

## **Effects of managed flows on Chinook Salmon (*Oncorhynchus tshawytscha*) in relation to run-timing, fertility, and fluctuations in water temperature and flow volume**

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We evaluated annual and seasonal patterns of run-timing in two genetically differentiated races of adult Chinook Salmon (*Oncorhynchus tshawytscha*) inhabiting the upper Trinity River, California. Our analysis provides evidence that highly managed flow regimes implemented since 2003 have 1) altered the pattern of run-timing in sympatric anadromous populations of spring- and fall-run Chinook Salmon, 2) resulted in significant differences among managed flow-types in relation to the taxon-specific “historical” post-dam baseline flow-type, 3) altered environmental measures of water temperature and flow volume, and 4) potentially affected hatchery-parental broodstock female average annual percent fertility associated with egg production. Additionally, counts of coded wire tagged spring- and fall-run adult Chinook Salmon were significantly correlated with total hatchery returns of all age classes of marked and unmarked fish, and all three groups of salmon exhibited a significant and negative decline in relative abundance since peaking in 2004. Trends in declining stocks of all Chinook Salmon coincided with establishment of the Trinity River Restoration Program in 2002 and subsequent highly managed flow releases including periodic pulsed augmentation flows beginning in 2003. Deviation away from the baseline flow pattern in run-timing occurred in spring-run fish by compression and movement of peak counts to earlier in the season; whereas in fall-run fish peak counts occurred earlier and later in the season relative to the baseline condition. Further, we show significant differences between the baseline flow pattern and managed flow hydrographs in both annual and seasonal measures of average daily water temperature, extremes in average daily water temperature, and average daily flow volume. Analyses of annual trends in hatchery records using generalized additive modeling also revealed a significant negative relationship between year and

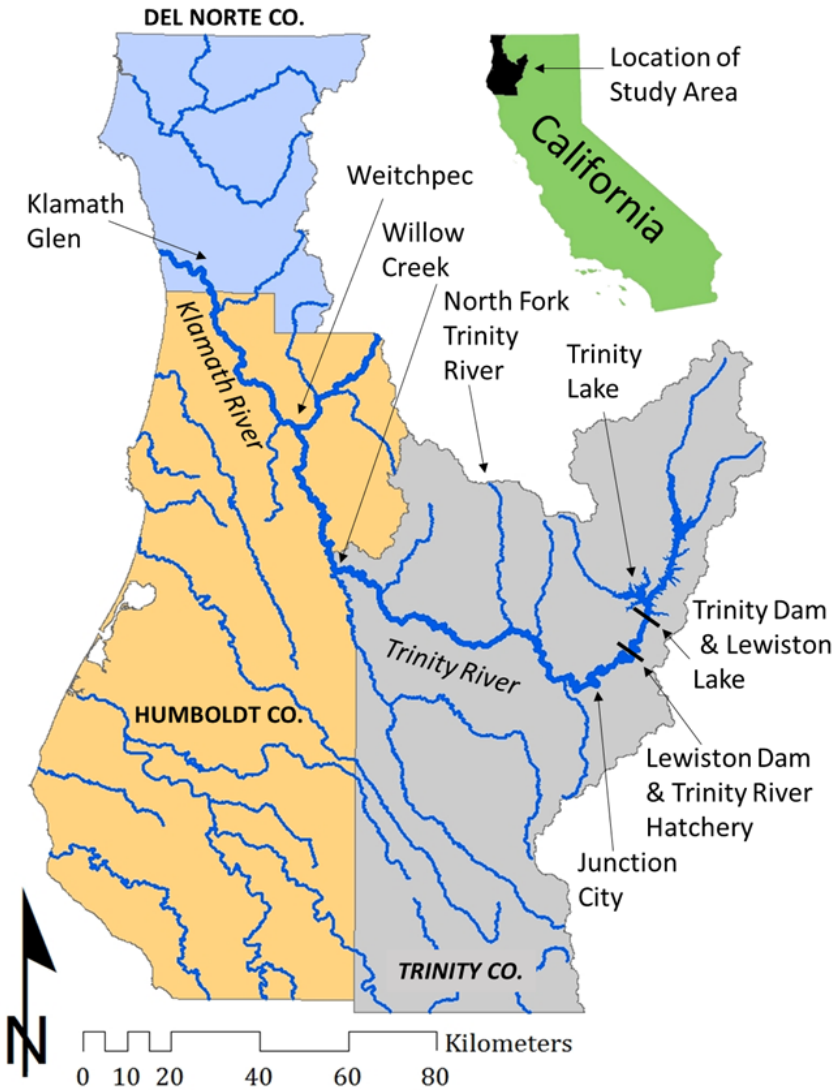
average annual percent fertility of hatchery raised parental broodstock associated with hatchery egg-take in both spring- and fall-run Chinook Salmon. Declining concordant trends in fertility suggest that these seasonally disjunct and genetically differentiated races of Chinook Salmon are tracking conditions in the upper Trinity River in parallel, which may in part be a function of the potentially negative consequences of altered flow on riverine ecosystem processes and the fisheries resources they support.

Key words: coded wire tag, fall-run Chinook Salmon, fertility, hatchery broodstock, managed flows, pulse flows, spring-run Chinook Salmon, Trinity River

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The Klamath River basin in Northern California has distinct populations of anadromous semelparous Chinook Salmon (*Oncorhynchus tshawytscha*). Trinity River is located in northwestern California and is the largest tributary in the Klamath River basin (Figure 1). Klamath River fall-run and Trinity River fall-run Chinook Salmon are allopatric populations, as both runs occur as adults in the Lower Klamath River and estuary during late summer and early fall. These populations separate geographically during migration upstream from the confluence of the Trinity River at the township of Weitchpec. Trinity River also has a sympatric population of spring-run Chinook Salmon that begins annual upstream migration as early as May. Separation of spring-run from fall-run Chinook Salmon in the Trinity River occurs through migration behavior and run-timing to the extent that these two runs appear to constitute separate genetic “races” (Kinziger et al. 2013). Historically, the size of the fall-run is typically much larger than the spring-run of Chinook Salmon. Artificial propagation programs in the upper Trinity River began in 1960 at the Lewiston Fish Trapping Facility, prior to completion of Lewiston Dam and Trinity River Hatchery (TRH) in 1963 (Murray 1962). Trinity River Hatchery has an operational egg-take allotment for spring-run Chinook of 3,000,000 eggs with a production goal of releasing 1.4 million (1,000,000 fingerlings and 400,000 yearlings); for fall-run Chinook the operational egg-take allotment is 6,000,000 (2,000,000 fingerlings and 800,000 yearlings; L. Glenn, personal communication 2016).

The Trinity River Restoration Program (TRRP), created by the Record of Decision, henceforth called “ROD” (USBR 2000), outlined a plan for restoration of 63.1 km (mainstem) of the upper Trinity River and its fish and wildlife populations (TRFES 1999). The Trinity River Mainstem Fishery Restoration Environmental Impact Statement was the basis for the ROD. The TRRP strategy for restoration included 1) flow management through manipulation of the annual hydrograph, 2) mechanical channel rehabilitation, 3) sediment management, 4) watershed restoration, 5) infrastructure improvements, 6) adaptive environmental assessment and monitoring, and 7) environmental compliance and mitigation. Timing, extent, volume of restoration flows, and annual water-year designations from 1995 through 2016 appear in Table 1. Information on the intended benefit of each restoration and pulsed flow augmentation hydrograph varies on an annual basis depending upon water availability and the particular restoration objective at the time of implementation (TRRP 2019). The primary objective of flow management on the upper Trinity River was to clean spawning gravels, build gravel bars, scour sand out of pools, provide adequate temperature and habitat conditions for fish and wildlife at different life stages, control riparian vegetation, and perform other ecological functions (TRRP 2019).



**FIGURE 1.**—Map showing counties, named tributaries ( $\geq 34$  km in length), major towns, and facilities mentioned in the text along corridors of both the Klamath River and Trinity River.

In 2003 the TRRP began implementing restoration flows, henceforth called “ROD flows” to accomplish their stated restoration strategy (Magneson 2013). In conjunction with annual ROD flows, the TRRP and United States Bureau of Reclamation (USBR) implemented additional late-summer pulsed augmentation flows, henceforth called “pulse flows” in 2003, 2004, and 2012 through 2016. In regulated rivers pulse flows are often referred to as artificial freshets (Hasler et al. 2014) used to encourage fish holding in estuaries to move into the mainstem segment of the river or aid upstream movements through fish-ways (Peterson et al. 2017). However, pulse flows in the Trinity River have historically been implemented

**TABLE 1.**—Attributes of ascending and descending limbs of hydrographs that characterized baseline PreROD, ROD, and Pulse flows for years 1995 to 2017. Rate of flow measured in cubic meters per second (m<sup>3</sup>/s) and flow release in hectare meters. For each hydrograph, a bench indicated a temporary holding steady of flow release volume and flattening of the hydrograph for at least one day. Rapidness indicated a steep and immediate increase or decrease in rate of flow, relative to a more prolonged or gradual increase or decrease in rate of flow. Abbreviations: NA = no data, shape of the ascending and descending limbs of the hydrographs: R = rapid, G = gradual, B = number of benches, and 2P = double peak. Digital data to verify online printed hydrographs for 1994 and 2001 were not available through the California Department of Water Resources, California Data Exchange Center website for the time-period encompassing by all 3-flow-types.

Year	Water year- type	Low release magnitude (m <sup>3</sup> /s)	Shape as- cending limb	Peak release magnitude (m <sup>3</sup> /s)	Restoration release (hect- are m)	Shape descending limb	Low release magnitude (m <sup>3</sup> /s)	Date and duration to base-flow	Total days
PreROD Flow (1994 - 2002)									
1995	NA	14	R	131	NA	G	27	25 Apr-22 May	28
1996	NA	9	R	144	NA	G, 1B	14	10 May-9 Jun	31
1997	NA	10	R	62	NA	G, 3B	13	2 May-2 Jul	62
1998	NA	47	R	192	NA	G	13	24 May-27 Jul	65
1999	NA	15	G	71	NA	G	13	8 May-18 Jul	72
2000	NA	9	R	66	NA	G	13	8 May-27 Jul	81
2002	normal	9	R	171	59,540	G	13	27 Apr-25 Jun	28
ROD Flow (2005 - 2011, 2017)									
2005	wet	8	R, 2B	197	79,880	G, 1B	13	27 Apr-22 Jul	87
2006	extra wet	8	G, 5B	286	99,900	G, 2B	13	16 Apr-22 Jul	98
2007	dry	8	R	135	55,963	G	13	25 Apr-25 Jun	62
2008	dry	9	R, 1B	183	80,016	G, 3B	20	22 Apr-15 Jul	85
2009	dry	8	R	125	54,952	G, 4B	12	24 Apr-6 Jul	74
2010	wet	9	R	194	81,003	G, 3B	12	22 Apr-2 Aug	102
2011	wet	7	R, 2B	329	89,033	G, 2B	13	26 Apr-1 Aug	98
2017	extra wet	9	R, 2P	326	101,536	G	13	22 Apr-11 Aug	112

TABLE 1.—Continued.

Year	Water year- type	Low release magnitude (m <sup>3</sup> /s)	Shape as- cending limb	Peak release magnitude (m <sup>3</sup> /s)	Restoration release (hect- are m)	Shape descending limb	Low release magnitude (m <sup>3</sup> /s)	Date and duration to base-flow	Total days
Pulse Flow (ROD-segment + pulsed augmentation flow; 2003, 2004, 2012 - 2016)									
2003	wet	9 + 13	R + R	73.9 + 51	55,272 + 4,194	G, 2B + G	12 + 13	29 Apr-22 Jul + 23 Aug-18 Sep	85 + 27
2004	wet	9 + 16	R + R	175.6 + 485	80,300 + 4,465	G, 4B + G	12 + 14	4 May-22 Jul + 21 Aug-14 Sep	80 + 25
2012	normal	9 + 13	R, 2B + R, 1B	172.2 + 39	79,817 + 4,811	G, 4B + R, 1B	13 + 13	4 Apr-26 Jul + 12 Aug- 20 Sep	114 + 40
2013	dry	8 + 13	R, 1B + R	125.2 + 74	55,741 + 2,294	G, 2B + R, 1B	13 + 13	13 Apr-25 Jun + 24 Aug-20 Sep	74 + 28
2014	critically dry	9 + 12	R, 1B + R, 1B	96.6 + 97	45,701 + 7,993	G, 1B + R, 1B	13 + 13	21 Apr-26 Jun + 15-25 Sep	67 + 11
2015	dry	9 + 19	R + R, 1B	240.8 + 83	55,593 + 5,908	G, 3B + R 1B	13 + 13	21 Apr-1 Jul + 20 Aug- 21 Sep	72 + 31
2016	wet	9 + 14	R, 2P + R, 1B	283.3 + 35	87,429 + 4,835	G + R, 2B	13 + 13	20 Apr-2 Aug + 24 Aug-28 Sep	105 + 36

based on the expectation of 1) large annual runs of fall-run Chinook Salmon into the lower and upper Klamath River basins, or 2) drier than normal hydrological conditions determined by water-year designations (Table 1). A third justification for this action was to specifically reduce the potential threat of a reoccurrence of the large pathogen-related fish kill that occurred in 2002 (Magneson and Chamberlain 2015, USBR 2015), although there have been no quantitative studies post-2003 to evaluate whether pulse flows have actually prevented another fish die-off in the lower Klamath River. Further, no study has demonstrated a clear relationship between pulse flows and fish movement (Thorstad and Heggberget 1998, Thorstad et al. 2003, Hasler et al. 2014, Peterson et al. 2017).

Recent information suggests that velocities and higher turnover rates of water associated with the magnitude and duration of additional water provided by pulse flows are more important than quality of additional cold water from the Trinity River intended to stimulate fish to move for prevention of disease in the lower Klamath River (Strange 2010, Peterson et al. 2017). Additionally, within the context of the National Environmental Protection Act, numerous assessments have determined no significant impact to populations of salmonids in the Trinity River from implementation of either ROD or Pulse flows, or a combination of both (USBR 2015, USBR 2016, and references therein). Importantly, however, there has been no assessment of the potential effects of intensely managed flow regimes on the pattern of seasonal run-timing or impacts to female reproductive performance, relative to the post-dam baseline flow pattern (henceforth called “PreROD flows”), for any population of adult anadromous species of salmonid in the Trinity River.

Thus, our specific objectives were fourfold. First, we compared annual counts of known-race coded wire tagged and adipose fin clipped (“marked”) hatchery recoveries of adult Chinook Salmon (henceforth called “CWT”), to expanded estimates of CWT adult fish, and all Chinook Salmon that return to the hatchery. This category includes all CWT adult marked and all age classes of marked and un-marked fish (henceforth called “total TRH returns”). Second, we assessed the annual distribution and relative abundance of both races of CWT adult Chinook Salmon and evaluated seasonal patterns in run-timing to identify any concordant patterns common to both races. Third, we tested three research hypotheses of significant differences among designated flow-types in relation to 1) annual and seasonal counts of Chinook Salmon, 2) environmental variables reflecting fluctuations in water temperature and flow volume, and 3) average annual percent fertility determined at the hatchery ( $AAPF = ([\text{total eggs taken} + \text{total eggs culled}] / \text{total eggs after pick})$ ):

$H_1$ : Annually managed flow regimes (hydrographs) implemented by the ROD have altered the run-timing of spring- and fall-run Chinook Salmon in the upper Trinity River.

$H_2$ : Annually managed flow regimes implemented by the ROD differ significantly among flow-types and have altered 1) average daily water temperature, 2) extremes in average daily water temperature, and 3) average daily flow volume in the upper Trinity River.

$H_3$ : Annually managed flow regimes implemented by the ROD have altered hatchery-parental broodstock female AAPF associated with egg production, which includes both hatchery-origin and potentially an unknown number of “wild” natural-origin fish mixed in with the hatchery egg collection.

Our fourth objective was to assess the potential impact of these extrinsic water temperature and flow volume variables on AAPF of hatchery parental broodstock. Importantly, we maintain that AAPF constitutes a “baseline” for performance-based comparisons, developed under controlled hatchery conditions, with in-river spawning of hatchery- and natural-origin stocks of both spring- and fall-run Chinook Salmon inhabiting the upper Trinity River.

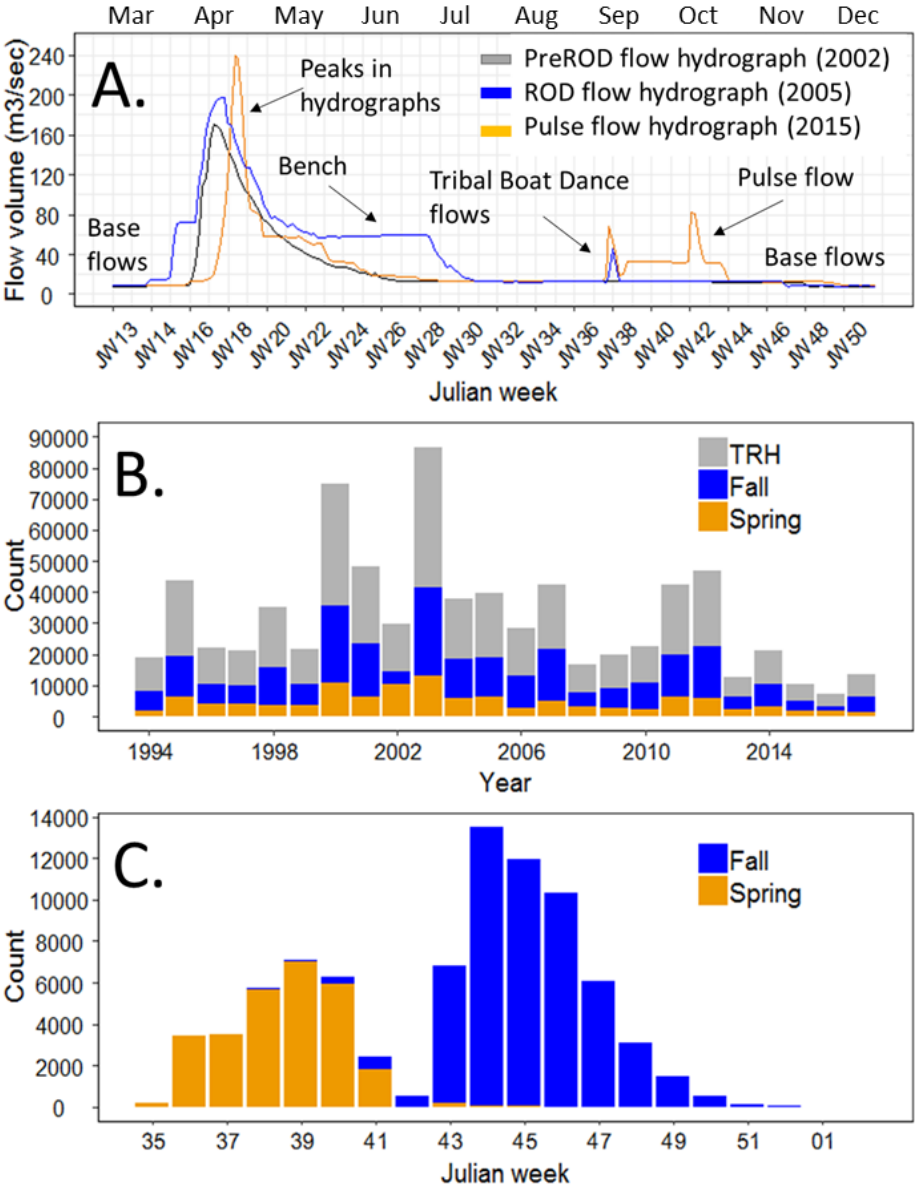
## MATERIALS AND METHODS

*Study area.*—Trinity River is located in northwestern California and is the largest tributary of the Klamath River (Figure 1). Construction of Trinity and Lewiston dams occurred in the early 1960s. Trinity Dam creates Trinity Lake (NAD 83, Zone 10N, UTM 519,964.7 m east and 4,516,719.7 m north), storing up to 3,022 m<sup>3</sup> of water (USFWS and HVT 1999). Lewiston Lake, formed by Lewiston Dam, is located 11.8 km downstream of Trinity Dam (river kilometer [rkm] 180; UTM 517,489.4 m east and 4,508,408.4 m north), which serves as a re-regulating reservoir for flow into the Trinity River and diversion into the Sacramento River Basin, comprising the Trinity River Division of the Central Valley Project. Lewiston Dam is the uppermost limit of anadromous fisheries on the Trinity River. From Lewiston Dam, the Trinity River flows approximately 180 kilometers before joining the Klamath River at the township of Weitchpec (UTM 440,575.2 m east and 4,559,590.2 m north). The Klamath River flows for an additional 70 rkm before entering the Pacific Ocean west of Klamath Glen. The upper Trinity River is the stretch from the confluence of the North Fork Trinity River to 63.1 km up stream to Lewiston Dam. Trinity River Hatchery is located immediately below Lewiston Dam; it releases approximately 4.3 million Chinook Salmon, 300,000 Coho Salmon, (*Oncorhynchus kisutch*), and 448,000 juvenile anadromous Rainbow Trout (*Oncorhynchus mykiss*) (henceforth called “steelhead”) into the Trinity River annually. Data presented herein, derive from counts of Chinook Salmon obtained at the hatchery as part of annual single mark recapture estimates conducted for both races of Chinook Salmon.

*Flow year-types.*—We used our designated flow-types to test our research hypotheses 1) baseline post-dam PreROD flows (1982 - 2002), 2) ROD flows (2005 - 2011, 2017), and 3) Pulse flows (2003, 2004, 2012 - 2016). Late summer pulsed flows were intended to cue up-river seasonal migration of Chinook Salmon out of the lower Klamath River to reduce risk of the epizootic of the ciliate parasite *Ichthyophthirius multifiliis*. Prior to 2003, there were no annually managed ROD or Pulse flows. Importantly, we note that each Pulse flow event was accompanied by a single ROD flow hydrograph (ROD flow plus Pulse flow), beginning in 2003. Thus, for each Pulse flow, effects of each pulsed augmentation are not completely separable or independent from effects of its companion ROD flow.

Since 2001, total restoration releases have included flows for 1) restoration, 2) Tribal Ceremonial Boat Dances, and 3) late summer pulse flows (Table 1). Ceremonial Tribal Boat Dance flows occur in odd years in ROD flows and just prior to any pulsed flow augmentation in Pulse flow years (Figure 2A). They are evident in each hydrograph, amount to  $\leq 0.6\%$  of the total release into the Trinity River (TRRP 2019) and are included herein as Pulse flows tier off the trailing ends of Ceremonial Boat Dance flow hydrographs when they occur. Shapes of the ascending limbs of ROD flow hydrographs were mostly rapid (19/15) with few years in which there were benches (7/15), all of which were associated with managed flows (Table 1). In contrast, shapes of the descending limbs of ROD flow hydrographs were generally gradual with numerous “benches” associated with virtually all managed flows (14/15). We designated benches in these hydrographs as indicating stabilization of water release for one or more consecutive days. There were two double peaked ROD flows (2016 and 2017; Table 1). All Pulse flows had rapid ascending hydrographs and at least one bench. Similarly, all descending limbs of Pulse flows were rapid with at least one bench. Spring and summer base flow releases historically equate to 13 m<sup>3</sup>/second.





**FIGURE 2.**—Line and bar graphs of A) examples of PreROD, ROD, and Pulse flow-type hydrographs showing characteristics described in Table 1. Also shown is the approximate timing of Julian weeks (JW) in relation to months. B) Annual fluctuations in total Trinity River Hatchery returns of all age classes of marked (CWT) and un-marked Chinook Salmon ( $n = 401,667$ ), and expanded estimates of CWT adult spring-run ( $n = 114,720$ ) and fall-run Chinook Salmon ( $n = 246,813$ ). C) Seasonal fluctuations in Julian week hard-counts of both races of CWT adult Chinook Salmon.



ROD flows generally occurred annually from late April to August, whereas conjoining Pulse flows mostly occurred from August to September. Actual timing, magnitude, and duration of ROD and Pulse flows varied in hydrologic characteristics, cubic meters per second ( $\text{m}^3/\text{s}$ ), and shape and duration of the hydrograph annually depending upon the specific intent of the management action (Table 1). Average duration of ROD flows approximated 89.8 days (range 62.0 - 112.0 days) from mid-April to early August and averaged approximately 221.9  $\text{m}^3/\text{s}$  (range 124.9 - 328.6  $\text{m}^3/\text{s}$ ) of flow at the top end of the hydrograph. Average duration of Pulse flows approximated 28.3 days (range 11.0 - 40.0 days) from mid-August to late September, and averaged approximately 61.1  $\text{m}^3/\text{s}$  (range 35.3 - 97.0  $\text{m}^3/\text{s}$ ) of flow at the top end of the hydrograph. For the same general monthly period, average duration of baseline PreROD flows approximated 52.4 days (range 28.0 - 81.0 days) from late April to late July, and averaged approximately 119.6  $\text{m}^3/\text{s}$  (range 62.3 - 192.3  $\text{m}^3/\text{s}$ ) of flow at the top of the hydrograph. Water summary data and typical flow release diagrams (hydrographs) teared to water-year type are available at the TRRP website (TRRP 2019, <http://www.trrp.net>).

*Study design.*—We compared counts of total TRH returns to known age and race CWT spring- and fall-run adult Chinook Salmon recovered from the hatchery. We “expanded” the counts of these CWT adult Chinook Salmon by standardizing, using specific CWT release group multipliers (expansion coefficients). This process generated expansion estimates for total TRH returns based on ratios of the total number of individual fish released for each release group for both spring- and fall-run adult CWT adult Chinook Salmon, divided by the total number of CWT adult fish released for each CWT value. Telemetered digital flow volume ( $\text{m}^3/\text{s}$ ) and water temperature data (degrees centigrade [ $^{\circ}\text{C}$ ]) were derived from the US Geological Survey (USGS) and the USBR Lewiston Water Quality Gauge (LWS), upper Trinity River at river-km 178.2 (UTM 516,634 m E and 4,507,678 m N, elevation 558 m), 1.7 rkm downriver from the Lewiston Dam and the hatchery. We downloaded digital data on average daily water temperature (ADWT) and average daily flow volume (ADFV) from the California Department of Water Resources, California Data Exchange Center (DWR 2018).

We used the LWS gauge data for several specific reasons. First, water temperature in the hatchery main intake is monitored daily and water temperature throughout the facility to the river effluent has historically been within 1 degree (D. Muir, personal communication). Thus, we assumed that thermal regimes in the hatchery closely mimic immediate in-river water temperatures, as both derive from water sources immediately out of Lewiston Lake. Second, this gauge is the “standard” used in all National Environmental Protection Act assessments and flow augmentations analyses of in-river average water temperature, specific to the upper Trinity River out of Lewiston Dam since 1997 (Zedonis 2009 and included references). Second, this gauge provides the best, most consistent, and detailed long-term digital information reflecting water temperature conditions used during each hatchery phase of egg production, juvenile grow-out, and release of all hatchery-produced Chinook Salmon assessed herein. Third, virtually all hatchery raised Chinook Salmon spawn within the first 3.2 km below the Lewiston Dam and hatchery (Rupert et al. 2016). Fourth, this section of the upper Trinity River consistently contains the largest densities of hatchery-origin Chinook Salmon spawning redds (Rupert et al. 2017a and 2017b). Thus, this gauge provides the best location for measuring water temperature conditions nearest to the hatchery for in-river spawning of hatchery-origin Chinook Salmon, and it is highly likely that other natural-origin co-occurring anadromous species of salmonids also spawn in this segment of the reach. Although punctuated up-and-down measurements using average daily water temperature may

approximate a bi-monthly framework for viewing average water temperature in the upper Trinity River, this metric does not identify or illustrate extremes in water temperature. Instead, we used the range of extreme variation in average daily water temperatures (minimum to maximum) to address the need for an index of water temperature variability (ADWTVI).

*Statistical analyses.*—A Shapiro-Wilk test of the hypothesis that annual counts of total TRH returns, and spring- and fall-run CWT adult Chinook Salmon derive from a normally distributed population was rejected for each group of fish (spring-run:  $W = 0.85$ ,  $P < 0.01$ ,  $n = 24$ ; fall-run:  $W = 0.85$ ,  $P < 0.01$ ,  $n = 24$ ; total TRH returns:  $W = 0.88$ ,  $P = 0.01$ ,  $n = 24$ ). In all three groups of fish, counts were skewed significantly to the right, consistent with a Poisson distribution. Thus, all subsequent non-regression statistical analyses of count data used non-parametric methods (McDonald 2014). Spearman's rank correlation ( $r_s$ ) was used to calculate strength and direction of the relationship between two variables, expressed as a monotonic relationship, whether linear or not (Corder and Foreman 2014). Although we provide and analyze expanded estimates of the relative abundance of fish based on CWT adult Chinook, we used non-expanded CWT adult fish for all follow-on statistical analyses and comparisons because these data are not estimates but hard-counts (Kilduff et al. 2015).

We analyzed trends in seasonal count data by use of Julian weeks (JW), defined as one of seven consecutive-day-sets of 52 weekly periods in a calendar year, beginning 01 January of each year. This procedure allowed inter-annual comparisons of identical weekly periods. Extra day in leap years was included in the ninth week. Wilcoxon signed-rank test computed from two-sided probabilities using approximate normal variates ( $Z$ ) evaluated the hypothesis that the median difference between pairs of Julian weeks was zero among different flow-types for each race of Chinook Salmon (Hasler et al. 2014, McDonald 2014). To determine if timing of seasonal migration in ROD and Pulse flows deviated from the baseline PreROD flow condition, we calculated a Percent Deviation Index (PDI) from total hard-counts:

$$\text{PDI for ROD flows} = \% \text{ROD flow count} - \% \text{PreROD flow count}$$

$$\text{PDI for Pulse flows} = \% \text{Pulse flow count} - \% \text{PreROD flow count}$$

To evaluate the specific pattern in timing of migration, we tested the hypothesis ( $H_1$ ) that counts of spring- and fall-run Chinook Salmon identified during individual Julian weeks were significantly different between flow-types. We attempted to standardize sampling effort by including in our analysis only those pairwise comparisons that had a sample size  $\geq 5$  for each flow-type. Pairwise comparisons of non-zero counts using Julian weeks as attributes were then evaluated by use of the Dwass-Steel-Christchlow-Fligner (*DSCF*) 2-tailed test (Critchlow and Fligner 1991) combined with the Holm adjustment for unplanned multiple comparisons (Holm 1979). We assessed annual trends in continuously distributed linear measures of water temperature and flow volume from 1995 through 2018, and seasonally by use of Julian weeks specifically from the flow schedule implemented from previous managed hydrographs (Table 1, JW13 - JW40).

We generated regression models for total TRH returns and counts of CWT adult Chinook Salmon by use of Generalized Additive Models (GAMs, R Core Team 2019, Wood 2017). GAMs are a semi-parametric extension of Generalized Linear Models (GLM) that are less restrictive in assumptions about the underlying distribution of data; thus providing an effective technique for assessing non-linear relationships between response and explana-

tory variables (Madsen and Thyregod 2011). Instead of estimating single parameters as in a GLM, a general unspecific function relates predicted transformed  $y$ -values to predictor values ( $x$ -values). GAM models assume the dependent variable is dependent on the univariate smooth term (function) of the independent variable, rather than the independent variable itself (Hastie and Tibshirani 1990). We used default settings degrees of freedom in our GAM-based analyses of counts and a thin plate-regression spline base-function as our smoothing technique with 10 degrees of freedom ( $k$ ). This method generally gives 1) the best mean square error performance and optimal smoother of any given basis dimension; and 2) it is advantageous because it is flexible and avoids the need to make prior assumptions about the shape of the function (Schluter 1988, Wood 2003, Wood 2017).

Response curves generated from each GAM show the relationship between the fitted function to the response scaled to zero.  $Y$ -axes based on partial residuals indicate the relative influence of each predictor on the prediction on the base of partial residuals. Smooths were “centered” to ensure model identity and summed to zero over covariate values. Statistics reported from each GAM were 1)  $\chi^2$ - or  $F$ -statistic (approximate significance of smooth terms) including  $P$ -value and 95% confidence band for the spline line (Nychka 1988); 2) adjusted regression coefficient for the model ( $R^2$  adj.), 3) estimated residual degrees of freedom (*Ref. d.f.*), and 4) proportion of null deviance explained (*Dev.Exp.*). We used Spearman’s rank correlation coefficient as a follow-on procedure to assess strength and significance of trends in counts delineated by smooth terms, because GAMs lack a statistical inference procedure and formal parameter of goodness of the fit, which makes interpretation of output potentially complicated (Diankha and Thiaw 2016). Because our count data were over-dispersed, we used the negative binomial error-structure (family = “nb” [link = “log”]) in construction of GAM models to establish the relationship between response variables and smoothed functions of predictor variables (Peterson et al. 2017, Wood 2017). In contrast, we used the gamma error-structure (family = “Gamma” [link = “log”]) to assess annual and seasonal (JW) fluctuations in ADWT, ADWTVI, and ADFV (Appendix I) and their mean values when compared to AAPF (Appendix II), as visual inspection of Q-Q plots of standardized residuals showed that all variables were only near normal in their distributions. Thus, we used non-parametric statistics to assess relationships among environmental variables, flow-types, and AAPF for each genetic race of Chinook Salmon. We evaluated the species-specific relationships between AAPF (response variable) and explanatory extrinsic water temperature and flow volume attributes individually and in paired combinations. We used the Akaike information criterion modified for overdispersed count data adjusted for small sample uncertainty ( $QAIC_c$ ) to select the most parsimonious GAM models for comparisons between AAPF and various individual and combined water temperature and flow volume effects (Akaike 1973, Burnham and Anderson 1998).

We assumed that the highest-ranking model was the most parsimonious given the limitations of our data, and subsequent models were ranked in relation to the most parsimonious model. Fourteen water temperature and flow volume models resulted from our investigation of the relationship between AAPF and environmental attributes (Table 2). This analysis allowed identification of potentially useful models, variables, and variable combinations potentially affecting AAPF in hatchery- and natural-origin stocks of both races of Chinook Salmon. We used autocorrelation analysis of residuals derived from GAM analyses of annual and seasonal Julian week counts to investigate the relationship of each time point to each previous time point in the distribution of annually and seasonally consecutive counts

**TABLE 2.**—Summary of approximate significance of smooth terms and statistics derived from generalized additive model (GAM) regressions of total Trinity River Hatchery returns and coded wire tagged (CWT) annual and Julian week (JW) counts of adult Chinook Salmon in relation to 1) average annual percent fertility (AAPF), 2) average daily water temperature (ADWT), 3) average daily water temperature variability index (ADWTVI), and 4) average daily flow volume (ADFV). For the GAM regression ( $\chi^2$ ) “nb” = a negative binomial error structure and GAM regression (F) “Gamma” = a gamma error structure. The Akaike information criterion modified for overdispersed count data adjusted for small sample uncertainty ( $QAIC_c$ ) was used to select the most parsimonious GAM models.

GAM (family = “nb”)	GAM $\chi^2$	Ref.d.f.	P-value	n	R <sup>2</sup> (adj.)	Dev.Exp.	$QAIC_c$
<u>Counts vs years (1994 - 2017)</u>							
Total TRH returns ~ year	18.9	3.3	< 0.01	24	0.27	46.1%	487.2
Spring-run ~ year	16.6	3.3	< 0.01	24	0.26	44.1%	367.3
Fall-run ~ year	16.3	3.6	< 0.01	24	0.25	44.3%	404.3
<u>Counts vs years (2003 - 2017)</u>							
Total TRH returns ~ year (2003 - 2017)	16.1	1.0	< 0.01	15	0.50	53.4%	302.9
Spring-run ~ year (2003 - 2017)	32.1	4.3	< 0.01	15	0.71	77.3%	234.7
Fall-run ~ year (2003 - 2017)	12.6	1.0	< 0.01	15	0.47	46.6%	253.8
<u>Counts vs Julian weeks (JW35 - JW02)</u>							
Spring-run ~ JW	67.9	4.2	< 0.01	12	0.85	82.3%	214.4
Fall-run ~ JW	664.2	5.7	< 0.01	19	0.93	98.0%	264.4
GAM (family = “Gamma”)	GAM F	Ref.d.f.	P-value	n	R <sup>2</sup> (adj.)	Dev.Exp.	$QAIC_c$
<u>AAPF vs year (1994 - 2014)</u>							
Spring-run AAPF ~ year	6.7	3.8	< 0.01	20	0.51	60.9%	130.1
Fall-run AAPF ~ year	5.2	3.0	< 0.01	19	0.46	50.6%	129.6
<u>Environmental variables vs year</u>							
ADWT ~ year	162.2	4.0	< 0.01	4,347	0.13	12.7%	12,040.7
ADWTVI ~ year	226.8	4.0	< 0.01	4,347	0.16	15.0%	8100.4
ADFV ~ year	10.8	4.0	< 0.01	4,458	0.01	1.6%	38838.5
<u>Environmental variables vs Julian week</u>							
ADWT ~ JW	413.2	4.0	< 0.01	4,347	0.28	28.1%	11228.7
ADWTVI ~ JW	274.3	4.0	< 0.01	4,347	0.16	18.1%	7935.7
ADFV ~ JW	442.0	4.0	< 0.01	4,458	0.38	47.7%	35846.1
<u>Between environmental variables</u>							
ADWT ~ ADWTVI	444.6	4.0	< 0.01	4,347	0.29	29.3%	11158.0
ADWT ~ ADFV	536.7	4.0	< 0.01	4,315	0.30	32.6%	10846.1
ADWTVI ~ ADFV	842.7	4.0	< 0.01	4,315	0.31	40.2%	6529.3

TABLE 2.—Continued.

<u>Run-specific AAPF vs each environmental variable</u>							
Spring-run AAPF ~ ADWT	11.8	3.9	< 0.01	20	0.64	74.6%	122.9
Spring-run AAPF ~ ADWTVI	8.1	2.4	< 0.01	20	0.50	53.9%	127.1
Spring-run AAPF ~ ADFV	0.5	1.0	= 0.48	20	0.02	2.6%	137.9
Fall-run AAPF ~ ADWT	13.7	3.9	< 0.01	19	0.68	79.0%	119.7
Fall-run AAPF ~ ADWTVI	7.6	1.6	< 0.01	19	0.35	37.3%	129.3
Fall-run AAPF ~ ADFV	0.2	1.0	= 0.63	19	0.78	1.2%	136.4
<u>Run-specific AAPF vs combinations of environmental variables</u>							
<u>Spring-run AAPF ~ ADWT + ADWTVI</u>							
ADWT	3.6	7.1	< 0.01	20	0.74	84.5%	124.6
ADWTVI	2.0	3.4	= 0.05	20			
<u>Spring-run AAPF ~ ADWT + ADFV</u>							
ADWT	11.4	3.9	< 0.01	20	0.62	75.1%	127.9
ADFV	0.1	1.0	= 0.73	20			
<u>Spring-run AAPF ~ ADWTVI + ADFV</u>							
ADWTVI	7.2	2.4	< 0.01	20	0.47	54.2%	130.9
ADFV	0.0	1.0	= 0.98	20			
<u>Spring-run AAPF ~ WT + ADWTVI + ADFV</u>							
ADWT	6.8	3.8	< 0.00	20	0.72	83.9%	130
ADWTVI	3.7	2.2	=0.05	20			
ADFV	0.4	1.0	=0.56	20			
<u>Fall-run AAPF ~ ADWT + ADWTVI</u>							
ADWT	9.8	3.8	< 0.01	19	0.74	83.8%	118.9
ADWTVI	6.3	1.0	= 0.03	19			
<u>Fall-run AAPF ~ ADWT + ADFV</u>							
ADWT	13.7	3.9	< 0.01	19	0.66	79.2%	125.2
ADFV	0.5	1.0	= 0.83	19			
<u>Fall-run AAPF ~ ADWTVI + ADFV</u>							
ADWTVI	10.8	1.0	< 0.01	19	0.36	38.9%	131.4
ADFV	1.3	1.0	= 0.27	19			
<u>Fall-run AAPF ~ ADWT + ADWTVI + ADFV</u>							
	10	3.8	< 0.00	19	0.76	85.70%	123.6
	8.0	1.0	< 0.01	19			
	1.7	1.0	= 0.22	19			

of total TRH returns and each race of Chinook Salmon (R Core Team 2019). A follow-on Box-Pierce ( $\chi^2$ ) test evaluated the extent of stationarity of the time series model (Box and Pierce 1970, Fuller 1976, Ljung and Box 1978). We accepted overall statistical significance at  $P \leq 0.10$  because sample sizes were generally small, despite the risk of higher false signals (Rubin and Cole 2009, Noymer 2008, Bartley et al. 2012, McDonald 2014). Moreover, we wanted a more “relaxed” threshold to act as an early “warning signal” given the importance of assessing annual and seasonal trends that have immediate management and economic implications in reference to oceanic conditions, regional climate change, local drought, and flow manipulation (Good et al. 2005, Gallagher et al. 2012).

## RESULTS

*Fluctuations in annual counts and expanded estimates.*—From 1994 to 2017, the hatchery recovered 27,821 (6.9%) spring-run and 55,196 (13.7%) fall-run CWT adult Chinook Salmon, which equates to 20.7% ( $n = 401,667$ ) of all Chinook Salmon recovered from the hatchery (total TRH returns). Annual expanded estimates for CWT adult spring-run fish totaled 114,720 (28.56%) and 246,813 (61.5%) for fall-run fish. For both races of CWT adult fish, the combined expanded estimate represented 90.0% of all Chinook Salmon that returned to the hatchery between 1994 and 2017, which equates to an average multiplier of 4.35493. Prior to brood year 2000, the percent of marked pre-release juvenile Chinook Salmon averaged 13.5% (range 11.3% [1998] - 15.1% [1999]) of total TRH returns annually. However, beginning with brood year 2000 production (2001 release groups), the hatchery implemented an annual 25.0% “constant fractional marking rate” of pre-release juveniles. Nevertheless, the full effect of 25.0% constant fractional marking at the hatchery did not occur until 2005, with the parental brood year 2000 age 5 cohort.

Analysis of counts of Chinook Salmon returning to the hatchery and counts of spring-run and fall-run CWT adult fish fluctuated considerably on an annual basis (Figure 2B). Peak counts in total TRH returns occurred in 2003, 2000, 2001, and 2012. Whereas the smallest number of Chinook Salmon occurred in 2016, 2015, 2013, and 2017. From 1994 to 2017, 50.0% ( $n = 24$ ) of the years had counts smaller than recorded during the massive fish die-off that occurred in the lower Klamath River in 2002 (CDFG 2004). Follow-on rank correlations between total TRH returns and expanded estimates of CWT adult fish were significant and positive for both races of Chinook Salmon (spring-run:  $r_s = 0.90$ ,  $P < 0.01$ ,  $n = 24$ ; fall-run:  $r_s = 0.92$ ,  $P < 0.01$ ,  $n = 24$ ), as well as the combined expanded estimate using both races of CWT adult Chinook Salmon simultaneously ( $r_s = 0.99$ ,  $P \leq 0.01$ ,  $n = 24$ ). Similarly, the relationship between total TRH returns and counts of CWT adult spring- and fall-run fish also were significant and positive ( $r_s = 0.88$ ,  $P < 0.01$ ,  $n = 24$  and  $r_s = 0.79$ ,  $P < 0.01$ ,  $n = 24$ , respectively) even though combined counts of CWT adult fish represent only 20.7% of total TRH returns.

Autocorrelation analyses of residuals for annual counts showed that all time points were contained within approximate 95% confidence levels of significance for each correlation in the autocorrelation function correlograms. These results were corroborated by the lack of significance in Box-Pierce tests for total TRH returns ( $\chi^2 = 1.11$ ,  $P = 0.29$ ,  $d.f. = 1$ ), and CWT adult spring-run ( $\chi^2 = 0.48$ ,  $P = 0.49$ ,  $d.f. = 1$ ), and fall-run fish ( $\chi^2 = 2.0$ ,  $P = 0.16$ ,  $d.f. = 1$ ). Thus, we found no evidence against time dependency for counts; as all three groups of Chinook Salmon appeared to represent stationary series of relatively constant autocorrelation



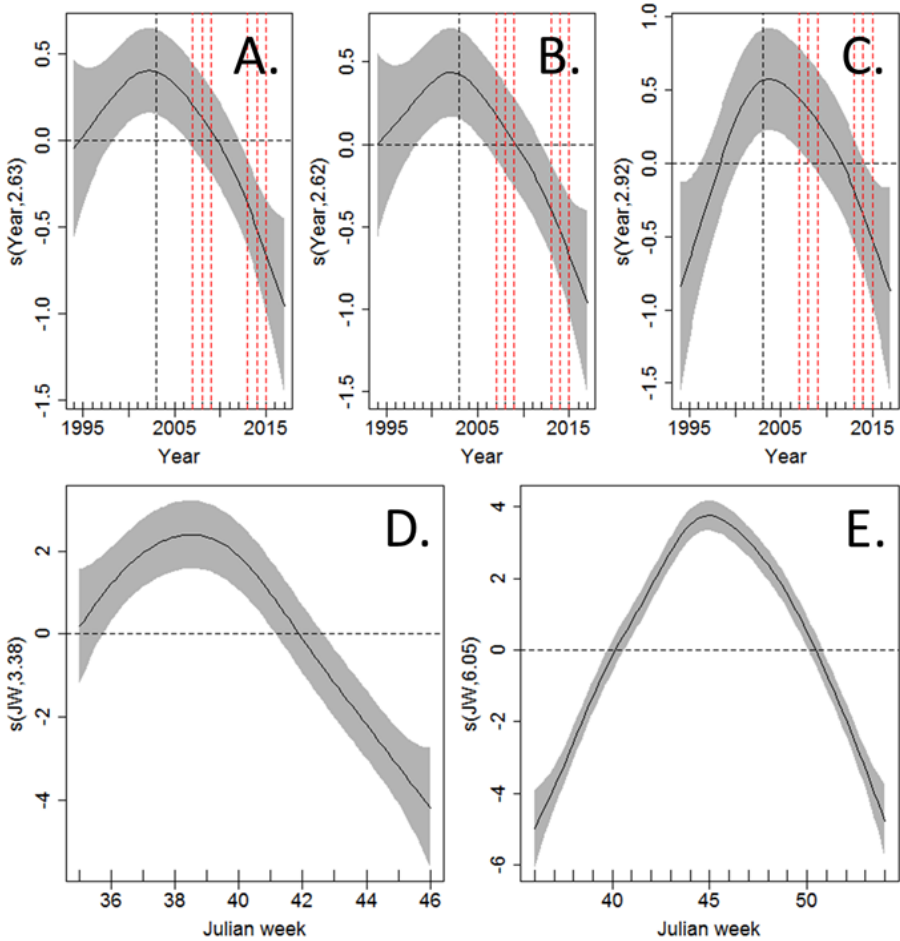
structure over time for the consecutive sequence of dates analyzed herein. Importantly, a stationary series for hatchery production likely will always occur for hatchery raised Chinook Salmon as TRH releases fingerlings and yearlings based on egg-take allotments established in the 1980s to meet fixed mitigation goals of 7,000 returning adult fall-run Chinook to the hatchery irrespective of annual hatchery escapement. Plots of partial residuals showed that annual counts of Chinook Salmon were nonlinear, and well defined by response curves for total TRH returns, and both races of CWT adult fish (Figure 3A, 3B, and 3C). All smooth terms were significant and deviance explained was  $\geq 44.1\%$  for each group of fish (Table 2). Additionally, there was a negative relationship between year and total TRH returns ( $r_s = -0.44$ ,  $P < 0.05$ ,  $n = 24$ ), and counts of spring-run CWT adult Chinook Salmon ( $r_s = -0.43$ ,  $P < 0.05$ ,  $n = 24$ ), but not between year and counts of fall-run CWT adult fish ( $r_s = -0.04$ ,  $P > 0.10$ ,  $n = 24$ ). For the annual sampling period shared by both races of CWT adult Chinook Salmon, the correlation between counts was significant and positive ( $r_s = 0.64$ ,  $P < 0.01$ ,  $n = 24$ ), indicating that both races exhibited concordant patterns in timing of annual migration.

However, for the annual sampling period from 2003 to 2017, a stronger negative trend was evident between year and counts in all groups of Chinook Salmon (total TRH returns:  $r_s = -0.67$ ,  $P = 0.01$ ,  $n = 15$ ; spring-run:  $r_s = -0.72$ ,  $P < 0.10$ ,  $n = 15$ ; fall-run:  $r_s = -0.65$ ,  $P = 0.01$ ,  $n = 15$ ). Similarly, all smooth terms were significant and deviance explained was  $\geq 46.6\%$  (Table 2). As expected, the strength of the correlation between counts of each group of fish from 2003 to 2017 was strong, significant, and positive (spring-run vs. total TRH returns:  $r_s = 0.91$ ,  $P < 0.01$ ,  $n = 15$ ; fall-run vs. total TRH returns:  $r_s = 0.99$ ,  $P < 0.01$ ,  $n = 15$ ; spring-run vs. fall-run:  $r_s = 0.85$ ,  $P < 0.01$ ,  $n = 15$ ). Thus, all age classes of marked (CWT) and un-marked fish have declined dramatically in relative abundance since 2003. Importantly, this concordant trend in declining stocks of Chinook Salmon began before the two disjunct periods of three consecutive years of regional drought as indicated by water year-type for 2007-2009 and 2013-2015 (3A, 3B, 3C; Table 1, TRRP 2019).

*Seasonal fluctuations in run-timing.*—Seasonal trends in counts of spring- and fall-run CWT adult Chinook Salmon also fluctuated on a weekly basis. In spring-run fish, fluctuations in seasonal run-timing ranged from early September through late November (JW36 - JW48, Figure 2C). Migrating fish occurred most frequently in the upper Trinity River and counted at the hatchery from early to mid-September through early October. There was a primary peak in late September, followed by an abrupt decline by mid-October, with some fish lingering in the upper reach into mid-November. In contrast, seasonal run-timing in fall-run CWT Chinook Salmon ranged from late September through early January (JW36 - JW01). Migrating fall-run fish occurred most frequently from mid-October through mid-November (Figure 2C), with the primary peak occurring in late October, followed by an abrupt decline through late November and early December.

Autocorrelation analyses of residuals for Julian week counts showed that all time points were contained within approximate 95% confidence levels of significance for each correlation in the autocorrelation function correlograms and by the Box-Pierce tests for both CWT adult spring-run ( $\chi^2 = 0.16$ ,  $P = 0.69$ ,  $d.f. = 1$ ) and fall-run ( $\chi^2 = 0.25$ ,  $P = 0.62$ ,  $d.f. = 1$ ) fish. Plots of partial residuals showed that seasonal trends in Julian week counts of spring- and fall-run CWT adult Chinook Salmon were significant, nonlinear, and well defined by response curves, with deviance explained  $\geq 82.3\%$  (Figure 3D and 3E, Table 2). Follow-on ranked correlation found a significant negative relationship between Julian weeks and counts of CWT adult spring-run fish ( $r_s = -0.62$ ,  $P < 0.01$ ,  $n = 12$ ) but not fall-run fish





**FIGURE 3.**—Response curves using GAM regression of annual fluctuations in the distribution of A) total Trinity River Hatchery returns, B) CWT adult spring-run, C) CWT adult fall-run fish, and seasonal fluctuations in Julian week (JW) counts of D) CWT adult spring-run and E) CWT adult fall-run Chinook Salmon. X-axes are labeled with the covariate name (cov) and y-axes by the covariate name and estimated degrees of freedom (edf) of each smooth ( $s[\text{cov}, \text{edf}]$ ). Plots show the relationship of the fitted GAM function to the response scaled to zero. Shaded areas indicate 2-times the point-wise standard error for each curve surrounding each fitted GAM function (black lines). Horizontal black dashed lines measure extremes above and below the mean. Vertical dashed black lines reference year 2003 and vertical dashed redlines reference 2-periods of three consecutive dry water-years reflective of regional drought (Table 1)

( $r_s = 0.06$ ,  $P > 0.10$ ,  $n = 19$ ). As expected, the relationship between counts of CWT adult spring- and fall-run fish was significant but negatively correlated for the weekly sampling period shared by these two seasonally semi-disjunct races of Chinook Salmon ( $r_s = -0.68$ ,  $P < 0.05$ ,  $n = 11$ ).

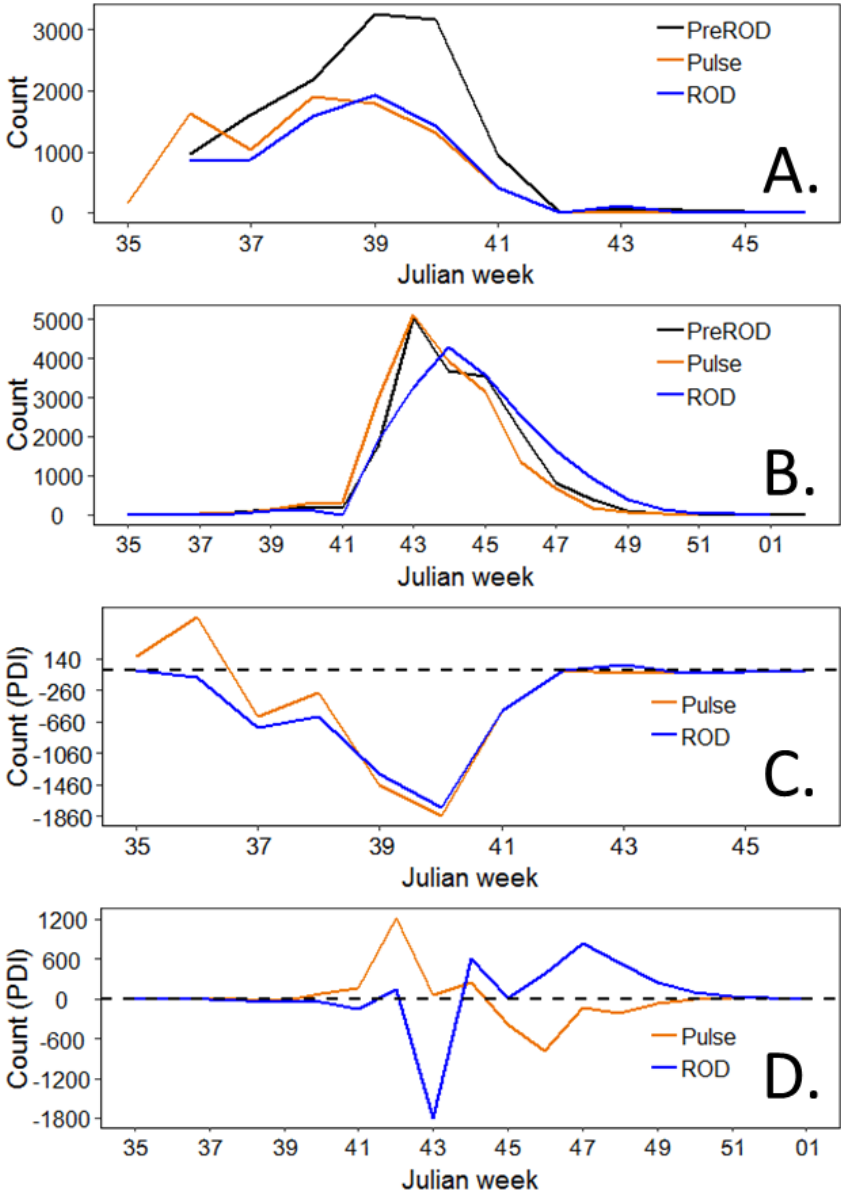
*Deviation in run-timing from the baseline flow-type.*—For CWT adult spring-run Chinook Salmon, counts of each flow-type were 1) baseline PreROD flow ( $n = 12,296$ ); 2) ROD flow ( $n = 7,248$ ) and 3) Pulse flow ( $n = 8,277$ ; Figure 4A). Deviation away from the baseline PreROD flow pattern in run-timing relative to other managed flow-types was

predominantly negative and occurred through 1) reduction in number of fish at the ascending limb of the baseline hydrograph, and 2) addition of fish along the declining central segment and trailing end of the baseline hydrograph (Figure 4C). Analysis of planned median differences in Wilcoxon sign-ranked tests of pairs of Julian week counts showed a significant overall difference in run-timing between baseline PreROD and ROD flows ( $Z = 2.6$ ,  $P < 0.01$ ,  $n = 12$ ) and between PreROD and Pulse flows ( $Z = 1.8$ ,  $P = 0.08$ ,  $n = 12$ ), but not between ROD and Pulse flows ( $Z = 1.0$ ,  $P = 0.36$ ,  $n = 12$ ). However, unplanned pairwise comparisons of individual Julian weeks showed several significant differences between flow-types. For example, of the 12 total Julian weeks encompassing the entire CWT adult spring-run (years 1994 - 2017), 66.7% (8/12) had sample sizes  $\geq 5$  for each flow-type (Table 3); of which four pair-wise comparisons showed significant differences between PreROD and ROD flows (JW43 - JW44) and PreROD and Pulse flows (JW40 - JW41, Figure 4C).

Counts of CWT spring-run adult Chinook Salmon, encompassing all deviations, both positive and negative, away from baseline PreROD flow pattern in run-timing, ranged from 5,156 fish (ROD flows) to 5,683 fish (Pulse flows, Table 4). Thus, the combined influence of both ROD and Pulse flow hydrographs affected 10,839 spring-run CWT adult Chinook Salmon relative to the baseline PreROD flow condition. This number equates to an estimated 47,203 total adult fish using the expansion coefficient or 11.8% of total TRH returns from 1994 to 2017. Strength of the correlation between spring-run fish affected by ROD flows and those affected by Pulse flows was significant and positive ( $r_s = 0.77$ ,  $P < 0.01$ ,  $n = 12$ ), indicating that both ROD and Pulse flows altered run-timing in the baseline PreROD flow pattern in parallel (Figure 4C).

For fall-run CWT adult Chinook Salmon, counts of each flow-type were 1) baseline PreROD flow ( $n = 18,086$ ), 2) ROD flow ( $n = 18,902$ ), and 3) Pulse flow ( $n = 18,208$ ; Figure 4B). Timing of migration for both ROD and Pulse flows also deviated from the historical baseline PreROD flow pattern of migration. Here, deviations were mostly positive and occurred through 1) addition of fish at both the ascending (early) and descending (late) limbs of the baseline PreROD flow hydrograph, and 2) reduction of fish within the center of the baseline PreROD flow hydrograph (Figure 4D). Median differences in planned pairs-wise comparisons of Julian week counts showed no significant overall difference in run-timing between baseline PreROD and ROD flows, PreROD and Pulse flows, or ROD and Pulse flows ( $Z = 1.2$ ,  $P = 0.24$ ,  $n = 19$ ;  $Z = 0.46$ ,  $P = 0.67$ ,  $n = 19$ ;  $Z = 0.66$ ,  $P = 0.52$ ,  $n = 19$ , respectively). However, of the 19 Julian weeks encompassing the entire fall-run for CWT adult Chinook Salmon, 11 (57.9%) had sample sizes  $\geq 5$  for each flow-type (Table 3). Of these unplanned pairwise comparisons 7 (63.6%) showed significant differences between PreROD and the ROD flows (JW39, JW43, JW45, JW47), PreROD and Pulse flows (JW41), and ROD and Pulse flows (JW46, JW47, JW48; Figure 4D).

Counts of fall-run CWT adult Chinook Salmon encompassing all deviations, both positive and negative, away from the baseline PreROD flow condition, ranged from 5,008 fish (ROD flows) to 3,412 fish (Pulse flows, Table 4). Hence, the combined influence of both ROD and Pulse flow hydrographs affected 8,420 fall-run CWT adult Chinook Salmon, relative to the baseline PreROD flow pattern of migration, which equates to an estimated 36,669 total fish using the expansion coefficient or 9.1% of total TRH returns from 1994 to 2017. Importantly, however, the relationship between fall-run fish affected by ROD flows and those fish affected by Pulse flows was significant and negatively correlated it was not strong ( $r_s = -0.41$ ,  $P < 0.08$ ,  $n = 19$ ; Figure 4D). These results indicate that ROD and Pulse



**FIGURE 4.**—Line graphs of seasonal fluctuations in counts of CWT adult A) spring-run and B) fall run Chinook Salmon; and counts of CWT C) adult spring-run and D) adult fall-run fish affected by both ROD and Pulse flows relative to the baseline PreROD flow pattern of run-timing, expressed as a function of the Percent Deviation Index (PDI). ROD and Pulse flow lines that plot above or below dashed horizontal black lines on the y-axes indicate addition or subtraction of fish from the taxon-specific baseline pattern of run-timing associated with the specific managed flow-type.

**TABLE 3.**—Results of the Dwass-Steel-Chritchlow-Fligner (*DSCF*) pairwise comparisons of nonzero coded wire tag marked (CWT) spring- and fall-run adult Chinook Salmon using Julian week (JW) counts as attributes to assess significance between baseline flow-types from 1994 to 2017. Only pairwise comparisons with Julian week count sample sizes  $\geq 5$  were included in our analyses. We adjusted raw *P*-values using the Holms adjustment method separately for each race and JW. Only those comparisons that were significant ( $P \leq 0.10$ ) appear in the table.

Julian week	Flow group ( <i>i</i> )	<i>n</i>	Flow group ( <i>j</i> )	<i>n</i>	DSCF statistic	<i>P</i> -value
Spring-run Chinook salmon						
JW37	Pre-ROD	9	Pulse	7	3.1	0.08
JW38	Pre-ROD	8	Pulse	7	3.1	0.07
JW39	Pre-ROD	9	Pulse	7	3.3	0.05
	ROD	8	Pulse	7	2.9	0.09
JW40	Pre-ROD	9	Pulse	7	4.0	0.01
JW41	Pre-ROD	9	Pulse	6	7.2	0.00
JW43	Pre-ROD	6	ROD	6	3.8	0.02
JW44	Pre-ROD	8	ROD	6	4.2	0.01
Fall-run Chinook salmon						
JW41	Pre-ROD	8	ROD	6	3.3	0.06
	Pre-ROD	8	Pulse	6	3.6	0.03
JW43	Pre-ROD	6	ROD	7	4.1	0.01
	ROD	7	Pulse	7	2.9	0.10
JW45	Pre-ROD	8	ROD	7	4.0	0.01
	ROD	8	Pulse	7	3.1	0.07
JW46	ROD	8	Pulse	7	3.3	0.05
JW47	Pre-ROD	8	ROD	7	5.0	0.00
	ROD	8	Pulse	7	4.1	0.01
JW48	Pre-ROD	8	ROD	7	3.1	0.07
	ROD	8	Pulse	7	3.6	0.03

flows altered run-timing in the baseline PreROD flow pattern of fall-run CWT adult fish at different times during the season (JW41 - JW44). Thus, annually managed hydrographs have affected approximately 20.9% (83,872/401,667) of total TRH returns of spring- and fall-run adult Chinook Salmon, relative to the baseline PreROD flow pattern since 2003.

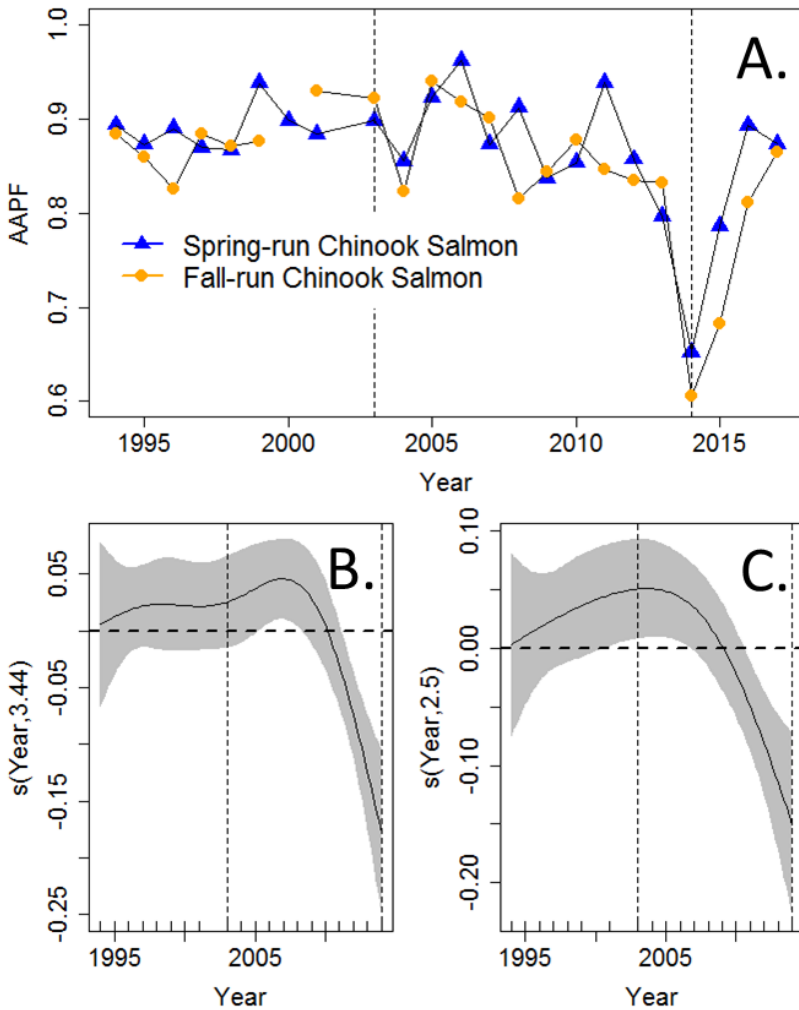
*Fluctuations in annual reproductive attributes of hatchery parental brood-stock.*—An average of 1,125.2 ( $n = 27,028$ ) spring-run and 1,972.9 ( $n = 43,403$ ) fall-run marked (CWT) and un-marked adult female Chinook Salmon were spawned annually at the hatchery from 1994 to 2017. Spring- and fall-run fish differed significantly in total number of adult females spawned (AFSPW:  $Z = 4.1$ ,  $P < 0.01$ ,  $n = 22$ ), a function of generally larger run-size in fall-run fish (Figure 2B and 2C) and AAPF ( $Z = 1.7$ ,  $P = 0.08$ ,  $n = 22$ ), but not in average eggs per ounce (AEPOZ;  $Z = 0.65$ ,  $P = 0.52$ ,  $n = 22$ ), or average eggs per female (AEPF:  $Z = 0.05$ ,  $P = 0.96$ ,  $n = 22$ ). All reproductive attributes except AEPOZ were significantly correlated between spring- and fall-run adult Chinook Salmon (AEPF:  $r_s = 0.80$ ,  $P < 0.01$ ; AFSPW:  $r_s = 0.52$ ,  $P = 0.02$ ; AAPF:  $r_s = 0.50$ ,  $P = 0.02$ ; AEPOZ:  $r_s = 0.33$ ,  $P = 0.13$ ).

**TABLE 4.**—Total counts (positive and negative) and total cumulative counts (positive + negative) by Julian week (JW) of spring- and fall-run CWT adult Chinook Salmon affected by ROD and Pulse flows, relative to the pattern in run-timing typical of taxon-specific baseline PreROD flows.

Julian week	Spring-run affected			Fall-run affected		
	ROD flows	Pulse flows	Total affected	ROD flows	Pulse flows	Total affected
JW35	0	165	165	0	0	0
JW36	-100	667	767	1	2	3
JW37	-733	-589	1,322	-3	-1	4
JW38	-594	-286	880	-4	3	7
JW39	-1,326	-1,469	2,795	-38	-7	45
JW40	-1,742	-1,858	3,600	-44	-21	65
JW41	-530	-530	1,060	-53	83	136
JW42	-8	-1	9	-160	168	328
JW43	54	-45	99	140	1,208	1,348
JW44	-45	-50	95	-1,794	53	1,847
JW45	-19	-19	38	597	250	847
JW46	-5	-4	9	24	-397	421
JW47	0	0	0	370	-795	1,165
JW48	0	0	0	837	-124	961
JW49	0	0	0	537	-215	752
JW50	0	0	0	256	-68	324
JW51	0	0	0	96	-16	112
JW52	0	0	0	40	-1	41
JW01	0	0	0	12	0	12
JW02	0	0	0	2	0	2

Average annual percent fertility began to decrease in 2005 in spring-run and in 2006 in fall-run Chinook Salmon (Figure 5A), and in both taxa it continued to decline through 2014. An increase in AAPF occurred in 2015 coincidental with changes in the methodology used in fertilization and incubation of fertilized eggs in response to declining fertility rates in Chinook Salmon eggs brood years 2012 to 2014 (personal communications L. Glenn, 2014; S. McCarn and S. Ballard, 2015 and 2017, respectively). The 2015 increase in AAPF continued through 2016, followed by a slight downturn in 2017. Prior to the change in measurement protocol, a well-defined downward trend in AAPF was evident in both races of adult Chinook Salmon (Figure 5B and 5C). In each group of fish, plots of partial residuals of AAPF versus year were nonlinear, well defined by response curves, significant, with deviance explained  $\geq 50.6\%$  (Table 2), indicating a significant negative annual trend in AAPF in both races of Chinook Salmon. This suggests that the pattern of AAPF was similar for both races, when AAPF drops for one race it also drops for the other race and vice versa.

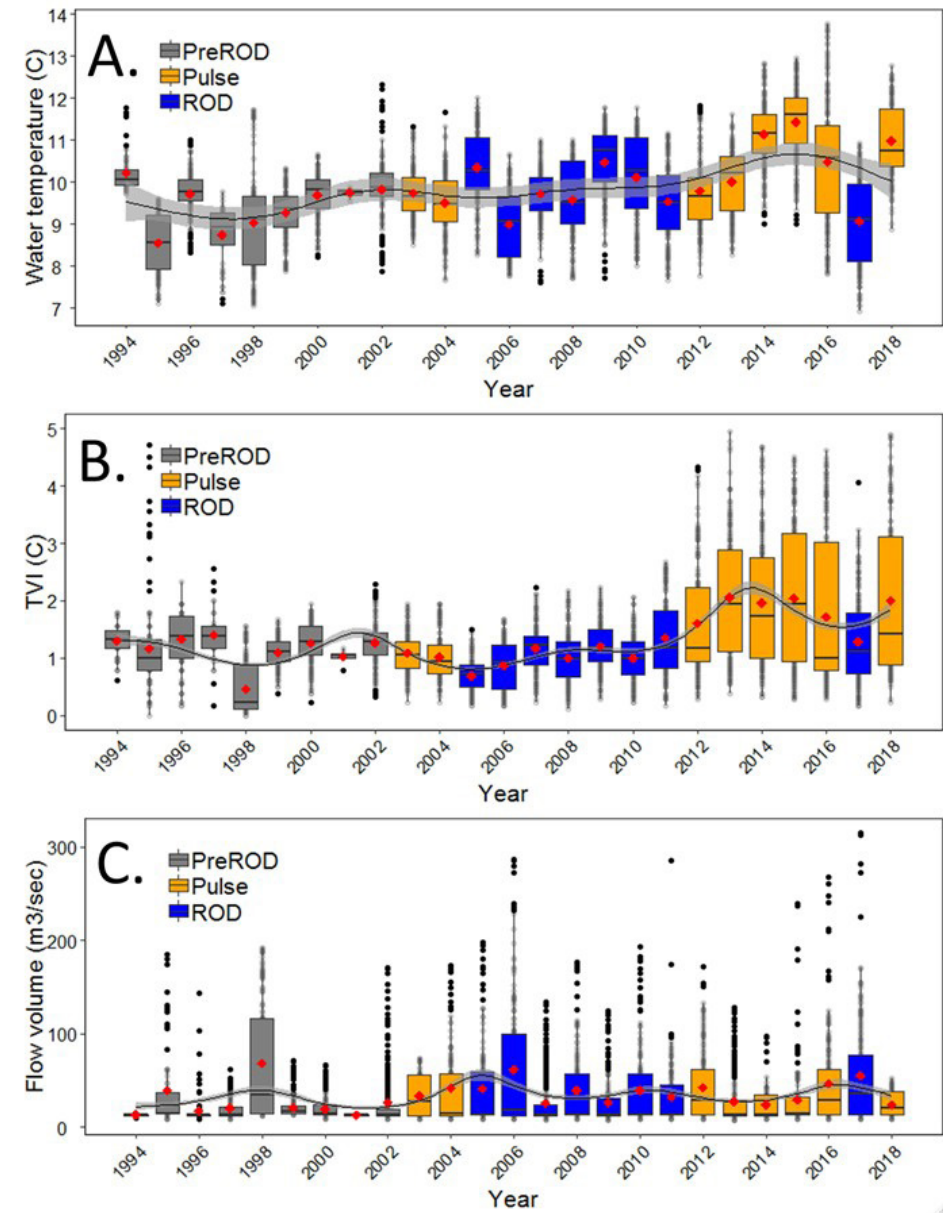
Additionally, autocorrelation analyses of AAPF for hatchery collected and reared Chinook Salmon eggs showed that all time points were contained within approximate 95% confidence levels of significance for each correlation in the autocorrelation function correlograms. This result was corroborated by follow-on Box-Pierce tests for both CWT adult spring-run ( $\chi^2 = 1.7$ ,  $P = 0.19$ ,  $d.f. = 1$ ) and fall-run Chinook Salmon ( $\chi^2 = 0.97$ ,  $P = 0.37$ ,  $d.f. = 0.32$ ). Thus, for the sequence of consecutive dates assessed herein, annual estimates of



**FIGURE 5.**—Line graphs of seasonal fluctuations in A) average annual percent fertility (AAPF) of adult female spring-run and fall-run Chinook Salmon measured at the Trinity River Hatchery, and response curves generated from regression using GAM for adult B) spring-run and C) fall-run fish. Plots show the relationship of the fitted function to the response scaled to zero. Shaded areas indicate 2-times the point-wise standard error for each curve surrounding each fitted GAM function (black lines). Vertical dashed black lines identify year 2003 and 2014.

AAPF for spring- and fall-run Chinook Salmon represented a stationary series of relatively constant autocorrelation structure over time.

*Fluctuations in water temperature and flow volume associated with flow-types.*—Regression using GAM showed a pattern of nonlinear variation in each variable used to assess annual trends in water temperature and flow volume (Figure 6). All smoothed year terms were significant for each annual response curve (ADWT, ADWTVI, ADFV), but deviance explained was not particularly robust among environmental variables examined (Table 2). Correlation analysis also indicated that annual trends in environmental variables were



**FIGURE 6.**—Regression of annual fluctuations in average daily A) water temperature (ADWT), B) temperature variability index (ADWTVI), and C) flow volume (ADFV) for each flow-type (PreROD, ROD, and Pulse). Boxplots display annual distributions of continuously distributed variables (gray colored points), including minimum, first quartile, median (horizontal line), third quartile, and maximum. Shaded areas indicate 2-times the point-wise standard error for each curve surrounding each fitted GAM function (black lines). Black “dots” at the end of the boxplot represent outliers and red diamonds represent the mean value of the distribution by year.



significant and positive for ADWT ( $r_s = 0.34$ ,  $P < 0.01$ ,  $n = 4,347$ ), ADWTVI ( $r_s = 0.18$ ,  $P < 0.01$ ,  $n = 4,347$ ), and ADFV ( $r_s = 0.07$ ,  $P < 0.01$ ,  $n = 4,458$ ), but the strength of the correlations were not particularly strong. These results show that all three environmental variables have increased over time for the above sequence of Julian weeks, with increases in flow volume exhibiting the weakest annual trend. As expected, whereas the relationship between ADWT and ADWTVI was significant and positive ( $r_s = 0.46$ ,  $P < 0.01$ ,  $n = 4,347$ ), both variables were inversely correlated with ADFV ( $r_s = -0.38$ ,  $P < 0.01$ ,  $n = 4,315$  and  $r_s = -0.67$ ,  $P < 0.01$ ,  $n = 4,315$ , respectively). Thus, as flow volume increased average water temperature and the range of variability in extreme water temperature decreased moving toward the end of seasonal run-timing for both races of Chinook Salmon.

Kruskal-Wallis ( $H$ ) non-parametric one-way analysis of variance (ANOVA) rank sum test identified significant overall differences among flow-types in all environmental variables, also reflected in both the mean and variance for each environmental variable (Table 5). For example, mean values of ADWT, ADWTVI, and ADFV were 1) PreROD flows (9.5° C, 1.1° C, 27.2 m<sup>3</sup>/s,  $n = 1,334$ ), 2) ROD flows (9.8° C, 1.0° C, 42.2 m<sup>3</sup>/s,  $n = 1,447$ ), and 3) Pulse flows (10.3° C, 1.5° C, 36.9 m<sup>3</sup>/s,  $n = 1,280$ ). Additionally, planned post-hoc multiple pairwise comparisons found significant differences between all flow-types in each environmental variable except between ROD and Pulse flows in ADWTVI and ADFV (Table 5). Mean values of each measure of water temperature were higher in Pulse flows than in baseline PreROD or ROD flows. Similarly, variance in ADWT and ADWTVI was higher in Pulse flows (1.3° C, 0.91° C) than in PreROD flows (0.61° C, 0.28° C) or ROD flows (1.00° C, 0.26° C). We note that in 2017, ROD flows resulted in lower values for both water temperatures variables and higher flow volume than in Pulse flow-years, consistent with the seven consecutive ROD flows from 2005 to 2011 (Figure 6). Whereas in the 2018 Pulse flow this pattern was reversed among environmental variables.

Nonlinear patterns of seasonal Julian week counts were also evident in each measure of water temperature and flow volume, as all smooth terms were significant for each response curve and deviance explained ranged from 18.1% (ADWTVI) to 47.7% (ADTV; Table 2). Here, volume of flow was driving the response in extreme variability in water temperature; and although significant, none of the relationships were strong between Julian week counts and ADWT ( $r_s = 0.41$ ,  $P \leq 0.01$ ,  $n = 4,347$ ), ADTVI ( $r_s = 0.11$ ,  $P \leq 0.01$ ,  $n = 4,347$ ), or ADFV ( $r_s = -0.11$ ,  $P \leq 0.01$ ,  $n = 4,458$ ). Shapes of the response curves showed elevated levels of ADWT and ADWTVI associated with the ROD-segments of Pulse flows across virtually the full spectrum of Julian week counts (Figures 7A and 7B). Elevated levels of ADWT and particularly ADWTVI were evident at the onset and during the decline in the ROD-segments of pulsed augmentations (JW13 - JW17, JW26 - JW38), which encompassed the entire spring-run and early onset of run-timing in fall-run Chinook Salmon (Figure 2C). However, ADWTVI decreased on the trailing end of the ROD-segments of Pulse flows (JW34 - JW37), then increased during the actual pulsed augmentations (JW38 - JW40). These extremes in water temperature variability are a function of an increase in ADFV during the same period (Figure 7C).

As expected, ROD flows exhibited the largest mean flow volume (42.2 m<sup>3</sup>/s) compared to PreROD (27.2 m<sup>3</sup>/s) or Pulse flows (36.9 m<sup>3</sup>/s), a pattern particularly evident for Julian week 17 to 24 (Figure 7C). ROD flows also exhibited greater variance in ADFV (2,225.7 m<sup>3</sup>/s) than either PreROD (1,132.9 m<sup>3</sup>/s), or Pulse (1,288.3 m<sup>3</sup>/s) flows. Apparent also was the large and concentrated distribution of outliers in ADFV clearly associated with year

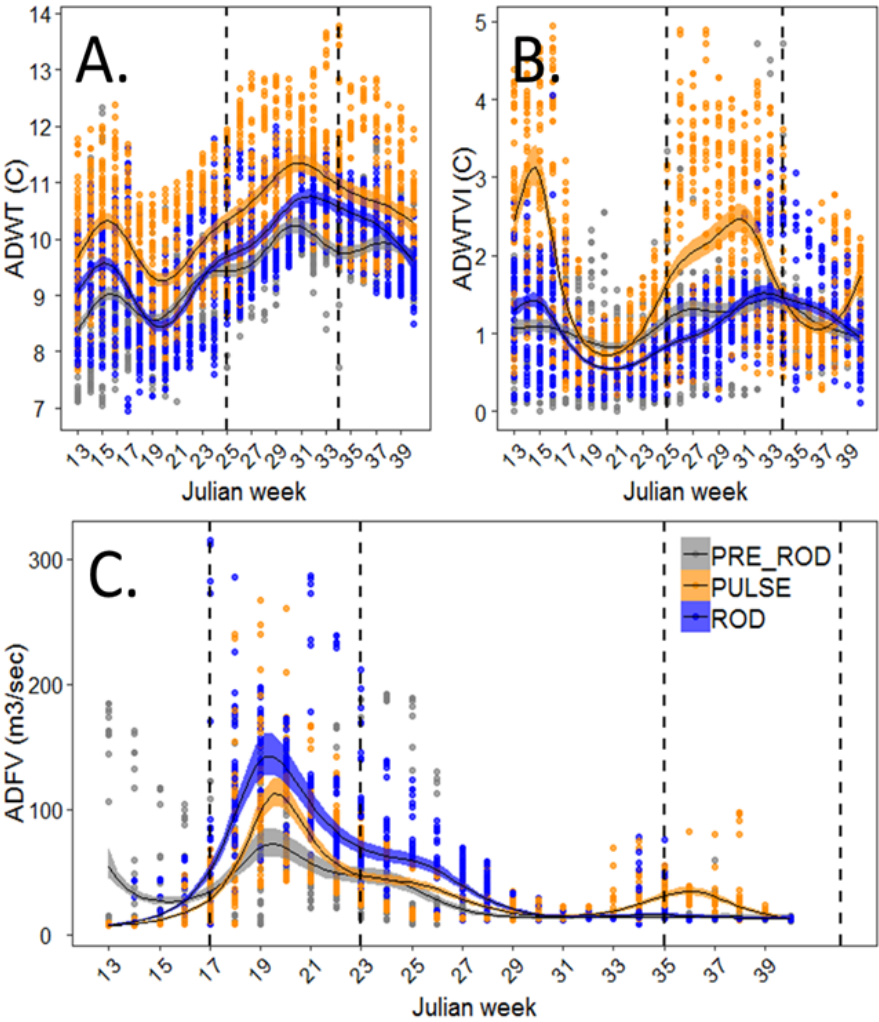
**TABLE 5.**—Non-parametric Kruskal-Wallis (*H*) rank sum one-way analysis of variance (ANOVA) tests followed by the Chritchlow-Fligner (*DSCF*) post-hoc multiple pair-wise comparisons tests of means between flow-types using 1) average daily water temperature (ADWT), 2) average daily water temperature variability index (ADWTVI), 3) and average daily flow volume (ADFV) for Julian weeks 13 to 40 (1995 - 2017; Table 1). Sample sizes for PreROD, ROD, and Pulse flows were *n* = 1,403, *n* = 1,510, and *n* = 1,545, respectively).

ADWT ( <i>H</i> = 321.8, <i>P</i> < 0.01, <i>d.f.</i> = 2)			
Group( <i>i</i> )	Group( <i>j</i> )	<i>DSCF</i>	<i>P</i> -Value
Pre-ROD	Pulse	26.294	0.00
Pre-ROD	ROD	43.035	0.00
Pulse	ROD	16.052	0.00
ADWTVI ( <i>H</i> = 132.1, <i>P</i> < 0.01, <i>d.f.</i> = 2)			
Group( <i>i</i> )	Group( <i>j</i> )	<i>DSCF</i>	<i>P</i> -Value
Pre-ROD	Pulse	-2.337	0.03
Pre-ROD	ROD	10.481	0.00
Pulse	ROD	14.498	0.00
ADFV ( <i>H</i> = 63.5, <i>P</i> < 0.01, <i>d.f.</i> = 2)			
Group( <i>i</i> )	Group( <i>j</i> )	<i>DSCF</i>	<i>P</i> -Value
Pre-ROD	Pulse	6.651	0.00
Pre-ROD	ROD	15.577	0.00
Pulse	ROD	12.784	0.00

2002 through 2016 (Figure 6C), which corresponded to 2002 the year of the massive fish kill in the lower Klamath River and all ROD and Pulse flows post-2002 to present. Further, the influence of Pulse flows and Ceremonial Tribal Boat Dance flows was clearly evident in ADFV, which spiked just prior to the “historical” peak in run-timing of spring-run adult Chinook Salmon (JW39, Figure 2A and 2C), and early arriving CWT fall-run adult fish (JW38 - JW40), which overlapped the trailing end of the spring-run (Figure 7C).

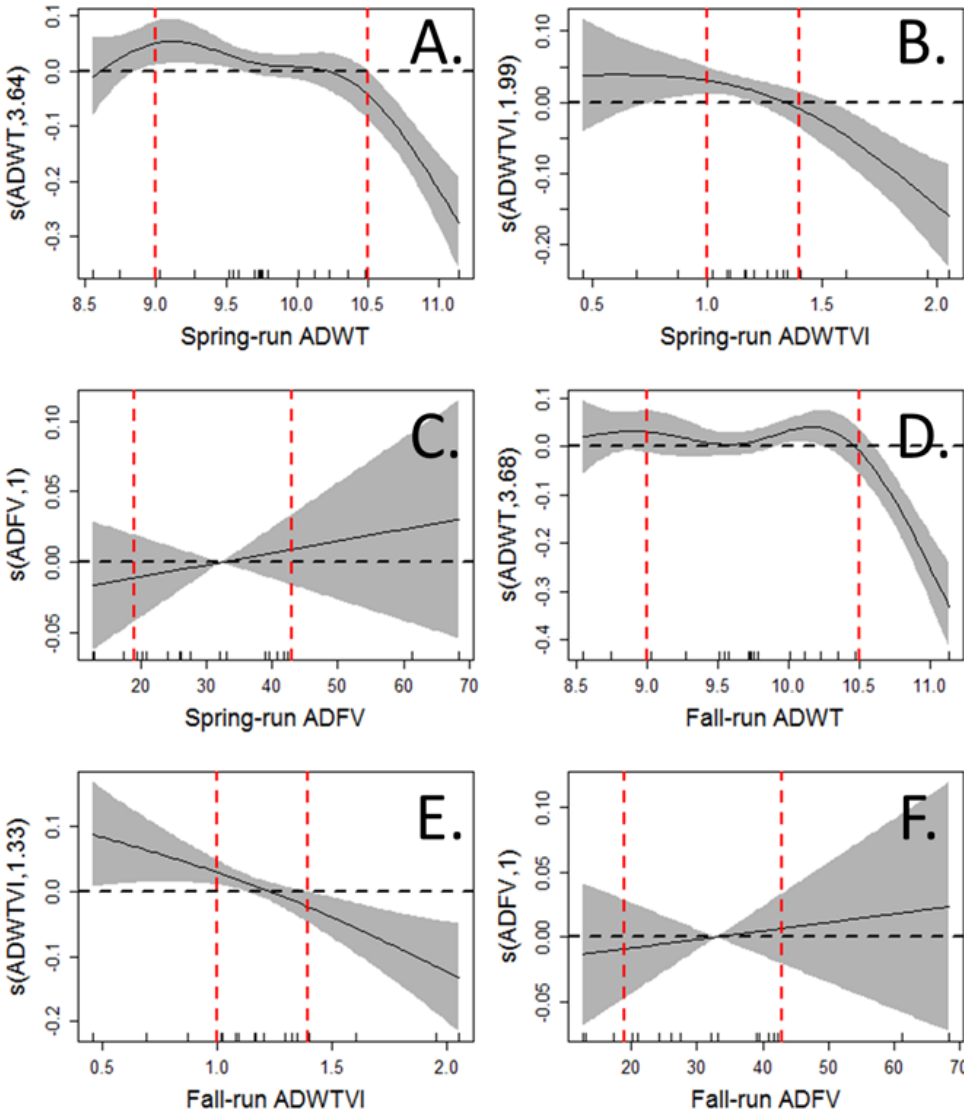
*Average annual percent fertility as a function of water temperature and flow volume.*— We assessed fluctuations in annual ADWT, ADTVI, and ADFV (1994 - 2017) separately and in combination, against annual fluctuations in AAPF using GAM (Table 2). Plots of partial residuals suggested concordant declining trends in AAPF for each environmental variable to each fitted GAM function for each race of Chinook Salmon (Figure 8A - 8B, and 8D - 8E, respectively). Shapes of response curves reflected a negative effect of ADWT and ADWTVI on AAPF, as smooth terms were significant for each water temperature gradient in each regression model, particularly ADWT (Table 2). Thus, as ADWT and ADWTVI increase AAPF decreases in relation to both environmental variables; whereas AAPF showed no significant trend in relation to variation in annual volume of flow. For each race of Chinook Salmon measures of model fit (*QAIC<sub>c</sub>*) were most efficient (parsimonious) using ADWT followed by ADWTVI, individually, in pairs, or in combination with ADFV, in the fitted function as nonlinear descriptors of the behavior in AAPF (Table 2).

For both races of Chinook Salmon, univariate histograms (rugs) at the base of each plot, showed that data points for ADWT were concentrated in their distribution between 9.0° C to 10.5° C (Figure 8A and 8C); whereas data points for ADWTVI ranged primarily



**FIGURE 7.**—Regression of seasonal Julian week (JW) counts among flow-types in response to average daily A) water temperature (ADWT), B) temperature variability index (ADWTVI), and flow volume (ADFV). Plots show the relationship of the fitted GAM function to each response variable. Shaded areas indicate 2-times the point-wise standard error for each curve surrounding each fitted function (black lines). Vertical (x-axis) black dashed lines correspond to Julian weeks referenced in the text.

between 1.0° C to 1.4° C (Figure 8B and 8D). Plots of partial residuals using GAM found no significant trends in AAPF in response to ADFV for either race of Chinook Salmon (Figure 8C and 8F, respectively), and most flow volume ranged between 19 m<sup>3</sup>/sec and 43 m<sup>3</sup>/second. Further, a significant positive relationship between spring- and fall-run fish suggests that AAPF may be a function of average and extreme measures of variability in water temperature, as AAPF in both races of fish tracked fluctuations in water temperature in a similar way, irrespective of changes in measurement initiated in 2015. For example, regression analysis using of AAPF between these two taxa resulted in GAM deviance explained ranging from 74.6% from 1994 to 2017 ( $F = 18.2$ ,  $Ref.df = 3.1$ ,  $P < 0.01$ ,  $n = 22$ ) to 73.2% from 1994 to



**FIGURE 8.**—Regression of seasonal Julian week (JW) fluctuations in average annual percent fertility (AAPF, 1994 - 2014) in response to 1) average daily water temperature (ADWT), 2) temperature variability index (ADWTVI), and flow volume (ADVF) for spring-run (8A, 8B, and 8C, respectively) and fall-run Chinook Salmon (8D, 8E, and 8F, respectively). GAM labels *x*-axes with the covariate name (cov) and *y*-axes by the covariate name and estimated degrees of freedom (edf) of each smooth ( $s[\text{cov}, \text{edf}]$ ). Plots show the relationship of the fitted function to the response scaled to zero. Shaded areas indicate 2-times the point-wise standard error for each curve surrounding each fitted GAM function (black lines). Vertical red dashed lines on *x*-axis correspond to various Julian weeks referenced in the text.

2014 ( $F = 21.8$ ,  $Ref.df = 2.1$ ,  $P < 0.01$ ,  $n = 19$ ). Similarly, follow-on correlation analysis of AAPF between taxa also showed and significant and positive relationship ( $r_s = 0.48$ ,  $P \leq 0.01$ ,  $n = 22$ ) for the period 1994 to 2017, irrespective of changes in the methodology used by the hatchery to measure this parameter.

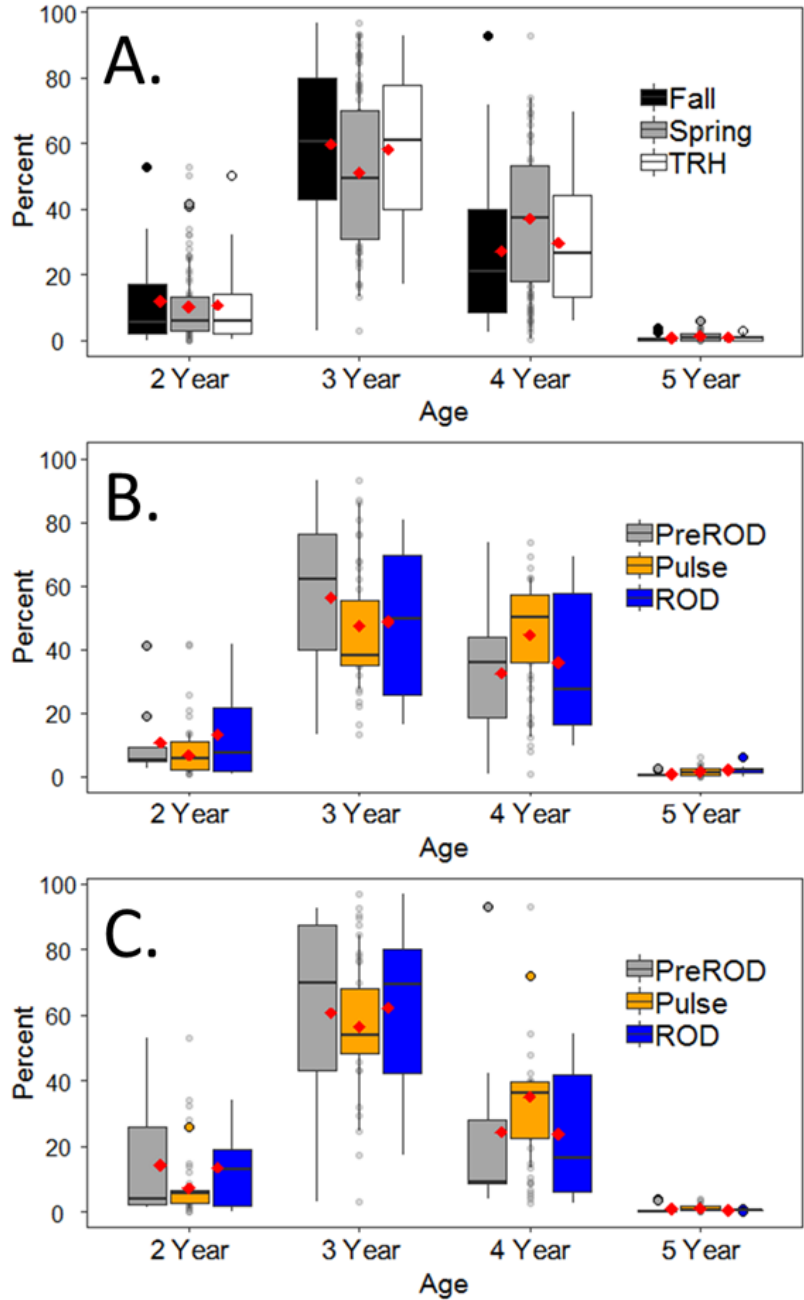
*Effects of flow-types on returning progeny.*—We found no significant difference in the proportion of fish assigned to each age class (ages 2 - 5) between total TRH returns, and expanded estimates of CWT adult spring- or fall-run Chinook Salmon from 1994 to 2017 (Table 6, Figure 9). Age class 3 followed by age class 4 composed the greatest proportion of fish in each group of Chinook Salmon. Similarly, except for age class five in spring-run Chinook Salmon, there was no significant correlation between year and age class for any group of fish or a significant difference among flow-types in the proportion of age classes for either race of Chinook Salmon (Table 6). However, unlike the direct effects of ROD and Pulsed flows on annual and seasonal fluctuations in run-timing, potential direct effects of managed hydrographs and their resulting temperature regimes on same-season reproduction are not immediately evident in annual counts of spring- or and fall-run Chinook Salmon, age 2, 3, 4, or 5-year old fish. For example, in 2012, a total of 24,374 Chinook Salmon returned to the hatchery (Table 7). These fish represented the four age cohorts (age 2, 3, 4 and 5-year-old fish) for hatchery-raised parental broodstock of brood-years 2007 through 2010. However, returning progeny of the 2012 Chinook Salmon hatchery-raised broodstocks comprise brood-years 2014 (age 2), 2015 (age 3), 2016 (age 4), and 2017 (age 5). Similarly, Chinook Salmon hatchery-raised parental broodstock in 2017 were derived from brood-years 2012 through 2015 parental brood-stock origin and will have returning progeny in 2019 through 2022.

DISCUSSION

*Implications of annual and seasonal fluctuations in counts.*—Results of our analyses showed a highly significant correlation between counts of known race CWT adult Chinook Salmon and total TRH returns of marked (CWT) and unmarked hatchery-origin fish of all age classes. Combined expanded estimates of CWT Chinook Salmon represented 90.0%

**TABLE 6.**—Results of the 1) Kruskal-Wallis ( $H$ ) rank sum tests ( $n = 24$ ,  $df = 2$ ) for differences in age classes and flow-types for Trinity River Hatchery total returns, and spring- and fall-run Chinook Salmon; and 2) Spearman's rank correlations ( $r_s$ ) between percentages of various age classes and year for both runs of Chinook Salmon.

2012 ( $n = 24,374$ )				2013 ( $n = 6,430$ )				2014 ( $n = 10,813$ )			
Parental stock		Returning progeny		Parental stock		Returning progeny		Parental stock		Returning progeny	
Age	Year	Age	Year	Age	Year	Age	Year	Age	Year	Age	Year
5	2007	2	2014	5	2008	2	2015	5	2009	2	2016
4	2008	3	2015	4	2009	3	2016	4	2010	3	2017
3	2009	4	2016	3	2010	4	2017	3	2011	4	2018
2	2010	5	2017	2	2011	5	2018	2	2012	5	2019
2015 ( $n = 5,341$ )				2016 ( $n = 3,650$ )				2017 ( $n = 7,013$ )			
Parental stock		Returning progeny		Parental stock		Returning progeny		Parental stock		Returning progeny	
Age	Year	Age	Year	Age	Year	Age	Year	Age	Year	Age	Year
5	2010	2	2017	5	2011	2	2018	5	2012	2	2019
4	2011	3	2018	4	2012	3	2019	4	2013	3	2020
3	2012	4	2019	3	2013	4	2020	3	2014	4	2021
2	2013	5	2020	2	2014	5	2021	2	2015	5	2022



**FIGURE 9.**—Distribution of age classes, expressed as a percentage of counts for A) total TRH returns ( $n = 401,667$ ), spring-run ( $n = 114,768$ ), and fall-run ( $n = 246,809$ ) Chinook Salmon; and in relation to different flow-types for B) spring-run (baseline PreROD = 50,835; ROD = 29,881; Pulse = 34,052) and C) fall-run (baseline PreROD = 95,952; ROD = 77,560; Pulse = 73,297) Chinook Salmon (1994 - 2017). Boxplots display annual distributions of continuously distributed variables (gray colored points), including minimum, first quartile, median (horizontal line), third quartile, and maximum. Colored “dots” at the ends of boxplots represent outliers as per flow-type and red diamonds represent the mean value of the distribution by year.

**TABLE 7.**—Annual counts of total returning Trinity River Hatchery spawned Chinook Salmon, age class, year of returning progeny, and parental source of broodstock for fish spawning from 2012 through 2017.

2012 ( <i>n</i> = 24,374)				2013 ( <i>n</i> = 6,430)				2014 ( <i>n</i> = 10,813)			
<u>Parental stock</u>		<u>Returning progeny</u>		<u>Parental stock</u>		<u>Returning progeny</u>		<u>Parental stock</u>		<u>Returning progeny</u>	
Age	Year	Age	Year	Age	Year	Age	Year	Age	Year	Age	Year
5	2007	2	2014	5	2008	2	2015	5	2009	2	2016
4	2008	3	2015	4	2009	3	2016	4	2010	3	2017
3	2009	4	2016	3	2010	4	2017	3	2011	4	2018
2	2010	5	2017	2	2011	5	2018	2	2012	5	2019
2015 ( <i>n</i> = 5,341)				2016 ( <i>n</i> = 3,650)				2017 ( <i>n</i> = 7,013)			
<u>Parental stock</u>		<u>Returning progeny</u>		<u>Parental stock</u>		<u>Returning progeny</u>		<u>Parental stock</u>		<u>Returning progeny</u>	
Age	Year	Age	Year	Age	Year	Age	Year	Age	Year	Age	Year
5	2010	2	2017	5	2011	2	2018	5	2012	2	2019
4	2011	3	2018	4	2012	3	2019	4	2013	3	2020
3	2012	4	2019	3	2013	4	2020	3	2014	4	2021
2	2013	5	2020	2	2014	5	2021	2	2015	5	2022

of total TRH returns from 1994 to 2017. We show that the pattern of annual fluctuations in counts of known race CWT adult fish was an accurate reflection of the annual hard-count of Chinook Salmon recovered from the hatchery, even though CWT adult fish only represent an average of 20.6% of total all TRH returns over the period we sampled. As such, we view the management practice of coded-wire tag marking of hatchery-raised fish as a reliable surrogate for assessing relative trends in populations of both races of Chinook Salmon, relative to un-marked hatchery-origin natural area spawning fish, particularly during years of low run size. Normally, fall-run Chinook Salmon represent the largest component of fish returning to the hatchery. However, in 2002, 2016, and 2017 returns of CWT adult spring-run Chinook Salmon at the hatchery exceeded counts of CWT adult fall-run Chinook Salmon. Potential explanations for these counts may be a function of the large die-off in 2002 of Chinook Salmon in the lower Klamath River or over harvesting of fish. In 2016 and 2017 there was no commercial ocean harvest or in-river sport harvest in 2017, except in the Hoopa Valley where Tribal take (*n* = 1,660), exceeded the allowed quota (*n* = 163, Thom 2018). Further, trends in relative abundance by use of GAM showed a concordant and significant downward monotonic trend in counts from 2003 to 2017 in all CWT adult spring- and fall-run, and total TRH returns of Chinook Salmon, coincidental with establishment of the TRRP in 2002 and subsequent ROD and periodic Pulse flows beginning in 2003.

*Implications of seasonal fluctuations in counts in relation to flow-type.*—Results of our analyses indicate that evidence exists to support the hypothesis (*H<sub>1</sub>*) that annually managed flow regimes implemented by the ROD have altered the pattern and timing of migration of spring- and fall-run Chinook Salmon in the Trinity River in a significant and concordant way beginning in 2003. Seasonal fluctuations in migration of each race of CWT adult Chinook



Salmon not only showed significant differences between baseline PreROD flows and ROD and Pulse flows, but we also observed significant differences between ROD and Pulse flows in both overall and individual Julian week comparisons, and in the number of counts affected by managed flows relative to the baseline condition. Thus, Pulse flows in combination with their associated companion ROD-segment appears to represent an important and independent factor affecting the temporal distribution of Chinook Salmon relative to a “purely” ROD flow hydrograph. As such, we maintain that annual ROD flows in combination with Pulse flow hydrographs have had significant direct and cumulative effects on the pattern of migration and run-timing of spring- and fall-run CWT adult Chinook Salmon in the upper Trinity River, relative to the pattern reflected in baseline PreROD flows. We also see these same annual and seasonal trends and flow effects in the sympatric potamodromous migration of the non-anadromous population of Brown Trout (*Salmo trutta*) in the upper Trinity River (Sullivan and Hileman 2018).

We hypothesize that effects of annually managed hydrographs have likely also alter run-timing of un-marked hatchery-origin and natural-origin spawning Chinook Salmon, which spawn in-river predominantly within the first 15 km of the upper Trinity River below Lewiston Dam and the hatchery, and increasingly down-river and outside mainstem TRRP restoration sites (Rupert et al. 2017a and Rupert et al. 2017b). Peterson et al. (2017) used a variety of environmental attributes to assess the relative influence of managed pulse flows to explain the magnitude of daily counts and proportions of fall-run Chinook Salmon in the Stanislaus River, California. They concluded that although managed pulse flows resulted in immediate increases in daily passages, the measured response was brief, representing only a small portion of the total run, relative to a stronger response between migratory activity and discharge levels. We view this phenomenon to be more reflective of annual ROD flows acting in concert with companion ROD-segments that are part of each Pulse flow hydrograph, as opposed to short-term pulsed augmentations. Viewed collectively, the combined influence of ROD and Pulse flow-types affected, both positively and negatively, the pattern of run-timing in both spring- and fall-run Chinook Salmon in a significant and concordant way, similar to synchrony in survival rates of Chinook Salmon and Coho Salmon in response to ocean conditions linked to coastal food webs (Kilduff et al. 2015, NOAA 2017).

*Other potential covariates.*—Although we focused specifically on the potential effects of a riverine system subjected to highly managed flow regimes, other covariates not studied also likely affect annual and seasonal patterns of relative abundance and timing of migration in salmonids in the upper Trinity River. For example, factors responsible for decreasing stocks of anadromous salmonids in both the Trinity and Klamath rivers, reference recent ocean conditions and regional drought (Dettinger and Cayan 2014, Diffenbaugh et al. 2015, Mann and Gleick 2015, Adams et al. 2017, NOAA 2017). However, yet to be fully documented or realized, is the degree to which these conditions pose threats to inland fisheries, as a function of changing climate. Importantly, we have shown that since 2001, 38.9% of regional water-years had “dry” or “critically dry” designations, including two periods of three consecutive dry water-years (Table 1). However, although major tributaries of the Trinity River Basin below the North Fork Trinity River may have suffered from the effects of drought, the mainstem Trinity River, which ends administratively at the confluence of the North Fork Trinity River, did not. This was because management of annual hydrographs resulted in release of flows down the Trinity River throughout all drought-years and tributary accretion of water for this segment of the mainstem is less relative to inflow from major

tributaries below the mainstem.

*Impact of altered run-timing on hatchery management.*—Run-size in Chinook Salmon has been a topic in numerous discussions focused on late summer hydrological augmentations (Turek et al. 2004, Strange 2010, NOAA and USFWS 2013). Yet, these considerations have not occurred in coordination with hatchery management practices. As such, what are the potential ramifications of altering the baseline PreROD flow run-time pattern on the distribution of 1) Chinook Salmon, 2) in-river spawning by hatchery-origin stocks, and 3) natural-origin spawning of “wild” Chinook Salmon? Historically, during baseline PreROD flows, timing of female egg ripening at the hatchery resembled a bell-shaped curve (unripe-ripe-overly ripe), with overly ripe females removed from the spawning matrix once egg-take allotments were approached (3 million spring- and 6 million fall-run Chinook Salmon). However, late summer pulse flows (2012 - 2016) have narrowed ripening curves such that they become negatively skewed, in which a high percentage of early arriving adult females have delayed gametic maturation (“green” females; L Glenn and J. Hileman, personal observations 2015). This situation narrows the spawning window and logistically limits flexibility in managing ripeness in females, particularly when most early arriving and unripe spring-run female Chinook Salmon suddenly become overly ripe (L. Glenn, personal communication, 2015). Additionally, during pulse flows, once spring-run females ripen, fall-run “green” females started arriving in abundance. A shift in ripening curves becomes even more problematic logistically because the hatchery is under a mandate to kill 100% of the Chinook Salmon that come through the hatchery fish trap, as there are no options for separating anesthetized fish, which are either killed or placed in holding tanks for gametic ripening.

Further, holding fish over in cement ripening ponds as a buffer in mitigating potentially low hatchery returns and increasingly earlier arriving spring- and fall-run Chinook Salmon directly exacerbates this practice, because holding ponds can only accommodate approximately 800 fish each. If there are too many unripe females early in a season, the hatchery is limited to holding females for a short duration for ripening before incurring highly density dependent mortality. Thus, if unripe female fish “trickle” into the hatchery for prolonged periods of time, held-over fish are processed multiple times for ripeness with ripe females removed for processing and unripe individuals put back into holding ponds. Consequently, if fall-run Chinook begin arriving prior to the annual temporal spawning break between races (October 15 and October 25), they are dispatched due to limited viability of adult fish in holdover ponds over the duration of the spawning break. Thus, Chinook Salmon are low-graded, such that at the end of egg-take for spring-run Chinook Salmon, all fish that look fresh “chrome” are euthanized. Thus, actions of managed flow regimes that alter the pattern and timing of migration in hatchery-raised Chinook Salmon matter tremendously, when these actions affect hatchery management logistical constraints and government mandates.

At present, there has been no comprehensive effort to collect data to measure in-river individual Chinook female ripeness. However, although, our study was not intended to examine relative adult female productivity between hatchery fish, or in-river spawning by hatchery or natural-origin “wild” fish (Hughes and Murdoch 2017), our analysis is an important step in identifying annual trends in measures of reproductive performance in Chinook Salmon, which has direct application for in-river spawning of both hatchery and natural-origin fish. By proxy, it is highly likely that similar ripening curves have shifted in both in-river spawning of hatchery-origin stocks and natural-origin spawning of Chinook Salmon.

This effort is important due to redd superimposition (Fukushima et al. 1998). For

example, in the upper Trinity River, redd superimposition mostly occurs below and within 3.2 km of Lewiston Dam, which consistently contains the largest densities of hatchery-origin Chinook and Coho Salmon (Rupert et al. 2016, Rupert et al. 2017a, Rupert et al. 2017b). This is also the area most affected by hydrological changes (Pulse flows) and extreme fluctuations in water temperature. Thus, if pulsed augmentation flows affect spawning Chinook Salmon at the hatchery, we predict that these actions will likely have an even greater effect on natural-area spawning redds. We agree with Rupert et al. (2016), that redd superimposition likely limits reproductive success of spring-run Chinook Salmon more than any other race or species of anadromous salmonid in the upper Trinity River (Hendry et al. 2003). Estimates of superimposition from 2015 to 2017 revealed significant and highly density dependent relationships (Rupert et al. 2016, Rupert et al. 2017a and 2017b) with severe superimposition occurring in relative proximity to Lewiston Dam where most in-river spawning of spring-run Chinook Salmon likely occurs.

*Implications of fluctuations in water temperature.*—Natural environmental influences determine river flow and water temperature in unregulated rivers, whereas in regulated rivers, flow and water temperature regimes can be highly altered by dam operations and water redistribution (Ward and Stanford 1979). Discharge of water from Lewiston Dam involves complex issues affected by political, economic, environmental, and biological factors. These processes are important role in regulating water temperatures downstream in the upper Trinity River. In-river water temperature is one of the most important environmental variables affecting salmonid biology (Carter 2005, Magnuson 2014, Magnuson and Chamberlain 2015). It influences feeding and growth rates (Hicks 2002, USEPA 2003), metabolism (Fry 1971, Beitinger and Fitzpatrick 1979), development, run-timing in anadromous and potamodromous migration in nonanadromous taxa (Hicks 2002, Beeman et al. 2012), spawning and rearing (USEPA 2001a, USEPA 2003), and availability of food (Ligon et al. 1999). Fluctuations in water temperature can block migration (CDFG 2004), and cause stress and lethality in fish (Elliot 1981, Li et al. 1994, USEPA 2001b, Myrick and Cech 2004, Barthalow 2005) leading to potential for disease in juvenile and adult salmonids (Guillen 2003, Lynch and Risley 2003, CDFG 2004, True et al. 2010). Moreover, depending on the flow release configuration of a dam (e.g., surface-spill, selective gates, or hypolimnetic), thermal characteristics of pulse flows can vary widely and must be considered relative to effects on all aquatic biota (Reiser et al. 2008).

Numerous reports have addressed fluctuations in water temperature in the upper Trinity River, but only in the context of average daily water temperature (Zedonis and Turner 2006, Zedonis and Turner 2008, Zedonis 2009, Scheiff and Zedonis 2010, Scheiff and Zedonis 2012, Magnuson 2013, USBR 2015). This was the metric used to determine potential direct, indirect, and cumulative effects to the affected environment associated with supplemental flow releases from Lewiston Dam in 2015 and 2016 (USBR 2016). Yet there has been no attempt to equate fluctuations in average daily water temperature or extremes in average daily water temperature in the upper Trinity River, to quantify, document, or evaluate potential effects to run-timing or reproductive output in anadromous salmonids associated with very divergent flow regimes initiated in 2003. As such, we do not agree that effects of ROD or Pulse flow augmentations on river stage, in-river water temperature, or the biology of this riverine system are fairly well known (Zedonis 2001), particularly as relates to Chinook Salmon.

Herein, we provide evidence in support our hypothesis ( $H_2$ ) that annually managed

flow regimes implemented by the ROD differ significantly among flow-types, which has altered average daily water temperature, and extremes in water temperature and volume of flow in the upper Trinity River. Further, we maintain that a major issue associated with declining stocks of Chinook Salmon is in part a function of extreme fluctuations in seasonal and daily maximum and minimum water temperatures associated with managed hydrographs initiated in 2003, in conjunction with diversions of water through Lewiston Dam into the Trinity River Division of the Central Valley Project (CVP). For example, from 2001 to 2017, 21,690,290 acre-feet of water was released from Lewiston Lake, of which 49.5% was diverted into the upper Trinity River below Lewiston Dam, and 50.5% was diverted to the CVP (Sacramento River, TRRP 2019), a river system never connected to the Klamath River Basin, but is part of the inter-basin water transfer program. Yet we are unaware of any analyses that address the overall effects to variable water temperature on migration timing, reproductive performance, or spawning of hatchery-origin or in-river natural-origin salmonids from this diversion policy relative to water released into the upper Trinity River.

To assist in this process we provide evidence in support of our hypothesis ( $H_3$ ) that annually managed flow regimes implemented by the ROD may effect hatchery-parental broodstock fertility associated with egg production at the hatchery, which includes both hatchery-origin and potentially an unknown number of “wild” natural-origin fish mixed in with the hatchery egg collection. For example, GAM analyses revealed 1) the potential importance of highly variable water temperatures in relation to a declining trend in AAPF in both races of hatchery-origin Chinook Salmon eggs, 2) significant differences in fluctuations in average daily water temperatures between flows, and 3) extreme fluctuations in maximum and minimum water temperatures on a daily or prolonged punctuated weekly basis. That eggs of both races of hatchery-reared Chinook Salmon exhibited concordant declining trends in AAPF in response to post-PreROD hydrological regimes suggests that these seasonally and genetically differentiated races of Chinook Salmon are tracking conditions in the upper Trinity River in parallel (Kinziger et al. 2013, USBR 2015). Viewed collectively, these results lead us to hypothesize that reduction in fertility in eggs of hatchery-reared Chinook Salmon is likely a function of extreme fluctuation in daily water temperature within the upper Trinity River, exacerbated by hydrological events attributable to annually managed flows. We believe that these issues need further investigation, particularly as relates to the potential effects on in-river 1) female reproductive viability in all salmonid populations in the upper Trinity River, including delayed maturation of females and reduced average annual fertility, and 2) spawning by hatchery-origin and natural-origin fish.

Additionally, evidence suggests that in-river hatchery-origin and natural-origin fish appear particularly susceptible to extreme fluctuations in water temperature. For example, from 2015 to 2017, in-river natural-origin spawning Chinook Salmon produced the lowest redd count and fewest Salmon carcasses recovered since inception of carcass surveys in 2002 (Gough and Rupert 2016, Rupert et al. 2017a, Rupert et al. 2017b). Although natural-origin Chinook Salmon spawn throughout the mainstem Trinity River, redds constructed by hatchery-origin fish were highly skewed toward the hatchery, as the number of hatchery-origin redds has decreased since 2002 throughout the mainstem and within TRRP restoration reaches (Rupert et al. 2017a and Rupert et al. 2017b). “Natural-origin” fish are those individuals that emerge as juveniles from each redd, as opposed to hatchery-reared individuals (Rupert et al. 2017a and 2017b). However, for the Trinity River, there is no accounting for 1) hatchery-origin fish not adipose fin clip marked in the 25% constant fractional pre-lease marking; or

2) Chinook Salmon that emerge from redds produced by ‘hatchery-origin’ parental stocks. Potential factor(s) responsible for reproductive trends described herein remain to be identified by more refined examination and experimentation, particularly as relates to in-river production of juvenile salmonids based on 1) quality of redds and 2) hatchery-origin versus natural-origin spawning (Hughes and Murdoch 2017). This need is timely, since from 2015 to 2017 total hatchery returns, CWT counts, and expanded estimates derived from CWT fish were the lowest recorded since 1994 for both races of Chinook Salmon (CDFW 2017a and CDFW 2017b). Similarly, natural-origin redd abundance, predicted to increase following restoration actions (TRRP and ESSA 2009, Rupert et al. 2017a), has not changed significantly from 2002 to 2016. Instead, natural-origin Chinook Salmon have reduced spawning activity in upper reaches of the mainstem and shifted spawning into more mid-river sections below restoration reaches, with no clear post-restoration response to TRRP rehabilitation sites with respect to abundance of natural-origin redds (Rupert et al. 2017a and Rupert et al. 2017b).

*Implications of future returns in progeny in relation to flow-types.*—Logistical constraints associated with management operations at hatcheries are integral to coordination and successful in-river management and restoration activities associated with overall viability of anadromous salmonid stocks in the upper Trinity River. Historically, such integration and coordination of hatchery operations has not been part of the Record of Decision (ROD) for the TRRP or a significant component of the long-term plan to protect salmonids in the Klamath River Basin (USBR 2015, USBR 2016). Unlike direct effects of ROD flows and Pulse flow augmentations on run-timing, effects of managed flows that cause altered and highly variable water temperature regimes that potentially impact reproductive output are not manifested in annual counts of Chinook Salmon until age 2-, 3-, 4-, and 5-year old fish. For example, 24,374 spawning Chinook Salmon returned to the in 2012. This cohort was comprised of individuals from brood-years 2007 through 2010; however, returning progeny of this cohort comprise brood-years 2014 (age 2), 2015 (age 3), 2016 (age 4), and brood-year 2017 (age 5). Similarly, counts documented in 2015 are in part a reflection of ROD flows and augmented Pulse flows implemented in 2012 and 2013, and progeny produced in 2016 are primarily a reflection of managed flows. In contrast spawning Chinook Salmon in 2017 will be entirely a reflection of managed flows with returning progeny in 2019 through 2022.

Thus, we hypothesize that flow management resulting in highly variable water temperatures that potentially affect AAPF in consecutive ROD and Pulse flows since 2012 will continue to influence annual counts of 2-, 3-, 4-, and 5-year old fish through 2022. Similarly, 3 to 4 brood-year cycle shifts and delays in response time also occurred in the distribution of redd counts in response to restoration activities in the upper Trinity River (Rupert et al. 2017a and Rupert et al. 2017b). We agree that the final judgment of success or failure of flow manipulations in managed river systems may ultimately be the actual numbers of returning naturally produced salmonids to the Trinity River and Klamath River Basin in general (Zedonis and Newcomb 1997). However, we also view hatchery-produced stocks as an integral baseline for performance-based comparisons with natural-origin stocks in evaluating the overall status of spring- and fall-run Chinook Salmon in the upper Trinity River. Development and enhancement of juvenile salmonid rearing habitat, as well as increasing numbers of juvenile salmonids produced within the upper Trinity River is a mandate of the TRRP. However, that mandate does not preclude the necessary requirement of assessing the long-term effects of managed ROD flows



and pulsed augmentation flows on run-timing or reproductive performance of hatchery spring- and fall-run Chinook as part of TRRP management actions.

Such issues have historically not been part of the overall effects analysis of the USBR Long-term Plan to Protect Salmon in the lower Klamath River EIS (USBR 2016), even though flows designed to facilitate such protection originate in the upper Trinity River. As of 25 July 2016, there are plans to address these issues for adult salmonids in the upper Trinity River or as part of any proposed environmental impact assessment (M. Paasch, personal communication, 2016). Further, in the most recent effects analysis, potential alteration of baseline PreROD pattern of run-timing in spring-run and fall-run Chinook Salmon, as well as sympatric populations of listed Coho Salmon and steelhead, were not examined in the most recent National Environmental Protection Act finding of no significant impact (USBR 2015, USBR 2016). Comparing the frequency distribution of migration parameters before, during, and after ROD and Pulse flow events would seem critical in discerning if a change in flow acts as a temporary stimulus or retardant to migration, or acts to alter the post-dam baseline seasonal run-time distribution pattern that we address herein. We contend that it is imperative that these issues be incorporated into future management and effects analyses of the overall impact of managed hydrographs associated with the upper Trinity River, particularly given the historically small run-size recorded for both races of Chinook Salmon since 2015.

*Management recommendations.*—Effective evaluation of annually managed flows and pulse flow augmentation on anadromous salmonids requires carefully designed field studies that include appropriate controls, which test specific hypotheses relevant to anadromous salmonids and their life history requirements. An integrated strategy includes comparative analyses and synthesis of potential impacts of managed flow regimes on timing of migration, population size, age structure, reproductive output, and survival of juvenile outmigrants (Peterson et al. 2017, Cyril 2018). Additionally, similar studies conducted concurrently on non-anadromous “control” species not affected by marine conditions may provide additional insight to flow management not observed in anadromous taxa (Sullivan and Hileman 2018). Close inspection of historical flow and project operational records in tandem with long-term biological data can provide insight into potential effects of planned management of pulse flow augmentation. A comparison of frequency distributions of migration parameters before, during, and after pulsed augmentation flows would help determine if a change in flow regimes acts either as a temporary stimulus or as a retardant to migration. Further, integration and coordination of experimental hatchery management and stocking practices with planned flow management, implemented of restoration actions, and other geomorphological events is crucial to this process. Comparative experimental studies on hatchery-raised fish conducted simultaneously with in-river natural-area spawning hatchery and “wild” fish would allow better understanding of relative annual population productivity in combination with managed flow releases used for conservation purposes in all relevant and connected segments of this highly regulated river system (Hughes and Murdoch 2017). Investigations of reproductive viability in female in-river Chinook Salmon from both hatchery parental brood-stocks and natural-area spawning fish will require refined methods of experimentation.

Long-term datasets that include a wide range of environmental conditions are particularly effective in allowing model linkages between environmental quality and biology of fish occurrence and production if rehabilitation of degraded riverine systems is a desired goal. However, altering measurement parameters used to evaluate reproductive performance (i.e.

AAPF) becomes problematic when it prevents monitoring of historical information critical in assessing trends in population viability, particularly when disconnected from in-river hydrological and geomorphological management of focal species. Herein, the change in measurement parameters used at the hatchery beginning in 2015 dramatically affected use of post-2014 data in adequately assessing the historical sequence we analyzed.

Research of this nature should continue for the longevity of any active large-scale geomorphological restoration program given the multitude of intrinsic and extrinsic co-variables impinging upon this riverine system. This need is particularly relevant given documented fluctuations in influential ocean conditions, climate change, regional drought, random drift, ongoing flow and water management policies, and increased environmental degradation and pollution of watersheds from illegal growing of marijuana throughout the upper Trinity River Basin (Welsh 2011, Kilduff et al. 2015, Rupert et al. 2017a, Rupert et al. 2017b, Mourad et al. 2018). Such actions are an integral part of any coordinated and monitored science-based adaptive management program, which is in large measure the original vision of the Record of Decision (USBR 2000), which outlined a plan for restoration of the Trinity River and its populations of fish and wildlife.

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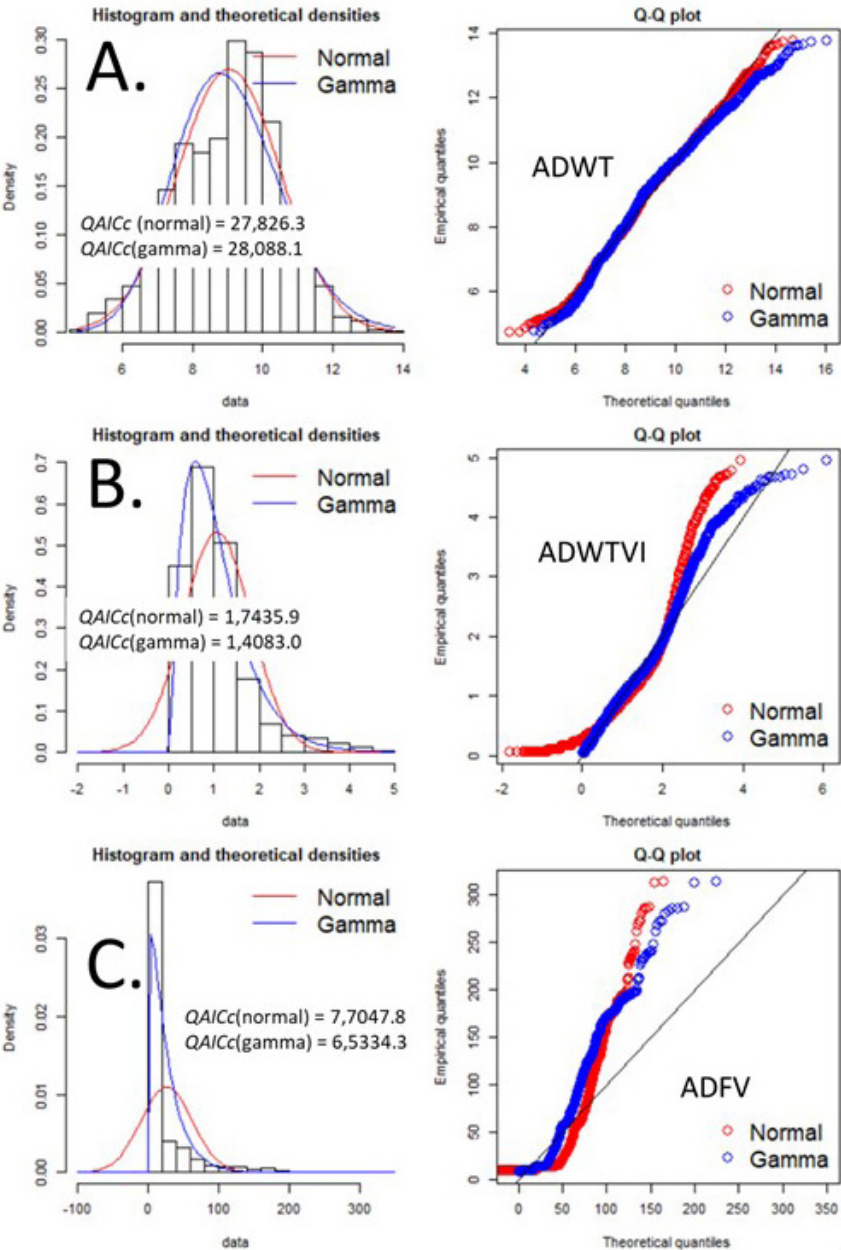
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**APPENDIX I.**—Normal quantiles plots and histograms of the frequency distribution both annually and seasonally (Julian weeks) of raw data for 1) averaged daily water temperature (ADWT,  $n = 4,347$ ), 2) average daily water temperature variability index (ADWTVI  $n = 4,347$ ), and 3) average daily flow volume (ADFV,  $n = 4,458$ ). Dashed black lines represent 95% confidence limits for the fitted normal quantile plots for each variable. We assume normality if all red points fall approximately along the reference black line.



**APPENDIX II.**—Normal quantiles plots and histograms of the frequency distribution of average annual values for 1) averaged daily water temperature (ADWT,  $n = 24$ ), 2) average daily water temperature variability index (ADWTVI,  $n = 24$ ), 3) average daily flow volume (ADFV,  $n = 24$ ), and average annual percent fertility (AAPF) for adult female spring-run ( $n = 23$ ) and fall-run ( $n = 22$ ) Chinook Salmon. Dashed black lines represent 95% confidence limits for the fitted normal quantile plots for each variable. We assume normality if all red points fall approximately along the reference black line. Outliers in AAPF represent the smallest annual measurements recorded for each race of Chinook Salmon.

