved predator avoidance and/or swimming capabilities (Brandes and McLain 2001; Woodson et al. 2013). Yet, recent findings have indicated an increased degree to which fry phenotypes contribute to adult populations (Miller et al. 2010; Sturrock et al. 2015) and bolster genetic and phenological diversity (Sturrock et al. 2020).

Here, acoustic telemetry data suggested residence time was greatest in the uppermost segment of Lower Putah Creek, where ground speed was reduced compared with other river segments. Increased residence time may indicate holding patterns by juvenile salmon prior to out-migration thus indicating that the upper reaches of habitat are suitable for juvenile rearing. Experimentally-tagged fish also traveled nearly three-fold faster in segment D when compared with other segments, despite notably slower water velocities. Segment D is broadly characterized by low gradient, warmer water temperatures, and increased abundance of non-native predators (e.g., Largemouth bass (*Micropertus salmoides*), Bluegill sunfish (*Lepomis macrochirus*), etc.) (Jacinto et al. *In revision*). Therefore, we speculate that increased ground speed in this segment may be caused by insufficient rearing habitat, a lack of holding habitat, or by the presence of predators.

Telemetry data also indicated that the road culvert and large beaver dam did not impede downstream movement relative to other segments. Conversely, passage proportions at the check dam

were reduced, when compared with other locations (Table 3). Replacement of flashboards at the check dam occurred several weeks before completion of juvenile outmigration; thus, preventing movement by outmigrating fish. While sample sizes were low, we observed very few juvenile salmon able to successfully navigate the check dam. Reduced water velocities towards passage obstructions can obscure cues used by juvenile Chinook salmon to navigate downstream, causing migratory delay, which is often associated with increased risk of mortality (Babin et al. 2021). Indeed, successful freshwater outmigration of juvenile Chinook salmon is a vulnerable period in their early life-history (Healey 1991) but is a primary driver in predicting abundance of returning adults (Michel 2018). Therefore, high mortality during this period or impaired outmigration of juvenile salmon will greatly limit the recovery of natal-origin salmon in Lower Putah Creek.

There were several limitations in our study. First, during carcass surveys, there is likely a compensatory observation effect such that it becomes more difficult to collect carcasses when there are fewer. Additionally, in our JSAT study, even using the smallest commercially available acoustic transmitter (ATS SS400), tag size limited our overall ability to tag and track smaller fish (i.e., any salmon <72-80 mm SL), which comprise the bulk of salmon sampled in the screw trap. Therefore, our study of outmigration success and behavior may be biased towards larger individuals captured later in the year.

Conclusions

Available historical information suggests that prior to dam construction, Putah Creek maintained a small but sporadic run of anadromous fishes, including Chinook salmon (Shapovalov 1947). Following implementation of the Accord, there has been a rise in the proportion of native fishes in Lower Putah Creek including the return of Chinook salmon (Kiernan et al. 2012; Jacinto 2020; Willmes et al. 2021b). Mimicking components of the natural flow regime and the use of cool water dam discharge has generated novel habitat for anadromous fishes within this ecosystem. In describing a recovering run of Chinook salmon in a reconciled ecosystem, we observed how passage barriers continue to constrain and

depress salmon migratory phenology and distribution. We also identified preferential selection of upstream habitats by spawning adults. Yet, while restoration projects in Lower Putah Creek have been successful in creating usable habitats, there is additional need to improve habitat conditions in the lower portions of the system. Additional restoration actions that further mimic the natural hydrograph and help reduce temperatures may also displace non-native predators, promoting a fuller longitudinal distribution of juvenile salmon habitat viability during outmigration. Further improvements to habitats could also expand spawning opportunities in the downstream sections of Lower Putah Creek.

Management Recommendations

This retrospective study provides new management-relevant information on the ecology of a recovering Chinook salmon population in a Central Valley stream. The work highlights several critical issues for managers to consider for improved adaptive conservation management. These include:

- 1) *Improve fish passage.* Current fish passage barriers in Putah Creek artificially constrain and depress salmon movement and access to habitat, possibly biasing genotypes capable of contributing to juvenile production. Therefore, we propose opening passage barriers during a wider migration window by leaving flashboards out longer or creating alternative migration routes (e.g., fish ladders or weirs). Further, the timing of barrier removal and reinstallation should be managed on an annual and adaptive basis. If passage barrier removal is delayed during fall, the initiation of a spring pulse flow could also be postponed allowing for sufficient juvenile growth prior to outmigration. Similarly, the reinstallation of the barrier should also be delayed allowing for juvenile outmigration before seasonal water impoundment begins.
- 2) *Improve water quality monitoring.* Water quality could be monitored in Putah Creek in real time and more broadly within the Yolo Bypass. Preventing fish kills like that observed in 2021 will be essential to the continued persistence of salmon within the system. Further, diminished water quality can functionally mimic physical fish passage barriers, precluding newly arriving salmon from accessing

suitable upstream spawning habitat. Improved real time water quality monitoring would allow water managers to increase flows or take other actions to more nimbly improve thermal-oxy conditions within the creek.

- 3) *Focus future restoration activities on downstream locations.* We observed limited habitat for adult spawning and juvenile rearing in Lower Putah Creek. Our data suggest that preferred habitats are concentrated in the most upstream reaches. Additional restoration actions focused on riparian and geomorphic processes may augment historical Accord actions (e.g., functional flow regimes; see Kiernan et al. 2012) by enhancing environmental water conveyance and reducing temperatures during critical periods.

We summarized the broad behavioral and phenological characteristics of a recovering run of native Chinook salmon in Lower Putah Creek following changes to flow management. Although we have begun to identify processes that drive ecological structure and function in Lower Putah Creek, a number of unknowns remain. Further research is necessary to develop flow targets that will support a diverse, sustainable, and adaptive riverscape. In general, however, our data demonstrate the importance of long-term ecological and water quality monitoring to generate sufficiently large datasets that provide managers with robust knowledge to predict and respond to native fish management obstacles.

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Tables

Table 1: Annual numbers of Chinook salmon sampled in Lower Putah Creek during adult carcass surveys and downstream out-migrant trapping, 2016 – 2021.

	2016	2017	2018	2019	2020	2021
Adult Chinook salmon carcasses recovered	126	208	211	1	70	81
Juvenile Chinook salmon sampled	*	215	33,513	26	200	5,078

Table 2: Total carcasses recovered by year and section in Lower Putah Creek and overall mean fork length calculated in centimeters (cm) for each year.

Year	Total Carcasses Recovered	Carcasses found in each section							Mean Fork Length (cm)
		A	B	C	D	E	F	G	
2016	126	78	39	8	1	NA	NA	NA	713.7
2017	208	130	32	40	6	NA	NA	NA	717.0
2018	211	148	42	21	0	NA	NA	NA	776.6
2019	1	1	0	0	0	NA	NA	NA	825.0
2020	70	23	0	0	0	40	7	0	807.0
2021	81	0	0	0	0	0	8	73	712.7

Table 3: Passage proportions of juvenile Chinook salmon at possible passage barriers in Lower Putah Creek in spring 2021 using unique transmitters to identify individual fish. River kilometer 0 is represented at point of ocean entry (the San Francisco Bay where it meets the Pacific Ocean).

Potential Passage Barrier	Approximate River kilometer (rkm)	Tags detected above barrier	Tags detected below barrier	Passage success rate
Beaver dam	154	70	54	77.1%

Road culvert	149	41	31	75.6%
Check dam	145	30	6	20.0%

Figure Legends

Figure 1: Map of lower Putah Creek illustrating reaches delineated for carcass surveys (labeled A – G).

Putah Diversion Dam represents the upper most boundary for accessible habitat by Chinook salmon in the creek. Data for the base layers from the National Hydrography and Watershed boundary dataset.

Figure 2: Map of Lower Putah Creek showing eight receiver locations and seven ecological reaches (A-G)

to assess juvenile outmigration in the spring of 2021, and location of the rotary screw trap (RST) which served as the release location for acoustically-tagged fish and three structures that represent passage impediments. Data for the base layers comes from the National Hydrography and Watershed boundary dataset.

Figure 3: Daily counts of recovered Chinook salmon carcasses in Lower Putah Creek, 2016-2021, red horizontal dashed lines indicates the timing of flashboard removal in each year. In 2021, all carcasses recovered were suspected of perishing prior to any spawning activity low in the system

Figure 4: Daily counts of Chinook salmon captured downstream of Lower Putah Creek in CDWR Toe Drain fyke trap below Lisbon Weir, 1999-2017. Vertical red line indicates date in the Putah Creek Accord that flashboards must be removed, December 15th. *Data provided by the CA Department of Water*

Resources Yolo Bypass Fish Monitoring Program:

<https://portal.edirepository.org/nis/mapbrowse?packageid=edi.233.2>

Figure 5: Qualitative density map of recovered carcass locations in each year; light blue represents areas where fewer carcasses were found while hot white indicates location of high carcass occurrences.

Figure 6: Annual counts of CWTs retrieved in Putah Creek, metadata associated with CWT serial numbers displayed as release locations (A), hatcheries of origin (B), and CWT age (C).

Figure 7: (A) Daily counts of juvenile Chinook salmon (red bars) captured in a Rotary Screw Trap in Lower Putah Creek in 2017 and 2019, two wet water year types with similar patterns of discharge, discharge is represented by the black line. (B) Daily counts of juvenile Chinook salmon (grey bars) captured in a Rotary Screw Trap in Lower Putah Creek in 2018, 2020, and 2021, varying water year types with similar patterns of discharge, represented by the black line. ***note the dissimilar primary y axis indicating divergent capture rates in each year*

Figure 8: Summarized Fulton's condition factors (K) of juvenile Chinook salmon captured in a Rotary Screw Trap in Lower Putah Creek, 2017 – 2021. $K=(100)/L^3$, where 'K' is condition factor, 'W' is weight of an individual fish (g), and 'L' is the fork length of fish (cm). Width of shaded area indicates proportion of data, and square indicates mean condition factor for that year.

Figure 9: (A) Summarized weekly fork lengths of juvenile Chinook salmon captured in a Rotary Screw Trap in Lower Putah Creek, 2018 and 2021. Box plot components: midline=median, boxes = first and 3rd quartile; whiskers= minimum/maximum values within 1.5*IQ range, points = outliers. (B) Length-frequency distributions of juvenile Chinook salmon captured in 2018 and 2021. (C) Scatter plot and regression line of juvenile Chinook growth data in 2018 and 2021.

Figure 10: Residence times within identified reaches in Lower Putah Creek in minutes. Box plot components: triangle=mean, midline=median, boxes = first and 3rd quartile; whiskers= minimum/maximum values within 1.5*IQ range, points = outliers. Left panel magnifies details between 0 and 5000 minutes to illustrate more clearly the interquartile ranges.

Figure 11: Mean daily dissolved oxygen at Lisbon Weir in the Yolo Bypass, located downstream of Putah Creek in the Toe Drain, from 1 October to 1 February in each year, 2017-2021. All water quality data downloaded from: <https://cdec.water.ca.gov/dynamicapp/wsSensorData>. Dashed line indicates 7mg/L threshold, solid vertical line is peak daily carcass count

Figures

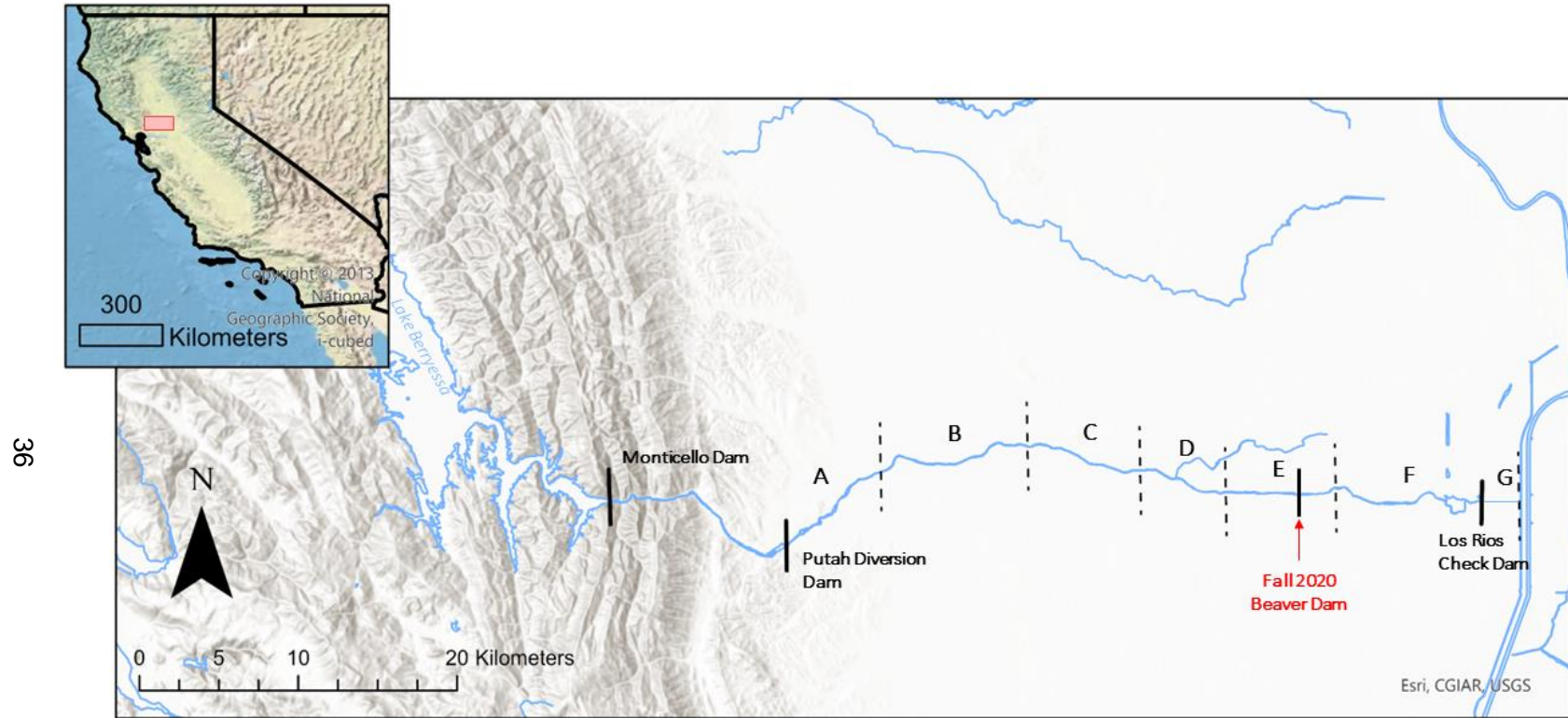


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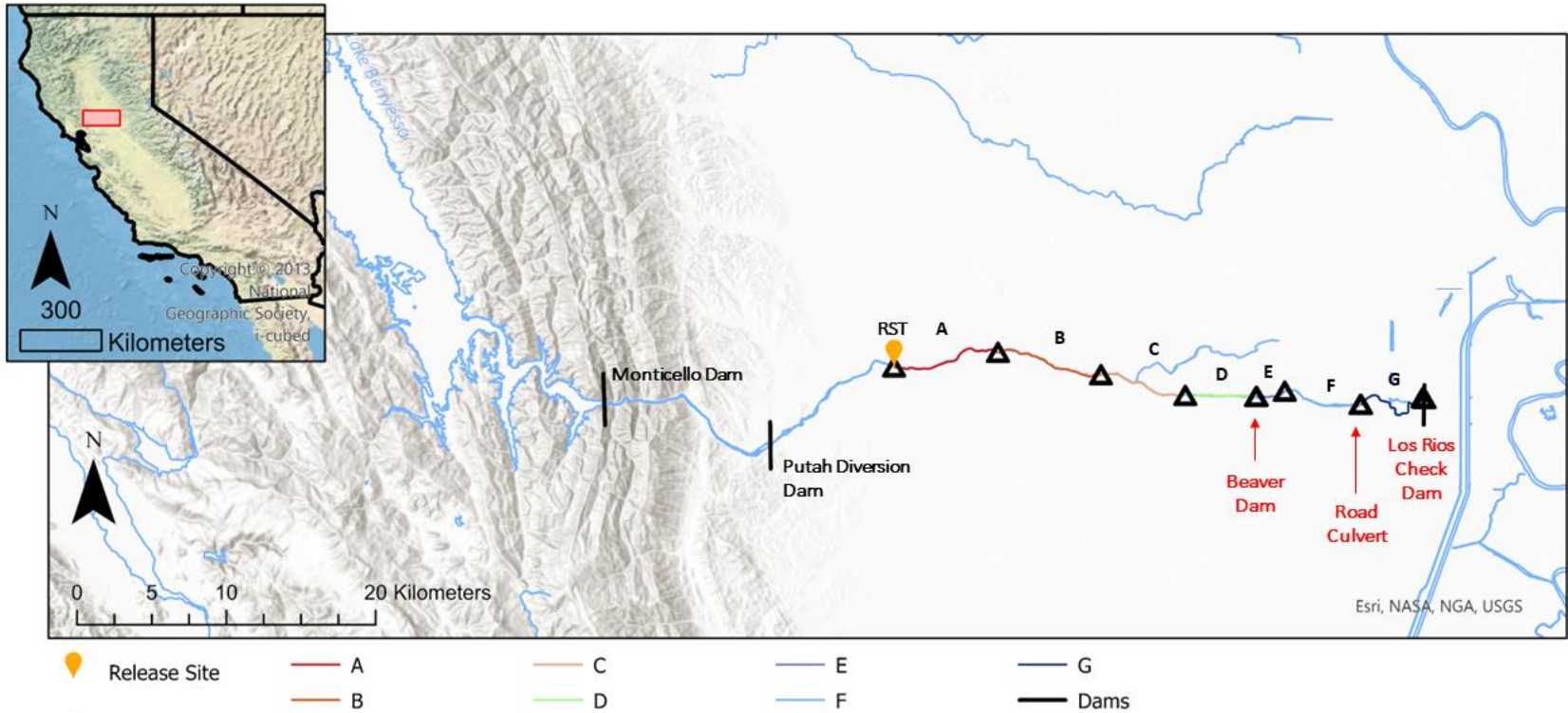


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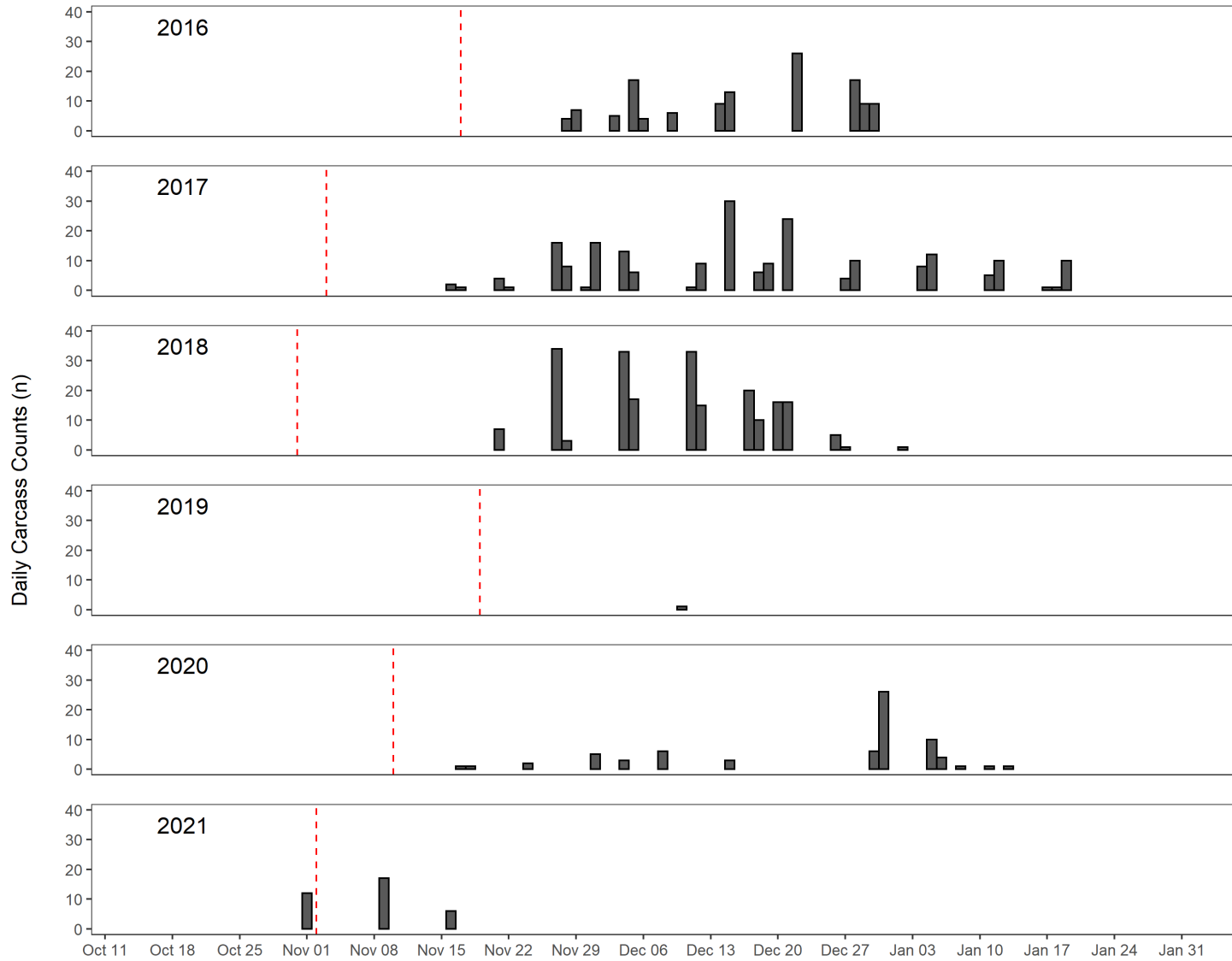


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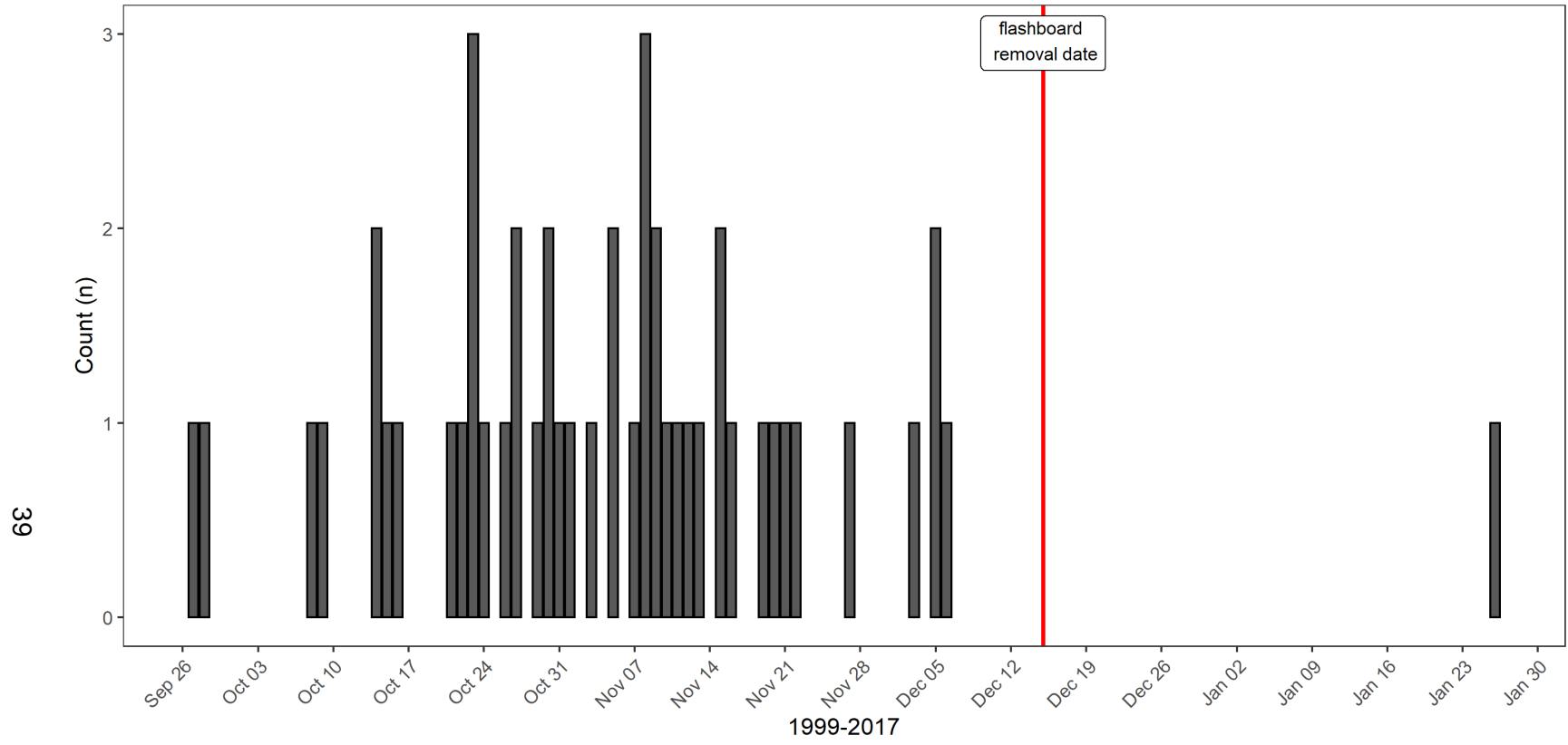


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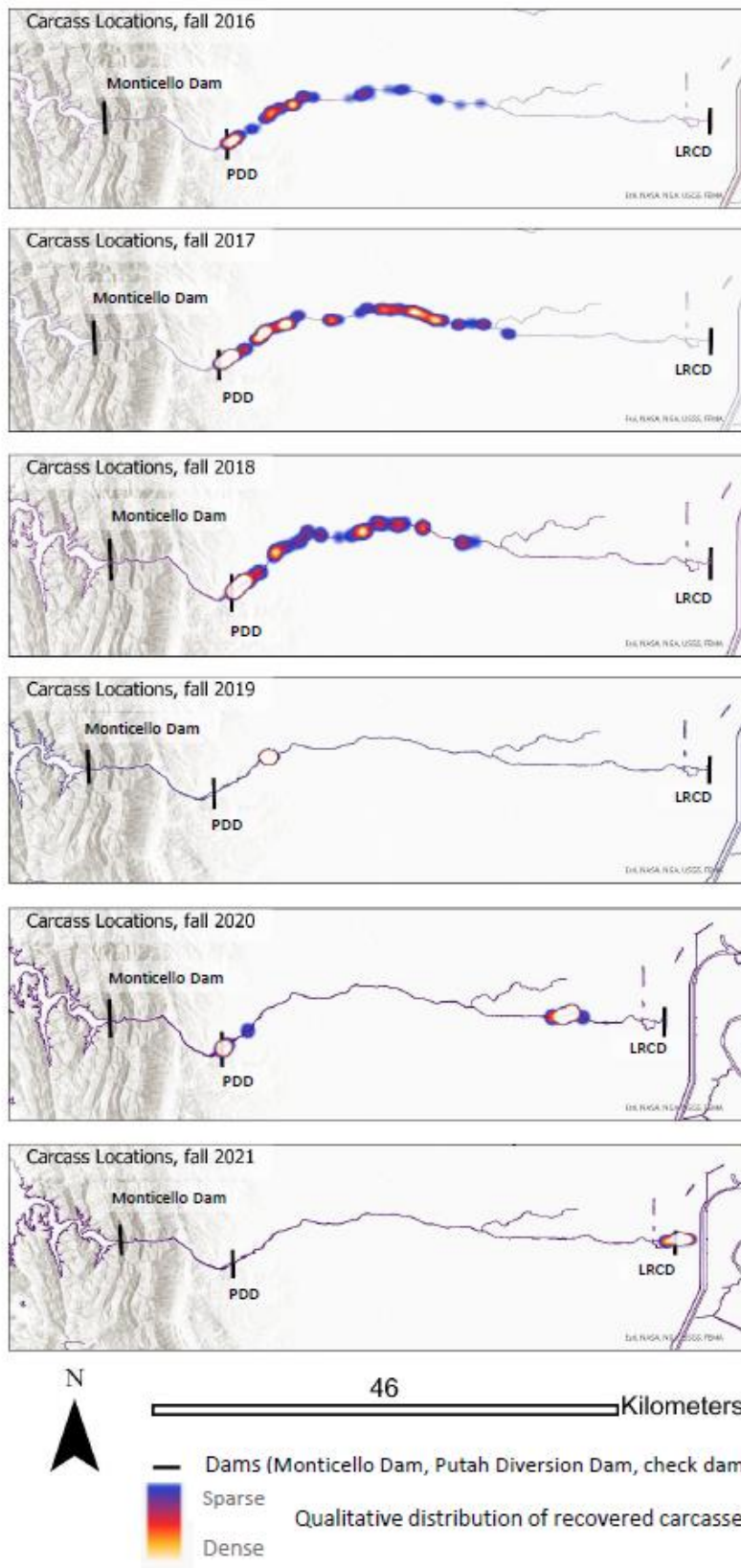


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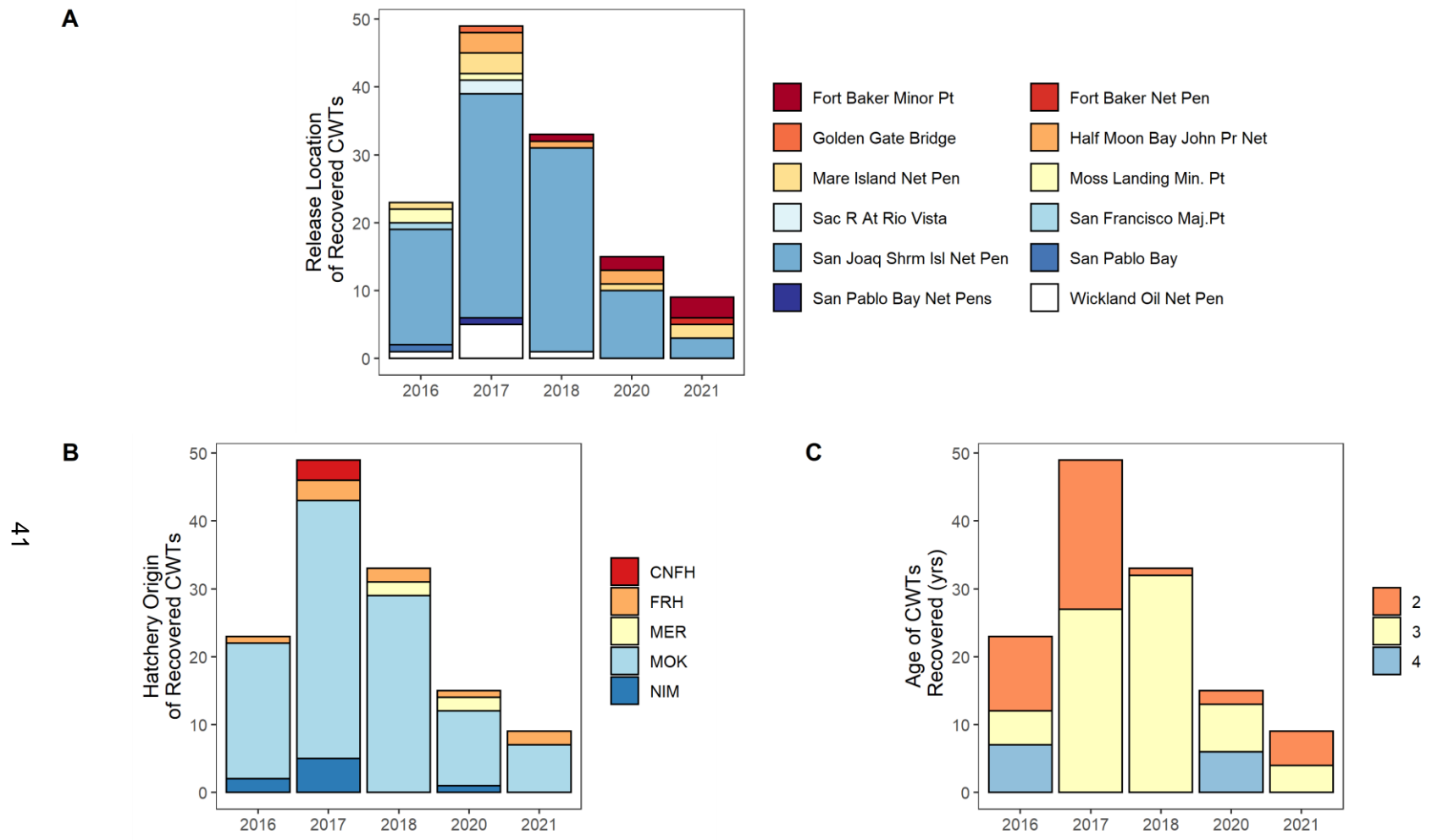


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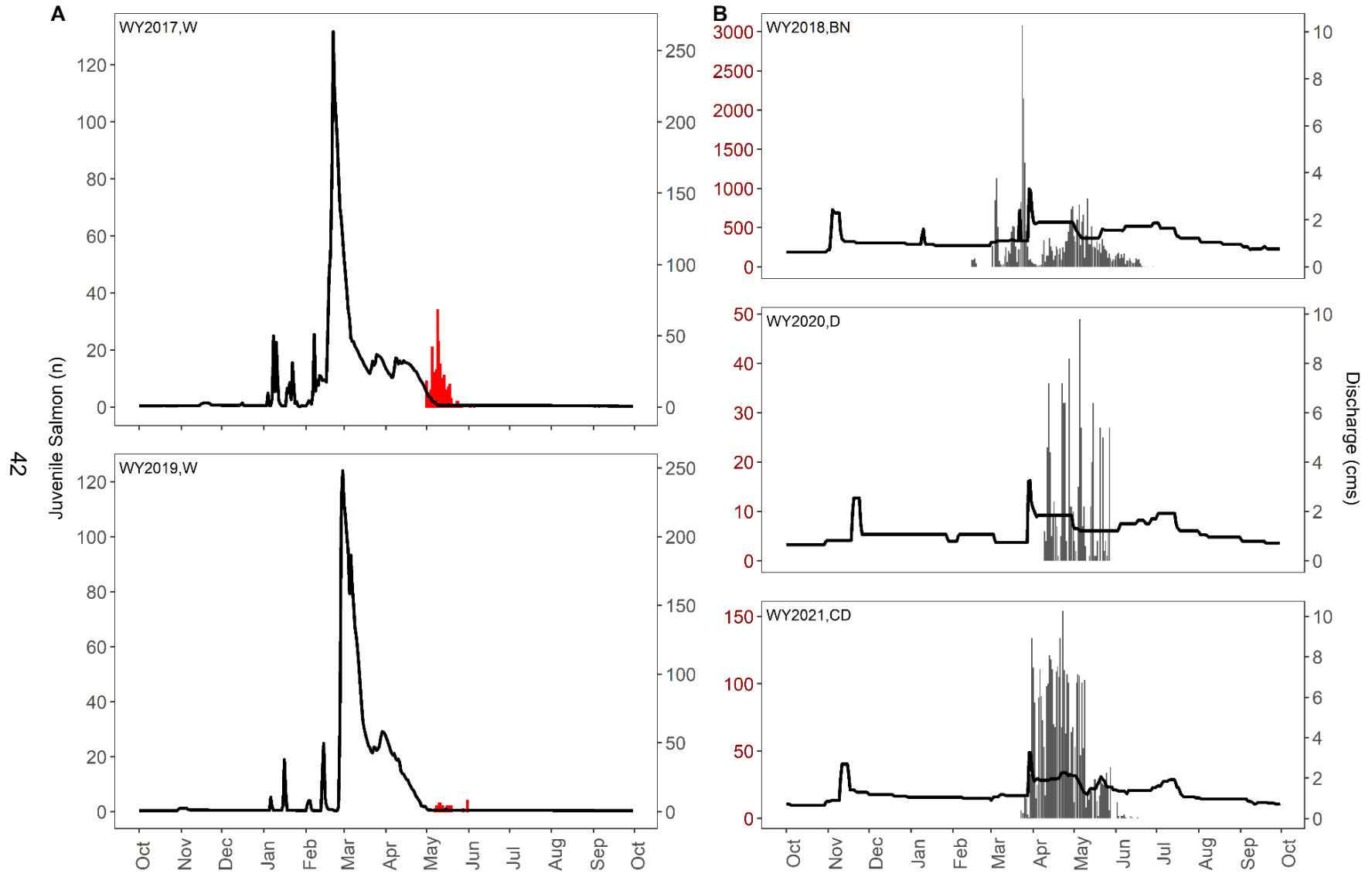


Figure 7

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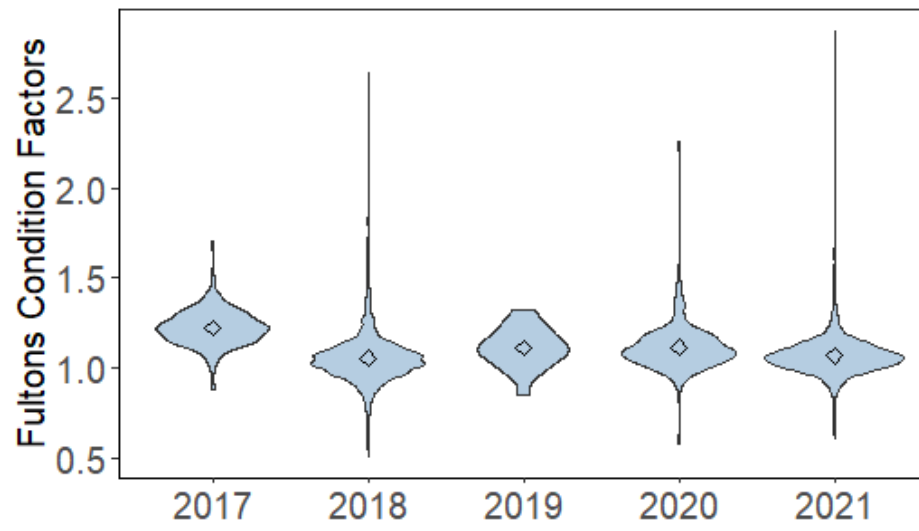


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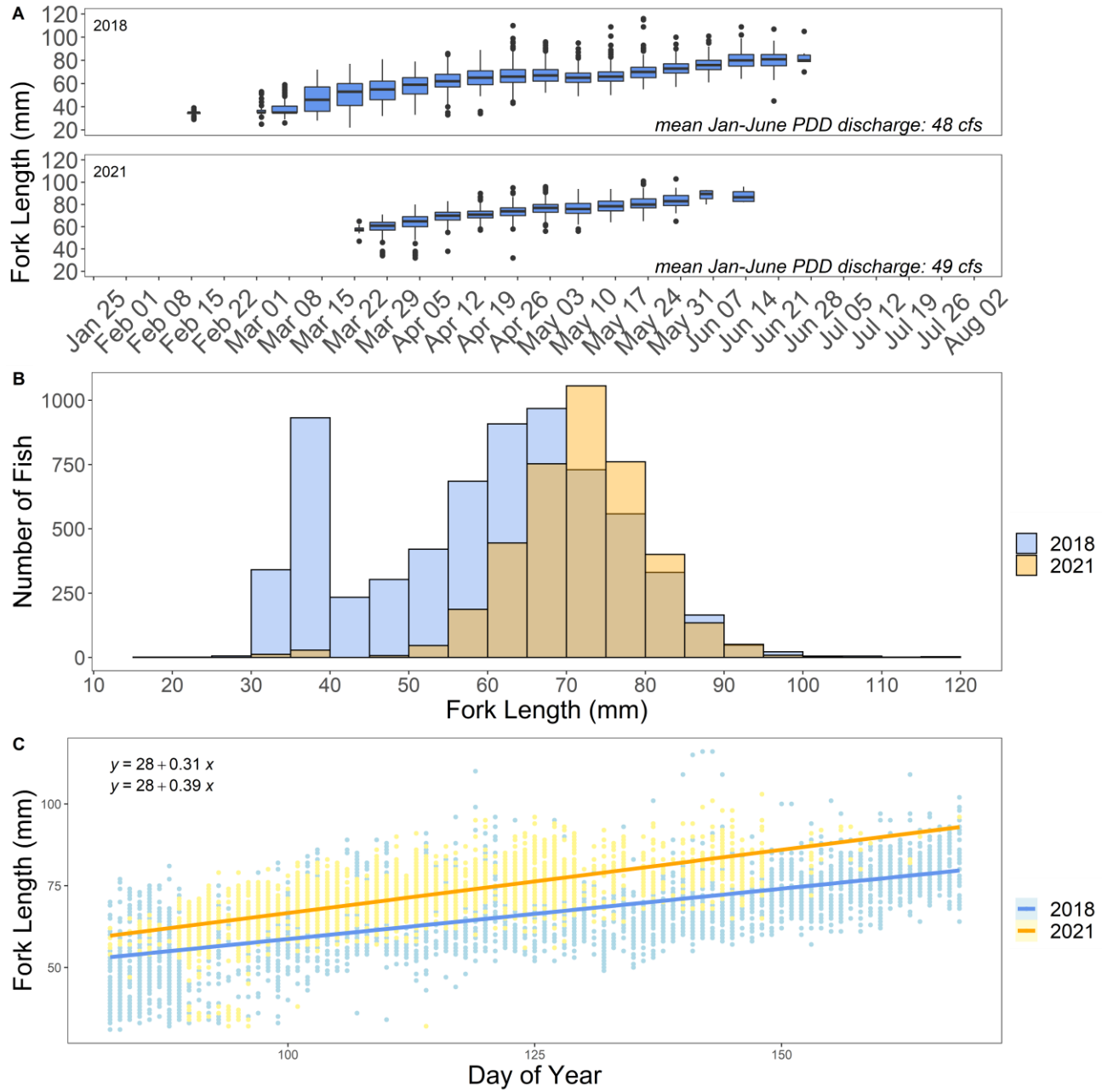


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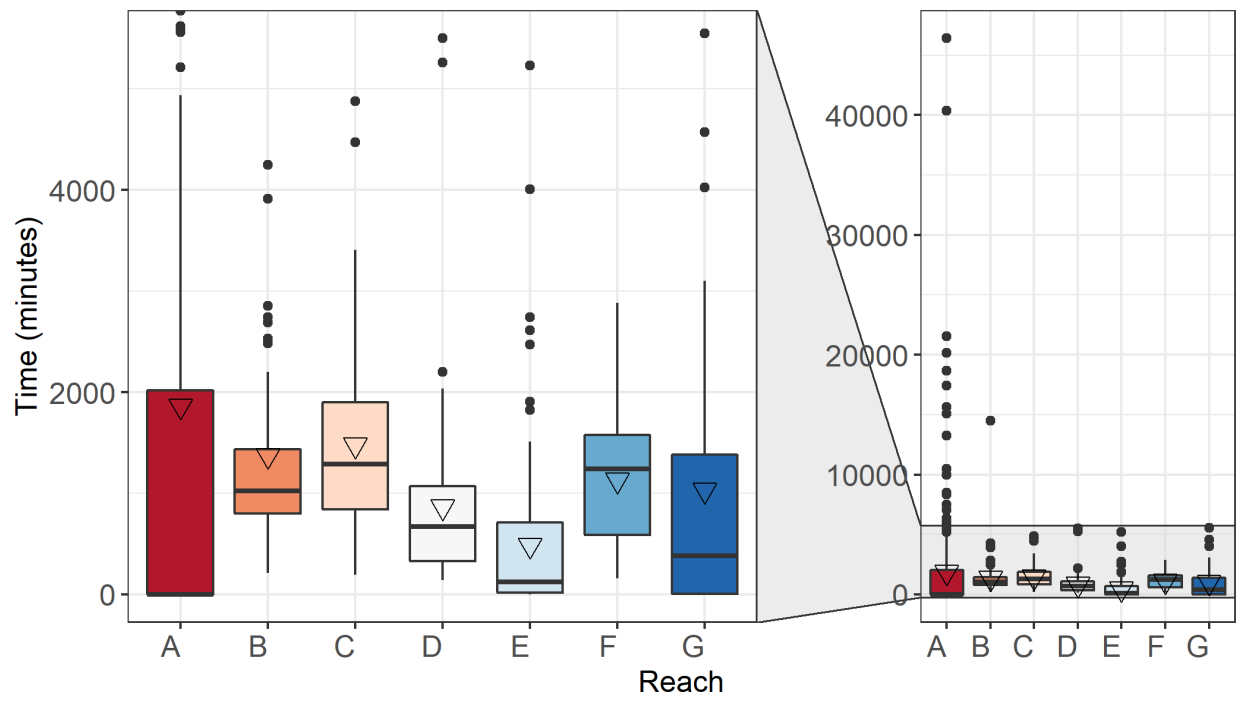


Figure 10

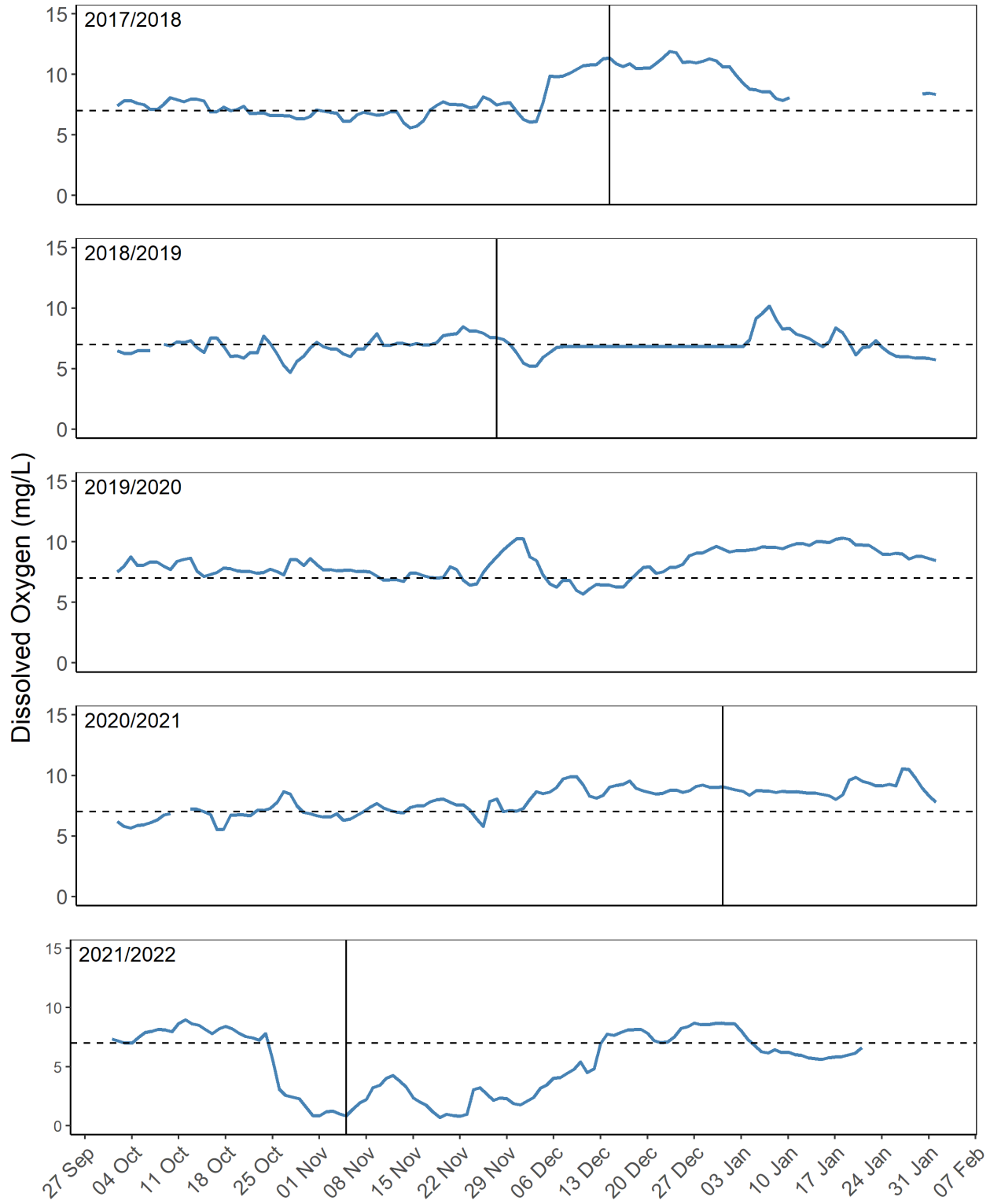


Figure 11