Comparative Analyses of Upstream Migration in a Multispecies Assemblage of Fish in Response to Highly Managed Flow Regimes

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Few, if any, studies have distinguished among anthropogenic factors (extrinsic drivers) acting on populations of sympatric species of fish within a single watershed or riverine system. Yet adaptive management requires knowledge of whether co-existing taxa with different life-histories are influenced by similar extrinsic as well as intrinsic factors to determine whether they vary in their population dynamics, hence conservation needs. Using data from weir and hatchery hard-counts, we evaluated the effects of anthropogenic-induced altered flow regimes in relation to annual and seasonal patterns of local migration and run-timing in a multispecies assemblage of adult fish inhabiting a large highly managed riverine system. Here, we test the hypothesis that annually managed flows (hydrographs) have altered the migration patterns and run-time schedules in a sympatric assemblage of six taxa composed of both anadromous and non-anadromous species inhabiting the upper Trinity River, California. Results of our analyses provide evidence to support our hypothesis that highly managed flow regimes implemented since 2003 have altered local migration and run-time schedules in a significant and concordant way among all species examined relative to species-specific baseline post-dam flow-type patterns. Whereas counts of all species fluctuated considerably on an annual basis, counts of all taxa decreased strongly and significantly from 2003 to 2018. This decrease coincided with establishment of the Trinity River Restoration Program in 2002 and subsequent highly managed hydrographs in combination with periodic pulse flow augmentations beginning in 2003, irrespective of two periods of three consecutive years of regional drought. We hypothesize that altered annual and seasonal patterns of local migration and run-timing in a suite of taxonomically and ecologically differentiated species with highly divergent life history strategies owing to local adaptation are likely a function of altered extrinsically-driven flow regimes on fluvial ecosystem processes and the fisheries resources they support. Our study suggests that further investigations into

the effects of flow management on migration and life history requirements in sympatric multispecies assemblages of non-anadromous and anadromous species of fish inhabiting the upper Trinity River are warranted and necessary for both hatchery- and natural-origin spawning fish, particularly if highly managed flow regimes continue indefinitely.

Key words: anadromous, baseline, fish, flow-type, managed flows, migration patterns, non-anadromous, pulse flows, river

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Riverine flow regimes are key drivers of lotic ecosystem structure and function (Bunn and Arthington 2002; King et al 2003; Kennard et al. 2007). In multispecies assemblages of non-anadromous and anadromous species of fish, temporal variation in hydrological events are also a significant driver of fish abundance, population dynamics, and patterns of migration (Biggs et al. 2005; McManamay et al. 2013; Walton et al. 2016). Such variability may severely constrain estimates of population size and interpretations of the effects of altered flows on seasonal patterns and timing of migration, habitat use, and rates of survival in resident taxa (Crisp 1993; Cunjak et al. 1998; Haxton et al. 2010). Additionally, the biotic integrity of freshwater fish assemblages generally decreases with increased anthropogenic alteration of natural flow patterns, which has contributed significantly to a decrease in both quality and quantity of salmonid spawning habitat (Poff et al. 1997; Poff and Zimmerman 2010). However, whereas numerous qualitative relationships have alluded to indirect benefits of extreme flow events, few such relationships are sufficiently well quantified or long-term for use in adaptive management (Naiman et al. 2008; Jager 2014; Quiñones et al. 2014; Brail et al. 2018). Moreover, assessments of the effects of flows have traditionally focused on discharge impacts over short time intervals (< 1 year), thus minimizing insight in anticipating longer-term effects (Holčík 1996; Walton et al. 2016). Indeed, Jager (2014) maintained that externally derived flow targets implemented without regard to specific mediating factors likely are suboptimal for resident fish.

Because flows in unregulated rivers in the western United States vary naturally in response to spring runoff from storms that historically occur relatively consistently during certain times of the year, populations of resident fish have generally evolved life history traits and habitat preferences adapted to natural pulsed-flow events (Rytwinski et al. 2017). Yet, pulse flows associated with highly managed flow regimes that occur outside the natural cycle can be problematic, as life history composition of fish assemblages historically adapted to regional habitat templates may be significantly altered downstream of dams in only a few decades owing to modifications in the timing of streamflow (Konrad et al. 2011; Mims and Olden 2013). Use of pulse flows to mimic natural hydrologic processes, mobilize sediments, habitat creation, or to elicit migration and spawning of fish is a common management strategy in highly regulated riverscapes (Peterson et al. 2017). Furthermore, seasonal variability in relative abundance and timing of migration of fish associated with annually managed flows allied with riverine restoration programs can be considerable (Platts and Nelson 1988; Holtby and Scrivener 1989; Bradford et al. 1997; Ham and Pearsons 2000; Bayley 2002). In California pulse flows were used in the Trinity River to minimize risk and spread of disease among adult upstream migrating Chinook Salmon (*Oncorhynchus tshawytscha*) in lower

reaches of the Klamath River (Strange 2007), and to create juvenile rearing habitats for salmonids in the upper Trinity River (Quiñones et al. 2014; Beechie et al. 2015). Elsewhere, flow regulation in tributaries of the Sacramento River resulted in delayed spawning and smolt migration, which contributed to declines in salmon populations (Keith et al. 2008).

Use of flow management, especially if the timing of which deviates from a region's historical natural hydrograph, requires understanding of the mechanisms by which altered flow regimes influence fish migration (Hasler et al. 2014; Jager 2014), particularly in river systems inhabited by multispecies assemblages of anadromous salmonids. This need is a prerequisite to enabling placement of a broad suite of covariate non-flow factors into perspective, which is particularly relevant to flow management related to riverine restoration actions, as it enables resource managers to better understand and evaluate their methodology (Baril et al. 2018). Further, knowledge of native fish movements and out-migrant survival through flow management in large river systems is especially important in management and listing status of anadromous salmonids given reduction in native stocks in northern California that have experienced declines due to environmental and anthropogenic factors regionally and elsewhere (Sommer et al. 2014; Adams et al. 2017; NOAA 2018).

As such, the objectives of our study were threefold. First, we assess annual fluctuations in relative abundance in a diverse assemblage of resident non-anadromous and anadromous species of fish, and evaluate temporal fluctuations in patterns of local migration and run-timing characteristic of a highly anthropogenic flow-regulated riverine system to identify any concordant patterns among taxa as a potential function of altered streamflow. Second, we evaluate the relationship between annual and seasonal fluctuations in relative abundance of fish in relation to variation in average daily water temperature and flow volume. Third, using results of our analyses, we test the research hypothesis (H_1) that annually managed flow regimes (hydrographs) in a highly regulated river system implemented beginning in 2003 have altered the post-dam baseline pattern of local migration and run-timing in counts of both non-anadromous and anadromous species of fish inhabiting the upper Trinity River, relative to their species-specific "historical" post-dam migration patterns.

METHODS

Study area

Trinity River is in northwestern California and is the largest tributary of the Klamath River system (Figure 1). Construction of Trinity and Lewiston dams occurred in the early 1960s. Trinity Dam creates Trinity Lake, storing up to 3,022 m³ of water. Lewiston Lake, formed by Lewiston Dam, is located 11.8 km downstream of Trinity Dam at river kilometer (rkm) 179.8, which serves as a re-regulating reservoir for flow to the Trinity River and diversion to 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 for approximately 180 kilometers before joining the Klamath River at the township of Weitchpec, California. The Klamath River flows for an additional 70 rkm before entering the Pacific Ocean near Klamath Glen. The upper Trinity River (mainstem) is the stretch from the confluence of the North Fork Trinity River to 63.1 km up stream to Lewiston Dam. Trinity River Hatchery (henceforth called "hatchery") is located immediately below Lewiston Dam and the Junction City Weir (henceforth called "weir") is located 135.8 rkm downstream from Lewiston Dam and the
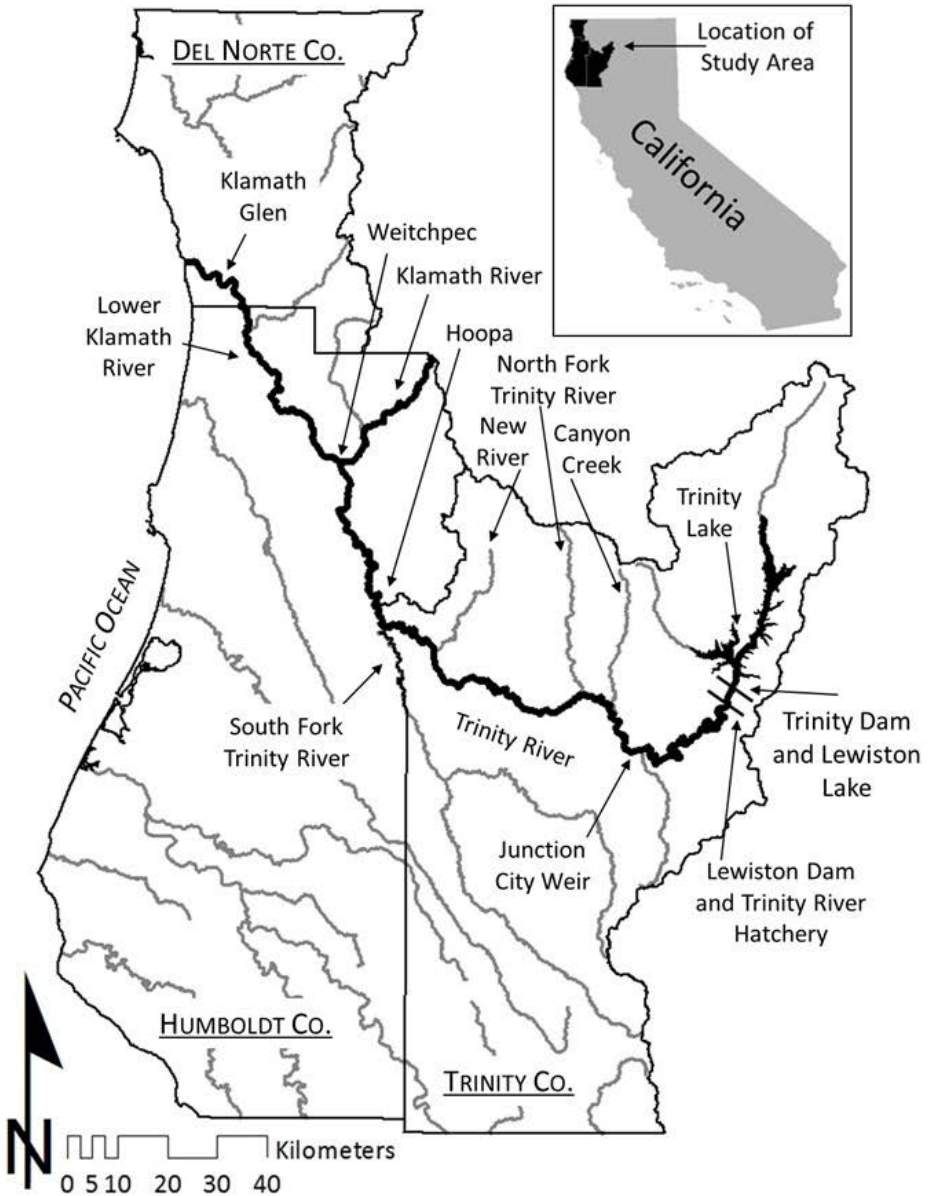
Figure 1. Map of the Klamath River, Trinity River, and other landmarks discussed in the text, encompassing the entire ranges of all species discussed herein. Area colored black in inset map is the study area pictured in main figure. Major rivers and streams that exceed 34 kilometers in length are colored gray.

hatchery. The upper 63.1 rkm of the Trinity River or "mainstem" ends at the confluence of the North Fork Trinity River and the Trinity River. This section of the river is the primary focus of restoration efforts by the Trinity River Restoration Program (TRRP).

Managed flows

The TRRP, created by the Record of Decision (henceforth called "ROD"; USBR 2000), outlined a plan for restoration of the 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. Since 2001, total restoration releases have included flows for 1) restoration, 2) Tribal Ceremonial Boat Dances, and 3) late summer pulse flows (Table 1, Figure 2). Ceremonial Tribal Boat Dance flows occur only in odd years in ROD flows and just prior to any pulsed flow augmentation in Pulse flow years. They are illustrated in each hydrograph and amount to < 0.6% of the total release into the Trinity River (Figure 2b and 2c; TRRP 2019). They are included herein as Pulse flows tier off the trailing ends of Ceremonial Boat Dance flow hydrographs when the latter occur.

Table 1. Attributes of ascending and descending limbs of hydrographs that characterized baseline PreROD, ROD, and Pulse flow-types for years 1995 to 2017. Rate of flow measured in cubic meters per second (m3/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.

Year	Water year-type	Low release magnitude (m^3/s)	Peak release magnitude (m^3/s)	Restoration release (hectare m)	Low release magnitude (m^3/s)	Date and duration to base-flow	Total days
			Pre-ROD Flow (1995 - 2002)				
1995	NA	14	131	NA	27	25 Apr-22 May	28
1996	NA	9	144	NA	14	10 May-9 Jun	31
1997	NA	10	62	NA	13	2 May-2 Jul	62
1998	NA	47	192	NA	13	24 May-27 Jul	65
1999	NA	15	71	NA	13	8 May-18 Jul	72
2000	NA	9	66	NA	13	8 May-27 Jul	81
2002	normal	9	171	59540	13	27 Apr-25 Jun	28
Average		**16.1**	**119.6**	**NA**	**15.1**		**52.4**
Minimum		**9**	**62**	**NA**	**13**		**28**

Table 1. continued.

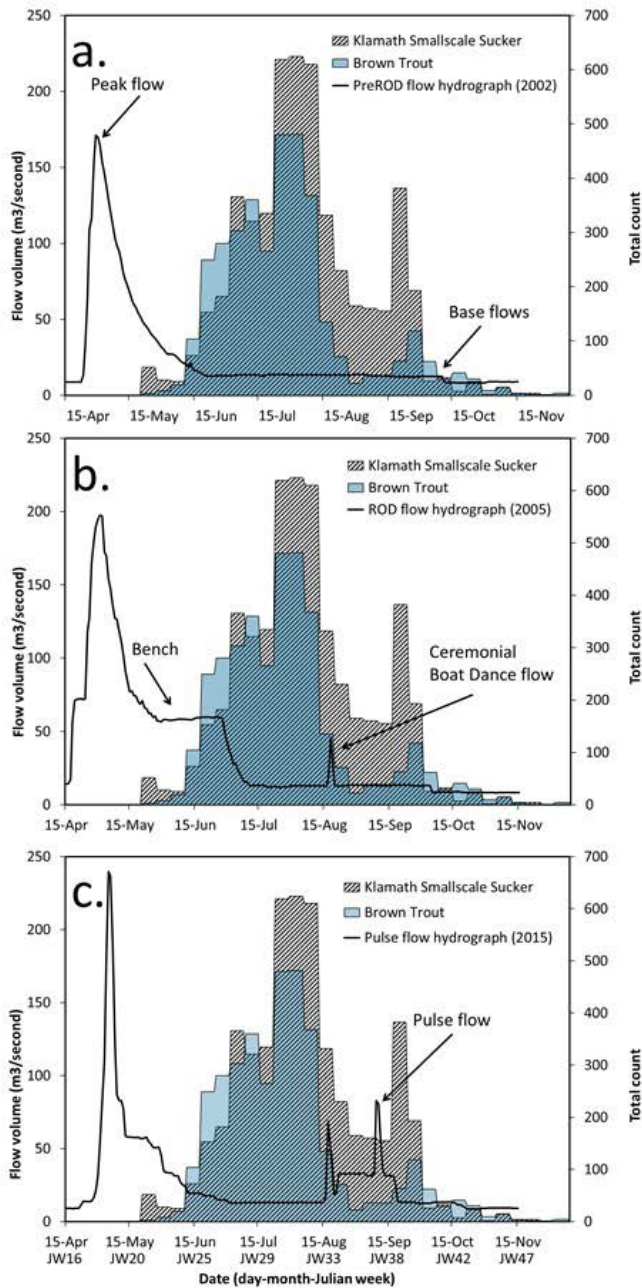| Year	Water year-type	Low release magnitude (m³/s)	Peak release magnitude (m³/s)	Restoration release (hectare m)	Low release magnitude (m³/s)	Date and duration to base-flow	Total days
Maximum		**47**	**192**	**NA**	**27**		**81**
ROD Flow (2005 - 2011, 2017)							
2005	wet	8	197	79880	13	27 Apr-22 Jul	87
2006	extra wet	8	286	99900	13	16 Apr-22 Jul	98
2007	dry	8	135	55963	13	25 Apr-25 Jun	62
2008	dry	9	183	80016	20	22 Apr-15 Jul	85
2009	dry	8	125	54952	12	24 Apr-6 Jul	74
2010	wet	9	194	81003	12	22 Apr-2 Aug	102
2011	wet	7	329	89033	13	26 Apr-1 Aug	98
2017	extra wet	9	326	101536	13	22 Apr-11 Aug	112
Average		**8.3**	**221.9**	**80285.4**	**13.6**		**89.8**
Minimum		**7**	**125**	**54952**	**12**		**62**
Maximum		**9**	**329**	**101536**	**20**		**112**
Pulse Flow (ROD segment): 2003, 2004, 2012 - 2016							
2003	wet	9	74	55272	12	29 Apr-22 Jul	85
2004	wet	9	176	80300	12	4 May-22 Jul	80
2012	normal	9	172	79817	13	4 Apr-26 Jul	114
2013	dry	8	125	55741	13	13 Apr-25 Jun	74
2014	critically dry	9	97	45701	13	21 Apr-26 Jun	67
2015	dry	9	241	55593	13	21 Apr-1 Jul	72
2016	wet	9	283	87429	13	20 Apr-2 Aug	105
Average		8.9	166.8	65693.3	12.7		85.3
Minimum		8	74	45701	12		67
Maximum		9	283	87429	13		114
Pulse Flow (Pulsed augmentation segment: 2003, 2004, 2012 - 2016)							
2003	wet	13	51	4194	13	23 Aug-18 Sep	27
2004	wet	16	485	4465	14	21 Aug-14 Sep	25
2012	normal	13	39	4811	13	12 Aug-20 Sep	40
2013	dry	13	74	2294	13	24 Aug-20 Sep	28
2014	critically dry	12	97	7993	13	15 Sep-25 Sep	11
2015	dry	19	83	5908	13	20 Aug-21 Sep	31
2016	wet	14	35	4835	13	24 Aug-28 Sep	36
Average		**14.3**	**123.4**	**4928.6**	**13.1**		**28.3**
Minimum		**12**	**35**	**2294**	**13**		**11**
Maximum		**19**	**485**	**7993**	**14**		**40**

Figure 2. Examples of hydrographs representative of the three flow type superimposed onto the historical migration pattern of Brown Trout (1982-2017) and Klamath Smallscale Suckers (1993-2017); a) PreROD flow (2002), b) ROD flow (2005), and c) Pulse flow (2015) and its companion late summer pulsed augmentation flow. Tribal Ceremonial Boat Dance flows occur in odd years. Approximate Julian week (JW) superimposed below dates on x-axis.

To date, shapes of the ascending limbs of ROD flow hydrographs were mostly rapid, with few years in which there were benches 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. 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). 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 m³/second. ROD flows generally occurred from late April to August, whereas conjoining Pulse flows mostly occurred from August to September (Figure 2). For the upper Trinity River, the actual timing, magnitude, and duration of each ROD flow and Pulse flow varied annually in hydrologic characteristics, cubic meters per second (m³/s), and shape and duration of the hydrograph depending upon the specific intent of varied management actions. 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 m³/s (range 124.9 - 328.6 m³/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 m³/s (range 35.3 - 97.0 m³/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 m³/s (range 62.3 - 192.3 m³/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).

Study design and sampling

To test H₁, we designated three annual flow groups (henceforth called "flow-types") 1) "baseline" PreROD flows (1982 - 2002), 2) ROD flows (2005 - 2011, 2017), and 3) Pulse flows (2003, 2004, 2012 - 2016, 2018) illustrated in Figure 2a, 2b and 2c, respectively). 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*, even though no quantitative studies post-2003 have definitively confirmed that augmentation by cold-water flows from the upper Trinity River have actually prevented another fish die-off in the lower Klamath River. 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 pre-pulse ROD flow segment.

Data and samples analyzed herein derive from two sources. First, we obtained all counts of anadromous co-occurring "wild" and hatchery stocks of native Coho Salmon (*Oncorhynchus kisutch*), spring- and fall-run Chinook Salmon, and anadromous Rainbow Trout (*Oncorhynchus mykiss*) (henceforth called "steelhead") from adult (> 32 cm fork length) returns to the hatchery. Second, we obtained daily trap-counts of adult non-anadromous Brown Trout (*Salmo trutta*) and Klamath Smallscale Suckers (*Catostomus rimiculus*) from the weir because both species do not enter the hatchery, are not "focal management" taxa, and are only encountered and counted at the weir. Adult Brown Trout and Klamath Smallscale Suckers (> 32 cm fork length) are considered "by-catch" at the weir, as target species

are anadromous salmonids, specifically spring-run Chinook Salmon. Sampling effort for all species based on size constraints at the weir has historically been relatively consistent from 1996 to 2018 (average = 55.1 trap days), except when weir operations are temporarily halted during ROD and Pulse flow years (beginning in 2003) until flows have subsided sufficiently to reinstate the weir (average trap-days post-2003 = 50.9). We provide detailed operation and efficiency estimates of the weir designed to assess only upriver movement of salmonids to the hatchery elsewhere (Sullivan and Hileman 2018).

Brown Trout and Klamath Smallscale Suckers in the upper Trinity River represent non-anadromous populations (Sullivan and Hileman 2018). Brown Trout are a piscivorous non-native species found in the Klamath Basin, introduced into tributaries in the lower Trinity River in 1893 to promote recreational angling (Dill and Cordone 1997; Sullivan and Hileman 2018). As such, this species has coexisted in sympatry with native anadromous salmonids in the Trinity River for over a century. Similarly, the Klamath Smallscale Sucker is native to the Trinity River. It is the most genetically unique phylogenetically and the least widely distributed geographically of all other species of suckers in the Klamath River Basin (Moyle 2002; Tranah and May 2006). Although both species display migratory behavior associated with availability of water and food, larval and juvenile development, water temperature, and spawning (Hohler 1981; Desjardins and Markle 2002; Hampton 2006; Pirrello 2011), information on extrinsic environmental factors that influence the pattern and timing of migration in response to altered flow regimes in both species of resident freshwater fish is relatively unknown.

Non-anadromous populations of Brown Trout and Klamath Smallscale Suckers in the Trinity River have acclimated or adapted to the Trinity River system for many years in sympatry with native anadromous species. Importantly, Brown Trout and Klamath Smallscale Sucker annual abundance, seasonal pattern and timing of migration, and response to changes in flow patterns derived from highly managed flow regimes involving pulsed augmentation flows are independent of any oceanic or marine influence. This condition is unlike anadromous species of co-occurring "wild" and hatchery stocks of native Chinook Salmon, Coho Salmon, and steelhead. Thus, for comparison with anadromous species we view Brown Trout and Klamath Smallscale Suckers as excellent "control" species for evaluating potential effects of managed hydrological variation within the upper Trinity River, which may provide insight into fisheries management of large, highly regulated riverine systems regionally or elsewhere. Importantly, that non-native brown trout are known to be piscivorous on juvenile salmonids is irrelevant to our assertion that they provide a valid "control" species, as steelhead (Naman 2008) and numerous terrestrial vertebrate species also readily consume both hatchery-produced and wild juvenile salmonids in the Trinity River (Sullivan and Hileman 2018). Yet no study has provided evidence of the relative degree of 1) predation by Brown Trout or 2) estimates of the availability and abundance of potential juvenile salmonid prey species in relation to other piscivorous taxa endemic or introduced into the Trinity River, including a recent bioenergetics model of Brown Trout predation in the Trinity River (Alvarez and Ward 2019). Further, understanding the basic pattern of migration and learning from the behavior of non-anadromous as well as anadromous resident species of fish in response to flow management is a prerequisite to enabling placement of a broad suite of covariate non-flow factors into perspective, which is particularly relevant to restoration actions, as it enables resource managers to better understand and evaluate their methodology and facilitated completion of the adaptive management process (Sullivan and Hileman 2019).

For Brown Trout (1982 - 2018, n = 3,614) and Klamath Smallscale Suckers (1993 - 2018, n = 5,156), we used the metric catch per unit effort (CPUE) in units of adult fish trapped per trap-day to estimate relative annual abundance and evaluate "population" trends over time (Sullivan and Hileman 2018). Estimates of CPUE derive from constant effort by-catch data collected at the weir (trap-counts). Although CPUE is not a measure of true abundance, it is an established indicator of relative abundance (Bonar et al. 2009; Arshad-Ul-Alam and Azadi 2015). Conversely, we used adult return hard-counts (henceforth called "counts") in our analysis of Coho Salmon (1990 - 2018, n = 153,872) and steelhead (1990 - 2018, n = 100,547). In contrast, adult return counts to the hatchery of coded wire tagged individuals (CWT) were used to evaluate known genetic race spring-run (1994 - 2018, n = 28,436) and fall-run (1994 - 2018, n = 56,749) Chinook Salmon. Importantly, counts of both spring- and fall-run coded wire tagged Chinook Salmon only represent an averaged marked subsample of approximately 20.7% of the total combined return to the hatchery of adult Chinook Salmon for each race (1994 - 2018, n = 41,1888), as currently only 25% of hatchery produced Chinook Salmon are coded wire tagged prior to release into the Trinity River below Lewiston Dam as juveniles (Sullivan and Hileman 2019). We used counts of coded wire tagged known race returns in our analysis to tease out definitive spring- and fall-run Chinook Salmon because there is frequently temporal overlap between returning adults of the two sympatric races in the autumn at the hatchery. Additionally, there is no other functional way to accurately determine racial segregation because there is no definitive external phenotypic difference between races of Chinook Salmon that would allow identification at the weir. Finally, counts of coded wire tagged known spring- and fall-run Chinook Salmon were used in lieu of estimates based on expansion equations (Kilduff et al. 2015; Sullivan and Hileman 2019).

Statistical analyses

All statistical tests performed used the R-suite of statistical programs (v3.5.2, R Core Team 2019). Prior to analysis univariate normality for annual fluctuations in the distribution of counts and CPUE estimates we conducted for all taxa, which were visually inspected by use of normalized (0.0, 1.0) quantile-quantile (Q-Q) and standardized residual plots. As expected, this assessment showed that all count and CPUE data were skewed significantly to the right, consistent with a Poisson distribution. A follow-on statistical evaluation by use of the Shapiro-Wilk's (W) test (McGarigal et al. 2000) similarly indicated that annual species-specific counts and CPUE data were not normally distributed (Brown Trout: W = 0.87, P < 0.01, n = 33; Klamath Smallscale Sucker: W = 0.88, P < 0.01, n = 24; CWT spring-run Chinook Salmon: W = 0.83, P < 0.01. n = 25; fall-run Chinook Salmon: W = 0.84, P < 0.01, n = 25; Coho Salmon: W = 0.88, P < 0.01, n = 29; steelhead: W = 0.82, P < 0.01, n = 29; Appendix I). Thus, all subsequent non-regression statistical analyses of count and CPUE data used non-parametric methods (McDonald 2014). For count and CPU data, we used the Spearman's rank correlation rho (r_s) 2-tailed test to calculate strength and direction of the relationship between two variables, expressed as a monotonic relationship, whether linear or not (Corder and Foreman 2014). Whereas the Pearson correlation coefficient (r_c) was used in all correlation analyses involving water temperature, flow, and other continuous metrics. The Wilcoxon signed-rank test (paired = "TRUE", zero method = "Pratt"; package "asht" v0.9.4) computed from two-sided probabilities using approximate normal variates (Z) for

all planned multiple comparisons, was used to evaluated the hypothesis that the median difference between pairs of Julian week counts was zero among different flow-types for each taxon of fish (Hasler et al. 2014).

We obtained telemetered digital data for 1) average daily water temperature (ADWT, degrees centigrade [Cº]) and 2) averaged daily flow volume (ADFV m³/s) from the United States Bureau of Reclamation, 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 (DWR 2018) for the sampling period 1994 to 2018 for which there were complete data for each variable. This gauge was the "standard" used in all National Environmental Protection Act (NEPA 1969) assessments and flow augmentation analyses of fluctuations in in-river average daily water temperature, specific to the upper Trinity River out of Lewiston Dam since 1997 (Magneson and Chamberlain 2014 and included references). Trends in seasonal count data were analyzed 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. To determine if timing of seasonal migration in species-specific ROD and Pulse flow-types deviated from their baseline PreROD flow pattern, we calculated a Percent Deviation Index (PDI) from total counts (Sullivan and Hileman 2019):

> PDI for ROD flows = %ROD flow count – %PreROD flow count
> PDI for Pulse flows = %Pulse flow count – %PreROD flow count

Generalized additive models

We assessed annual trends in continuously distributed linear measures of ADWT and ADFV from 1994 through 2018, and seasonally by use of Julian weeks specific to the documented presence (counts) of each species as a function of species-specific migration or run-time schedules (JW21 - JW13). Generalized additive models (GAM, Package "mgcv" v1.8-28, Wood 2017) were used in regression of hatchery counts and weir CPUE data for all species as described in detail elsewhere (Hastie and Tibshirani 1990; Madsen and Thyregod 2011; Sullivan and Hileman 2019). Response curves generated from each GAM showed the relationship between the fitted function to the response scaled to zero. Statistics reported from each GAM were 1) F- or χ^2- statistics (approximate significance of smooth terms) including P-values and 95% confidence bands for spline lines (Nychka 1988), 2) adjusted regression coefficients for each model (R^2 adj.), 3) estimated residual degrees of freedom (Ref. d.f.), and 4) proportion of null deviance explained (Dev.Exp.). We used the 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 (Package "AER" v1.2-6), the negative binomial error-structure (family = "nb" [theta = NULL, link = "log']) was used in construction of GAM models to establish the relationship between response variables and the smoothed functions of predictor variables (Wood et al. 2016; Wood 2017; Lipp 2016). In contrast, the gamma error-structure (family = "Gamma" [link = "log"]) was used to assess error distributions of annual and seasonal (JW) fluctuations in ADWT and ADFV (Package "fitdistrplus" v1.0-14). The Akaike information

criterion (QAICc, Package MuMIn v1.43.5) modified for overdispersed count data adjusted for small sample uncertainty was used to select the most parsimonious error distribution for each environmental attribute, as well as GAM models for comparisons between counts, and individual and combined water temperature and flow volume effects (Akaike 1973; Burnham and Anderson 1998). Whereas, a Gaussian error-structure (family = "gaussian" [link = "identity"]) was used to plot difference curves (Package "itsadug" v2.3) using GAM model predictions of the number of counts that deviated from the species-specific baseline PreROD flow-type as a result of both ROD and Pulse flows, because these data included both positive and negative numbers (Cox 2017). We set statistical significance for all analyses at $P < 0.05$.

Autocorrelation analysis of residuals derived from GAM analyses investigated the relationship of each time point to each previous time point in the distribution of consecutive annual counts in relative abundance for all species (Package "forecast" v8.3 and "stats" v3.6.0). Visual inspection of these results showed that all time-points were contained within approximate 95% confidence levels of significance for each correlation in the autocorrelation function correlograms (Appendix II). Additionally, follow-on Box-Pierce test (χ^2) tests and augmented Dickey-Fuller tests (SDF) evaluated the extent of stationarity of the time series models (Fuller 1976; Ljung and Box 1978). Each of these analyses indicated no evidence of non-zero autocorrelations in the in-sample forecast errors at any lag-point for any taxon (Coghlan 2019). Because we found no evidence against time dependency for any species, we concluded that annual counts of all species represented stationary series of relatively constant autocorrelation structure over time for the sequence of consecutive years analyzed herein. Importantly, a stationary time series likely will always occur for Trinity River Hatchery raised salmonids as numbers of hatchery released fingerlings and yearlings are based on egg-take allotments established in the 1980s to meet fixed mitigation goals of returning adult Chinook Salmon, Coho Salmon, and steelhead to the hatchery irrespective of annual hatchery escapement (Sullivan and Hileman 2019).

RESULTS

Annual fluctuations in relative abundance

Annual fluctuations in CPUE estimates in Brown Trout and Klamath Smallscale Suckers from the weir, hatchery counts of coded wire tagged known race spring- and fall-run Chinook Salmon, and hatchery counts of Coho Salmon and steelhead all fluctuated considerably on an annual basis (Figure 3a-3f). Peaks in relative abundance generally exhibited increasing trends beginning early in 2002. Plots of partial residuals showed that annual counts were non-linear and well defined by response curves (Figure 4a-4f), as all smooth terms were significant, and deviance explained ranged from 42.1% (Brown Trout, spring-Run Chinook Salmon) to 64.8% (steelhead). Additionally, 60.0% (n = 15) of all planned pair-wise correlations among species were significant and positively correlated indicating that most species exhibited similar annual patterns for the years that they shared in our sample (Table 2).

However, from 2003 to 2018 GAM regression showed that the strength of the relationship between year and counts and CPUE estimates was strong, significant, and negative for all non-anadromous and anadromous species irrespective of the reduction in years sampled. Concordance in these data indicate that all taxa have declined abruptly in relative abundance since 2003, irrespective of divergent life history strategies (Table 2). Importantly,
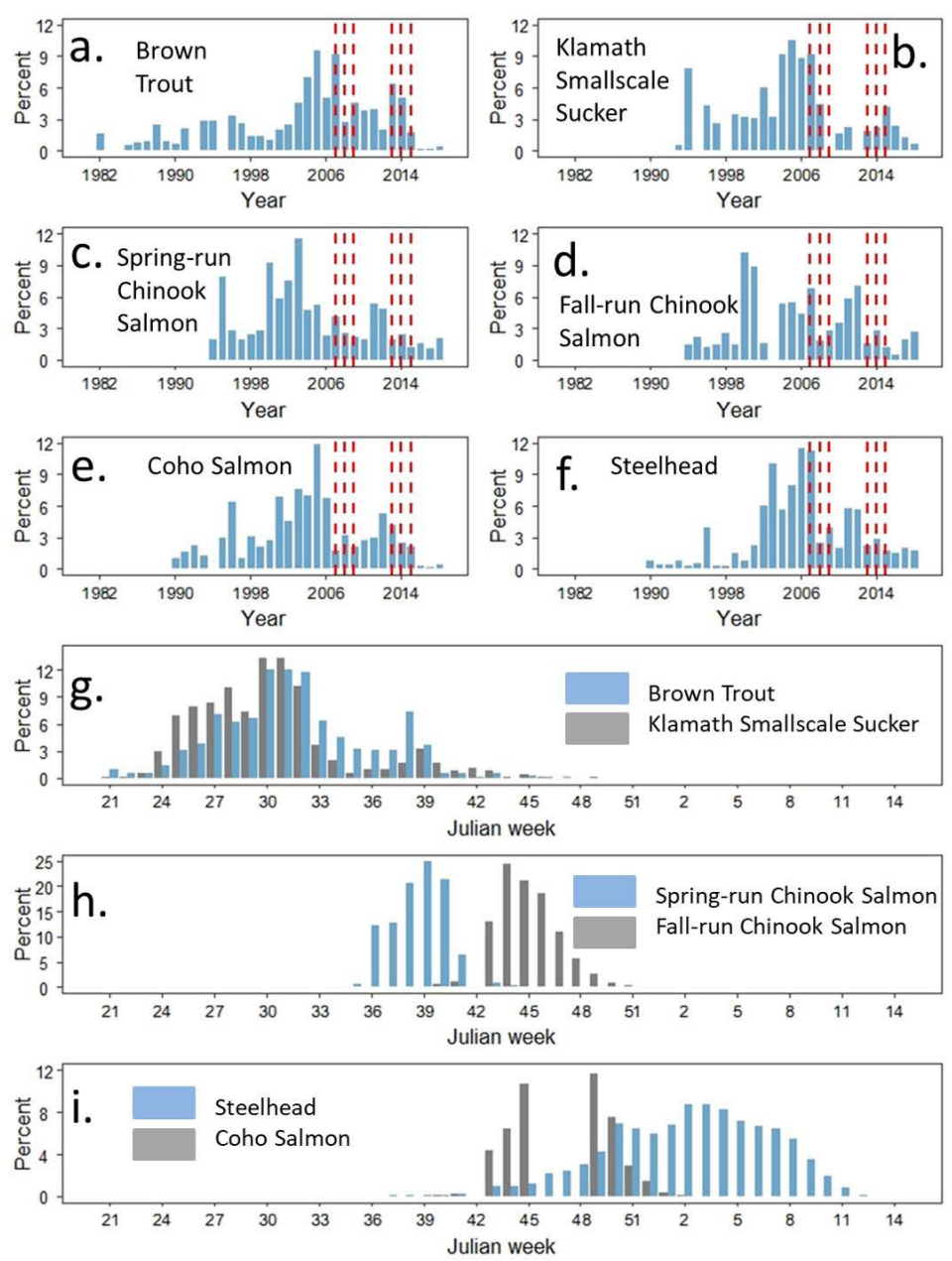
Figure 3. Bar charts of the percentage of annual and seasonal Julian week (JW) fluctuations in total adult counts of Brown Trout (a and g), Klamath Smallscale Suckers (b and g), spring-run Chinook Salmon (c and h), fall-run Chinook Salmon (d and h), Coho Salmon (e and i), and steelhead (f and i). Vertical dashed red lines reference two periods of three consecutive years of drought (2007-2009, 2013-2015).
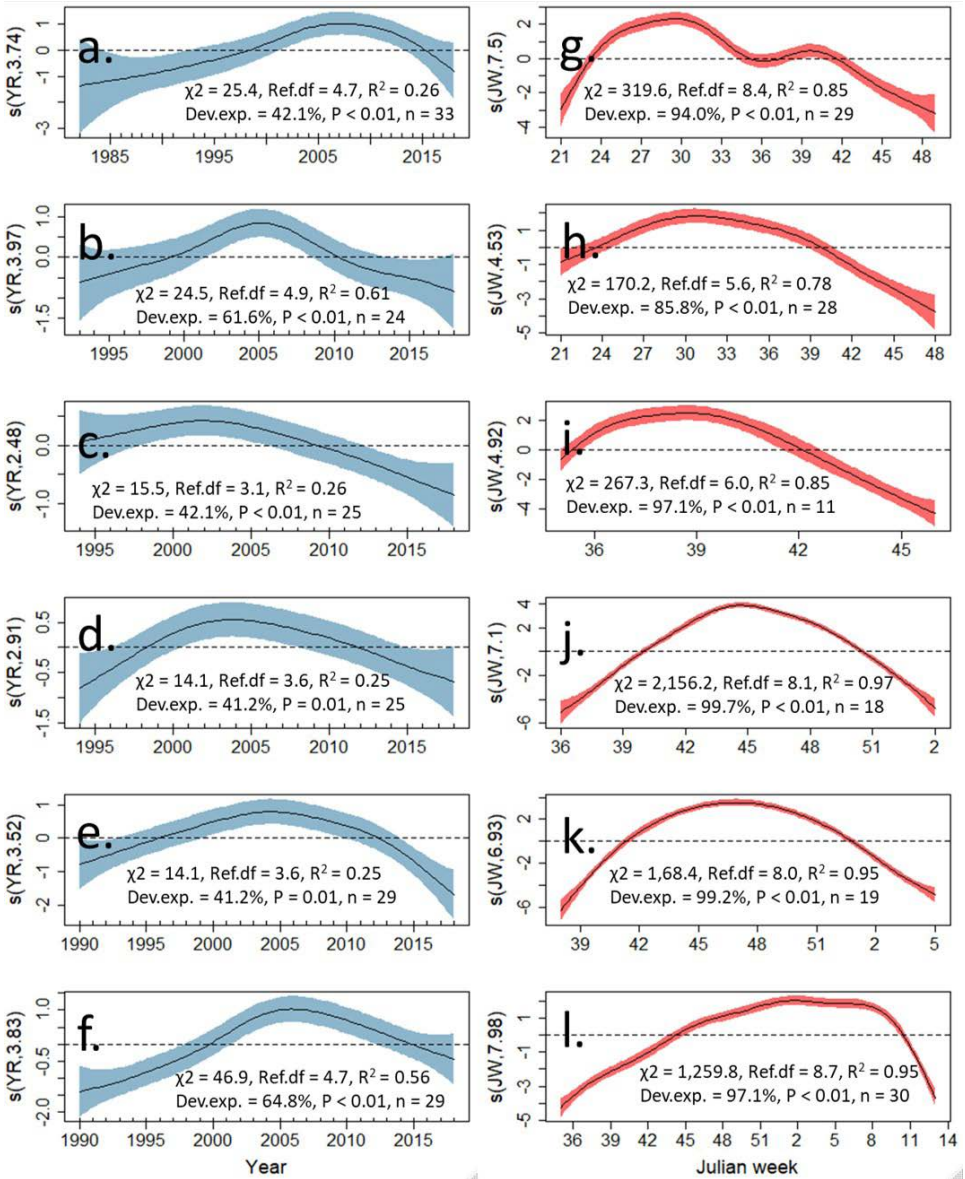
Figure 4. Partial residual response curves (centerline) generated from GAM regression of total annual counts and CPUE estimates (a - f), and seasonal Julian week (JW) counts (g - l) for each species of fish. Each plot shows the relationship of the fitted function to the response scaled to zero, including approximate 95% point-wise standard error bands for each curve of the factor level. Y-axes (log-scaled) are based on partial residuals indicating the relative influence of each year sampled (explanatory variable) on the relative abundance of counts (prediction). X-axes (independent variable/predictor) are labeled with the covariate name; whereas Y-axes (outcome/dependent variable) are labeled by the covariate name (cov) and estimated degrees of freedom (edf) of each of the smooths (i.e., s[cov,edf]); and smooths are "centered" to ensure model identity and sum to 0 over covariate values).

Table 2. Planed Spearman rank correlations Coefficients (rs) of 1) annual catch per unit effort (CPUE) and counts of all fish at the Trinity River Hatchery (hatchery) and Junction City (weir) for Brown Trout (BT, 1982 - 2018), Klamath Smallscale Sucker (KSS, 1993 - 2018), spring-run Chinook Salmon (SRC, 1994 - 2018), fall-run Chinook Salmon (FRC, 1994 - 2018), Coho Salmon (COS, 1990 - 2018), and steelhead (STH, 1990 - 2018); 2) CPUE and counts from the hatchery and weir from 2003 to 2018; and 3) seasonal Julian week (JW) variation in counts from 1994 to 2018. Correlations coefficients are below the diagonal and P-values are above the diagonal; P-values: * < 0.05, ** < 0.01, *** < 0.001.

Group	YR	BT	KSS	SRC	FRC	COS	STH
Years specific to taxa							
Year (n = 37)		0.04*	0.31	0.03*	0.82	0.97	0.01**
Brown Trout (n = 33)	0.36		0.05*	0.04*	0.01**	< 0.01***	< 0.01***
Klamath Smallscale Sucker (n = 24)	-0.22	0.40		0.13	0.56	0.06	0.01**
Spring-run Chinook Salmon (n = 25)	-0.44	0.42	0.32		< 0.01***	< 0.01***	0.06
Fall-run Chinook Salmon (n = 25)	0.05	0.53	0.13	0.63		0.02*	0.01**
Coho Salmon (n = 29)	0.01	0.69	0.39	0.63	0.47		< 0.01***
Steelhead (n = 29)	0.48	0.75	0.53	0.39	0.51	0.61	
Years and taxa (2003 - 2018)							
Year (n = 16)		< 0.01***	< 0.01***	< 0.01***	0.01**	< 0.01***	< 0.01***
Brown Trout (n = 16)	-0.76		0.12	< 0.01***	< 0.01***	< 0.01***	< 0.01***
Klamath Smallscale Sucker (n = 16)	-0.78	0.41		0.15	0.32	0.11	0.03*
Spring-run Chinook Salmon (n = 16)	-0.71	0.80	0.38		< 0.01***	< 0.01***	< 0.01***
Fall-run Chinook Salmon (n = 16)	-0.65	0.86	0.26	0.85		0.02*	< 0.01***
Coho Salmon (n = 16)	-0.78	0.73	0.41	0.70	0.56		0.01**
Steelhead (n = 16)	-0.80	0.79	0.55	0.79	0.84	0.65	
Julian weeks (JW21 - JW14) and years specific to taxa							
Julian week (n = 46)		0.01**	0.01**	0.07	0.95	0.74	0.02*
Brown Trout (n = 29)	-0.48		< 0.01***	< 0.01***	0.02*	< 0.01***	< 0.01***
Klamath Smallscale Sucker (n = 28)	-0.51	0.85		0.01**	< 0.01***	< 0.01***	< 0.01***
Spring-run Chinook Salmon (n = 11)	-0.57	0.96	0.71		0.02*	< 0.01***	0.07
Fall-run Chinook Salmon (n = 18)	0.02	-0.65	-0.80	-0.72		< 0.01***	0.87
Coho Salmon (n = 19)	-0.08	-0.93	-0.85	-0.93	0.73		0.87
Steelhead (n = 30)	0.44	-0.77	-0.85	-0.56	0.04	-0.04	

this continuing trend in declining stocks of sympatric non-anadromous and anadromous fish inhabiting the upper Trinity River initiated prior to the two periods of three consecutive years of regional drought as indicated by water year-type for 2007 through 2009 through 2013 to 2015 (Table 1; TRRP 2019).

Seasonal fluctuations in Julian week counts

Fluctuations in seasonal Julian week counts increased early in the migration or run-timing cycle then declined late in the season for all non-anadromous and anadromous species (Figure 3g-3i). Plots of partial residuals showed that counts associated with seasonal migration and run-timing were non-linear and well defined by response curves, as deviance explained was > 85.8% in all taxa (Figure 4g-4l). Initiation and termination of seasonal migration in non-anadromous Brown Trout and Klamath Smallscale Suckers ranged from mid-May through early December (JW21 - JW49). Whereas in anadromous salmonids initiation of seasonal run-timing ranged from late August to early January (JW36 - JW2) in spring- and fall-run Chinook Salmon, from mid-September to late March (JW38 - JW5) in Coho Salmon, and from late August through late March (JW35 - JW13) in steelhead. However, we note that initiation of annual hatchery counts does not start until the fish ladder opens at the beginning of September. Thus, based on count data presented herein seasonal migration in Brown Trout and Klamath Smallscale Suckers, and run-timing in steelhead were the most drawn-out migratory patterns of all the species evaluated.

Brown Trout and Klamath Smallscale Suckers overlapped significantly in their seasonal Julian week pattern of migration (Table 2). Regression analysis using GAM indicated that the timing of migration in Brown Trout passing through the weir equated to 51.3% of the deviance explained in timing of migration of Klamath Smallscale Suckers trapped at the weir during the same time period ($\chi^2 = 33.4$, Ref.df = 3.7, P < 0.01, $R^2 = 0.74$). Moreover, seasonal Julian week migration in both Brown Trout and Klamath Smallscale Suckers was significant and positively correlated with run-timing in spring-run Chinook Salmon but significant and negatively correlated with all other anadromous salmonids (Table 2). Intersection of species-specific run-timing in spring- and fall-run Chinook Salmon was minimal. However, historically some overlap between these genetically differentiated races occurs from mid-September through mid-November (Figure 3h, JW38 - JW46, Kinziger et al. 2013).

Coho Salmon and fall-run Chinook Salmon also exhibited a significant and positive relationship in run-timing with migration in fall-run Chinook Salmon equating to 51.4% of the deviance explained in Coho Salmon ($\chi^2 = 24.6$, Ref.df = 3.1, P < 0.01, $R^2 = 0.27$). Presence of steelhead in the upper Trinity River system encompassed run-timing of both Chinook Salmon and Coho Salmon. Yet, steelhead did not exhibit a similarly significant pattern of seasonal run-timing with any other anadromous species except marginally with early arriving spring-run Chinook Salmon; whereas the relationship in seasonal migration with both non-anadromous Brown Trout and Klamath Smallscale Suckers was highly significant but negative (Table 2).

Fluctuations in water temperature and flow volume

Regression analysis of raw environmental data using GAM reviled significant positive trends in annual fluctuations in ADWT, but significant negative trends in annual fluctuations in ADFV (Figure 5a). Yet the proportion of the null deviance explained in both variables

was low and follow-on correlations indicated that the strength of the relationships between year and each variable was extremely weak (Table 3). Whereas GAM analyses of seasonal Julian week fluctuations in ADWT and ADFV identified significant negative trends in both environmental variables, particularly ADWT. However, for each comparison much larger percentages of the null deviance were explained by seasonal variation in ADWT and ADFV compared to annual variation in these two environmental attributes (Table 3, Figures 5b and 5c).

Fluctuations in water temperature and flow volume in relation to counts of fish

Against this background, there were no significant trends in counts or CPUE estimates of each species of fish in relation to annual fluctuations in ADWT or ADFV based upon results of GAM regression or ranked correlation analyses (Table 3). Conversely, counts of Brown Trout, Klamath Smallscale Sucker, and spring-run Chinook Salmon exhibited significant positive trends in relation to seasonal Julian week fluctuations in ADWT (Table 3, Figure 5b). This pattern was a function of increased species-specific counts associated with early spring and late summer patterns of migration, coincidental with relatively warm water temperatures from approximately mid-July to late August (JW30 - JW34).

In contrast, counts of steelhead showed a significant negative relationship with ADWT, as a function of progressively late fall and early winter run-timing in association with comparatively colder water temperatures beginning in late October (JW45) through the coldest water-months from January to early February (JW51 - JW5, Table 3, Figure 5b). In comparison, counts of Fall-run Chinook Salmon and Coho Salmon exhibited no significant trends in relation to seasonal Julian week variation in ADWT following ROD and Pulse flow-type events and a return to base-flows in late fall (Table 3, Figure 3h and 3i, Figure 5c). As relates to seasonal Julian week fluctuations in ADFV, only counts of Fall-run Chinook Salmon and Coho Salmon exhibited a significant negative relationship with this variable. Whereas the marginally significant and positive correlation between CPUE and ADFV in Klamath Smallscale Suckers appears to represent only a small segment of the terminal end of local migration in response to seasonal peaks in odd year Tribal Ceremonial Boat Dance flows and companion or individual Pulse flow events after 2003, which also appear to promote local migration in Brown Trout (Figure 2c, Figure 5c; Sullivan and Hileman 2018).

Additionally, the proportion of null deviance explained in seasonal Julian week variation in relative count abundance by ADWT was greater than when count data were regressed against ADFV for each taxon (Table 3). Further, the proportion of null deviance explained improved greatly by combining the two environmental attributes in all species. Combining environmental variables in a composite GAM model for spring-run Chinook Salmon was not possible as there were more coefficients than the number of Julian week samples. However, combining ADWT with ADFV in model regressions did not appreciably improve all measures of relative fit for each predictive species-specific model as measured by the QAICc information criterion (Table 2). For example: 1) seasonal and local migration in Brown Trout appeared more aligned with warmer water in association with pulsed flow augmentations; 2) run-timing in Coho Salmon appeared closely affiliated with a return to base-flows in the fall on post-pulsed augmentation flows; and 3) run-timing in steelhead appeared more closely aligned with an increase flows late in the season in conjunction with the onset of winter storms and accretion of cold water derived from watersheds of the upper Trinity River basin.
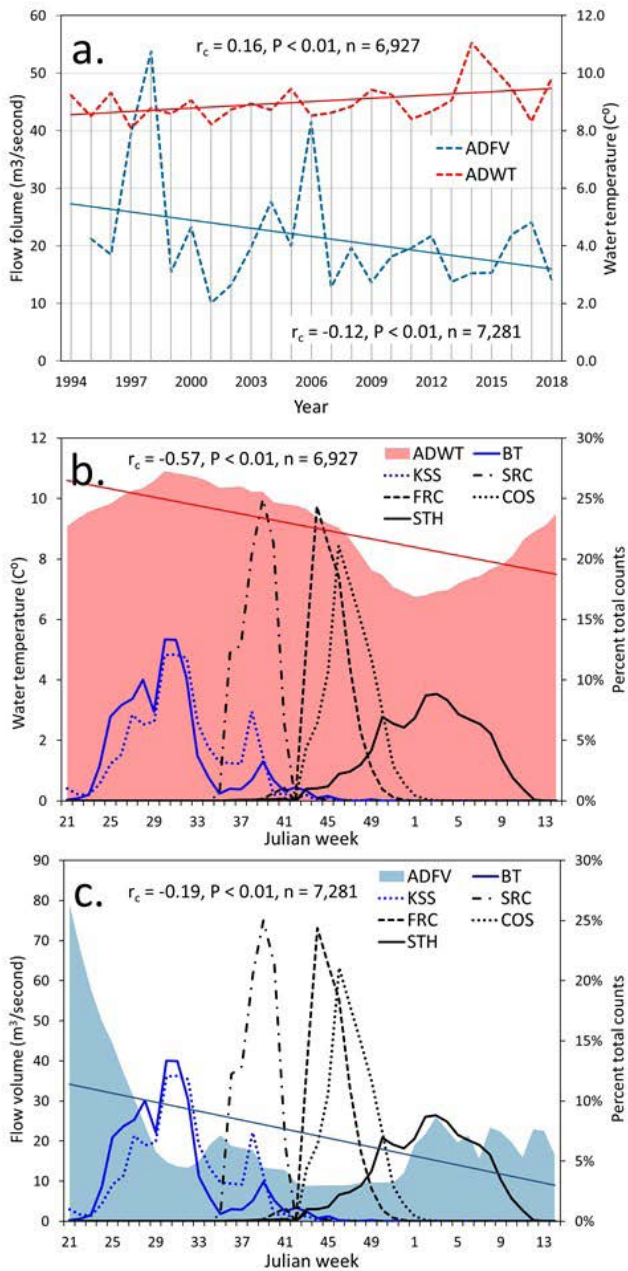
Figure 5. a) Mean values of annual fluctuations in average daily water temperature (ADWT) and averaged daily flow volume (ADFV) from 1994 to 2017 and for Julian weeks (JW) 21 to 14, which encompasses sampling dates for both hatchery and weir. Seasonal JW fluctuations in counts of salmon and steelhead and catch per unite effort (CPUE) for Brown Trout and Klamath Smallscale Suckers from 1994 to 2018 are superimposed onto mean values of b) ADWT and c) ADFV. Coho Salmon = COS, spring-run Chinook Salmon = SRC, fall-run Chinook Salmon = FRC, steelhead = STH, Brown Trout = BT, and Klamath Smallscale Sucker = KSS.

Table 3. Summary of approximate significance of smooth terms and statistics derived from generalized additive model (GAM) regressions of count and CPUE data for fish in relation to year (YR) and Julian week (JW), and raw data for averaged daily water temperature (ADWT) and flow volume (ADFV). Statistics reported for each GAM were 1) GAM F- or the GAM χ^2- statistic (approximate significance of smooth terms), P-value, 2) adjusted regression coefficient for the model (R^2 adj.), 3) estimated residual degrees of freedom (Ref.d.f.), 4) proportion of null deviance explained (Dev.Exp.), Akaike information criteria (QAICc), and parametric Pearson correlations (rc) or nonparametric Spearman rank correlations (rs) for each comparison; NA = no data.

Regression comparisons	GAM statistics (family = "Gamma")					QAICc	Pearson correlation		
	GAM F	P-value	Ref.df	R^2-adj	Dev.Exp. (%)		r_c	P-value	n
Environmental variables vs. year (1994 - 2018) and Julian week (JW21 - JW14) for all raw data									
ADWT ~ YR	47.2	<0.01***	9.0	0.06	5.6	24,653.5	0.16	<0.01***	6,927
ADFV ~ YR	48.2	<0.01***	9.0	0.06	11.5	55,847.1	-0.12	<0.01***	7,281
ADWT ~ JW	1602	<0.01***	9.0	0.67	67.4	17,533.4	-0.57	<0.01***	6,927
ADFV ~ JW	190.8	<0.01***	9.0	0.25	41.6	52,657.3	-0.18	<0.01***	7,281
	GAM statistics (family = "nb")					QAICc	Spearman rank correlation		
	GAM χ^2	P-value	Ref.df	R2-adj	Dev.Exp.		r_s	P-value	n
Annual counts or CPUE estimates vs. mean values of ADWT (1994 - 2018)									
Brown Trout YR CPUE ~ ADWT	0.2	0.70	1.0	0.04	0.6	97.7	-0.12	0.58	24
Klamath Smallscale Sucker YR CPUE ~ ADWT	0.7	0.41	1.0	0.03	2.8	110.3	-0.07	0.76	23
Spring-run Chinook Salmon YR counts ~ ADWT	3.3	0.07	1.0	0.01	10.2	384.5	-0.31	0.13	25
Fall-run Chinook Salmon YR counts ~ ADWT	1.9	0.17	1.0	0.01	6.5	424.0	-0.22	0.29	25
Coho Salmon YR counts ~ ADWT	0.4	0.54	1.0	0.03	1.1	473.9	-0.14	0.51	25
Steelhead YR counts ~ ADWT	0.6	0.42	1.0	0.03	2.0	455.2	-0.01	0.96	25
Annual counts or CPUE estimates vs. mean values of ADFV (1995 - 2018)									
Brown Trout YR CPUE ~ ADFV	0.1	0.86	1.4	0.04	1.9	95.9	-0.01	0.98	23
Klamath Smallscale Sucker YR CPUE ~ ADFV	2.4	0.12	1.0	0.08	10.2	105.0	0.09	0.69	22

Table 3. continued.

Regression comparisons	GAM statistics (family = "Gamma")						Pearson correlation		n
	GAM F	P-value	Ref.df	R²-adj	Dev.Exp. (%)	QAICc	r_c	P-value	
Spring-run Chinook Salmon YR counts ~ ADFV	0.9	0.32	1.0	0.03	3.3	372.4	-0.06	0.76	24
Fall-run Chinook Salmon YR counts ~ ADFV	0.2	0.62	1.0	0.04	0.9	410.1	0.00	0.99	24
Coho Salmon YR counts ~ ADFV	0.1	0.92	1.0	0.05	0.1	455.8	0.07	0.74	24
Steelhead YR counts ~ ADFV	0.1	0.77	1.0	0.04	0.3	438.9	-0.24	0.25	24
Seasonal Julian week counts vs. mean values of ADWT (1994 - 2018)									
Brown Trout JW counts ~ ADWT	107.3	<0.01***	5.5	0.58	77.8	298.4	0.83	<0.01***	29
Klamath Smallscale Sucker JW counts ~ ADWT	95.1	<0.01***	1.0	0.76	72.3	301.5	0.88	<0.01***	28
Spring-run Chinook Salmon JW counts ~ ADWT	78.0	<0.01***	3.4	0.67	83.5	202.2	0.62	0.04*	11
Fall-run Chinook Salmon JW counts ~ ADWT	305.2	<0.01***	6.5	0.86	93.9	266.7	-0.02	0.94	18
Coho Salmon JW counts ~ ADWT	70.7	<0.01***	4.8	0.70	67.8	337.1	-0.02	0.94	19
Steelhead JW counts ~ ADWT	147.9	<0.01***	3.2	0.92	75.8	488.5	-0.93	<0.01***	30
Seasonal Julian week counts vs. mean values of ADFV (1995 - 2018)									
Brown Trout JW counts ~ ADFV	37.6	<0.01***	5.7	0.10	51.3	322.3	0.28	0.14	29
Klamath Smallscale Sucker JW counts ~ ADFV	73.2	<0.01***	7.5	0.28	68.8	330.3	0.39	0.04*	28
Spring-run Chinook Salmon JW counts ~ ADFV	54.3	<0.01***	3.1	0.81	81.4	195.5	0.46	0.15	11

Table 3. continued.

Regression comparisons	GAM statistics (family = "Gamma")						Pearson correlation		n
	GAM F	P-value	Ref.df	R^2-adj	Dev.Exp. (%)	QAICc	r_c	P-value	
Fall-run Chinook Salmon JW counts ~ ADFV	148.2	<0.01***	1.4	0.63	83.1	258.1	-0.93	<0.01***	18
Coho Salmon JW counts ~ ADFV	59.1	<0.01***	2.9	0.54	64.6	329.9	-0.79	<0.01***	19
Steelhead JW counts ~ ADFV	0.6	0.45	1.0	0.03	1.8	528.1	0.10	0.62	30
Seasonal Julian week counts vs. combinations of environmental variables (1995 - 2018)									
Brown Trout JW counts ~ ADWT + ADFV									
ADWT	47.9	<0.01***	2.9	0.69	83.5	303.6	NA	NA	29
ADFV	15.8	<0.01***	4.4				NA	NA	
Klamath Smallscale Sucker JW counts ~ ADWT + ADFV		<0.01***							
ADWT	93.3	<0.01***	1.0	0.82	88.1	298.1	NA	NA	28
ADFV	24.4	<0.01***	3.8				NA	NA	
Fall-run Chinook Salmon JW counts ~ ADWT + ADFV		<0.01***							
ADWT	137.1	<0.01***	4.0	0.88	98.1	249.7	NA	NA	18
ADFV	31.0	<0.01***	1.9				NA	NA	
Coho Salmon counts JW counts ~ ADWT + ADFV									
ADWT	394.6	<0.01***	8.8	0.96	99.7	411.5	NA	NA	19
ADFV	653.1	<0.01***	4.0				NA	NA	
Steelhead JW counts ~ ADWT + ADFV		<0.01***							
ADWT	205.1	<0.01***	1.0	0.38	81.2	495.0	NA	NA	30
ADFV	19.4	<0.01***	2.3				NA	NA	

Seasonal fluctuations among flow-types in relation to Julian week counts

Results of Wilcoxon signed-rank tests for planned multiple comparisons showed a significant overall effect between all flow-types for some but not all species of fish (Table 4). For example, Brown Trout and Klamath Smallscale Suckers showed significant differences in counts between PreROD and Pulse flow-types and between ROD and Pulse flow-types, spring-run Chinook Salmon showed significant differences between PreROD and ROD flow-types, and steelhead showed significant differences between PreROD and ROD flow-types and between PreROD and Pulse flow-types. In contrast, fall-run Chinook Salmon and Coho Salmon did not show any significant differences between flow-types in the paired distribution of Julian week counts.

Comparative analysis of the effects of both managed flow-types on the baseline species-specific PreROD flow pattern of seasonal migration on resident species of fish showed that from 44.5% (Coho Salmon) to 66.3% (steelhead) of the cumulative counts (positive + negative counts) were affected by managed flow hydrographs from 2003 to 2018 (average = 56.2%, Table 5). For ROD-affected flow-types this varied from an addition of counts to the baseline PreROD flow pattern from 99.6% in steelhead to 0.9% in spring-run Chinook Salmon (average = 56.0%). For species-specific Pulse-affected baseline flows addition of counts varied from 31.2% in Coho Salmon to 98.9% in spring-run Chinook Salmon (average = 61.3%). In relation to total hard-counts from both hatcheries returns and the weir for the period 2003 to 2018, variation in the number of fish affected by managed flow-types fluctuated from 21.7% in coded wire tagged fall-run Chinook Salmon to 63.8% in coded wired tagged spring-run Chinook Salmon (Table 5). Thus, the total number of counts for all species affected both positively and negatively by managed flow-types from 2003 to 2018 was estimated to be approximately 237,506 individuals. However, recall that counts of coded wire tagged adult Chinook Salmon assessed herein represent only 21.7% (85,185/243,154) of the total hatchery return of all marked and unmarked fish of all age classes. Thus, for both spring-and fall-runs of this species the actual count of individual adult Chinook Salmon affected by managed flow regimes would be considerable larger, approximating a 4.43688 multiplier of the coded wire tag count for each genetic race comprising the total hatchery return from 2003 to 2018.

Deviation in counts from species-specific baseline flow patterns

Percent deviation indices generated for each taxon showed when and how managed flow-types deviated from their species-specific baseline PreROD flow patterns (Figure 6). For example, the PreROD migration pattern in Brown Trout deviated both positively and negatively from a reduction in counts at the ascending limb of the baseline PreROD flow owing to both ROD and Pulse flows. Yet both managed hydrographs added counts along the declining central and trailing segments of the baseline PreROD flow pattern. In Klamath Smallscale Suckers deviation away from the baseline flow pattern resulted from a decrease in counts by managed flows prior to the peak in the baseline, followed by an increase in counts mid-season and ending with a series of alternating increases (ROD flows) and decreases (Pulse flows) throughout the remainder of migration cycle. In spring-run Chinook Salmon Pulse flows added counts to the baseline pattern early in migration, followed by a decrease in counts by both ROD and Pulse flows throughout the balance of the baseline flow. Conversely, in fall-run Chinook Salmon Pulse flows added counts to the baseline early in the

Table 4. Wilcoxon signed-rank tests (Z) for planned multiple comparisons between pairs of Julian week counts among different flow-types (groups) for each taxon of fish; n = number of Julian weeks per flow-type used in each comparison; P-values: * < 0.05, ** < 0.01, *** < 0.001.

Taxon	PreROD vs ROD		PreROD vs Pulse		ROD vs Pulse	
	Z	P-value	Z	P-value	Z	P-value
Brown Trout (n = 29)	0.4	0.72	2.1	0.04*	2.5	0.01*
Klamath Smallscale Sucker (n = 28)	1.2	0.24	2.1	0.04*	3.1	< 0.00***
Spring-run Chinook Salmon (n = 11)	2.5	0.01**	1.6	0.12	1.4	0.16
Fall-run Chinook Salmon (n = 18)	1.1	1.00	0.0	1.00	0.9	0.40
Coho Salmon (n = 19)	1.3	0.22	1.3	0.24	1.6	0.11
Steelhead Trout (n = 30)	4.4	< 0.00***	3.8	< 0.00***	1.5	0.13

season declining at the end of run-timing; whereas ROD flows reduced counts mid-season but then increased counts late in the season. In Coho Salmon, however, deviation away from the baseline PreROD flow occurred primarily through addition of counts by ROD flows and to a lesser degree by Pulse flows early- to mid-season, the exact opposite of what occurred in fall-run Chinook Salmon, followed by a reduction in counts primarily from Pulse flows near the end of run-timing. Finally, in steelhead both ROD and Pulse flows added counts to the baseline PreROD flow pattern midway through the season, which continued throughout most of the remaining run-timing cycle, primarily in association with ROD flows. Species-specific Julian weeks in which counts were most commonly affected by ROD and Pulse flow-types are shown in Table 5.

Also apparent as a function of correlation analyses (Figure 6, Table 2), was the observation that managed flows imparted similar effects to baseline PreROD flow patterns of migration in non-anadromous Brown Trout and Klamath Smallscale Suckers, which have highly divergent life history strategies but are similar in timing of their seasonal migrations. Whereas alterations of baseline flow patterns in anadromous species by managed flows that have more similar life histories strategies compared to anadromous taxa, were highly dissimilar as a function of divergent run-time schedules (Mims and Olden 2013; Rytwinski et al. 2017), particularly Coho Salmon and steelhead. As such, Julian weeks in which baseline PreROD flow patterns were most frequently affected by managed flows were clearly a function of the timing of species-specific migration in non-anadromous taxa or run-timing in anadromous salmonids (Table 5).

Additionally, in spring-run Chinook Salmon, steelhead, Brown Trout, and Klamath Smallscale Suckers additions and deletions of counts to their corresponding baseline PreROD flow-type patterns were significant and positively correlated (Figure 6). These data indicate that for these species managed flow-types altered their companion baseline flows in similar ways along the seasonal spectrum of Julian weeks, albeit to different degrees. Conversely, in fall-run Chinook Salmon and Coho Salmon there was no significant correlation between ROD and Pulse flow-types in how hydrographs altered their corresponding baseline PreROD flow-types.

Finally, using species-specific difference curves GAM model predictions identified the specific Julian weeks that were significantly different statistically (at alpha = 0.05) between managed flow-types (Figure 7). This analysis closely mirrored the graphic illustrations

Table 5. Species-specific 1) total and percent of the cumulative counts (positive + negative) of fish for both flow-types (ROD and Pulse) that have affected the baseline PreROD flow pattern as a function of managed hydrographs; 2) total and percentage of cumulative counts of ROD and Pulse flow-types separately; 3) comparison of total and percent of affected counts relative to the total Trinity River Hatchery return counts from 1994 through 2018; and 4) Julian week (JW) sequences in which the PreROD flow pattern was most commonly affected and modified by managed flow-types since 2003.

Taxa	Cumulative count both flow-types			Cumulative count ROD flow-type				Cumulative count Pulse flow-type				Total hatchery/weir count (2003 - 2018)		Most common Julian weeks	
	n	Affected (%)	Pulse (%)	n	Add (%)	Delete (%)		n	Add (%)	Delete (%)		n	Affected (%)	Sequence	%
Brown Trout	1,249	62.0	38.0	775	68.4	31.6		474	35.7	64.3		2,459	50.8	28JW - 33JW	64.1
Klamath Smallscale Sucker	2,082	58.1	41.9	1,209	74.0	26.0		873	36.0	64.0		3,500	59.5	25JW - 36JW	68.7
Spring-run Chinook Salmon	10,292	49.9	50.1	5,140	0.9	99.1		5,152	98.9	1.1		16,140	63.8	36JW - 41JW	96.2
Fall-run Chinook Salmon	8,391	56.3	43.7	4,728	58.6	41.4		3,663	72.9	27.1		38,663	21.7	43JW - 49JW	91.2
Coho Salmon	54,931	44.5	55.5	24,439	34.3	65.7		30,492	31.2	68.8		96,201	57.1	43JW - 50JW	87.1
Steelhead	42,705	66.3	33.7	28,299	99.6	0.4		14,406	93.3	6.7		80,543	53.0	49JW - 6JW	71.0

derived by use of our percent deviation indices. For example, in non-anadromous species significant differences between ROD and Pulse flow GAMs for Brown Trout occurred JW26 and from JW29 to JW34 and for Klamath Smallscale Suckers from JW28 to JW38 (Figure 7a, 7b) In anadromous species there were no significant differences between managed flows in spring-run Chinook Salmon, but in fall-run Chinook Salmon significant differences occurred from JW41 to JW44 (Figure 7c, 7d). In Coho Salmon significant differences between ROD and Pulse flow-types occurred from JW45 to JW46 and from JW48 to JW50, and in steelhead from JW50 to JW8 (Figure 7e, 7f).
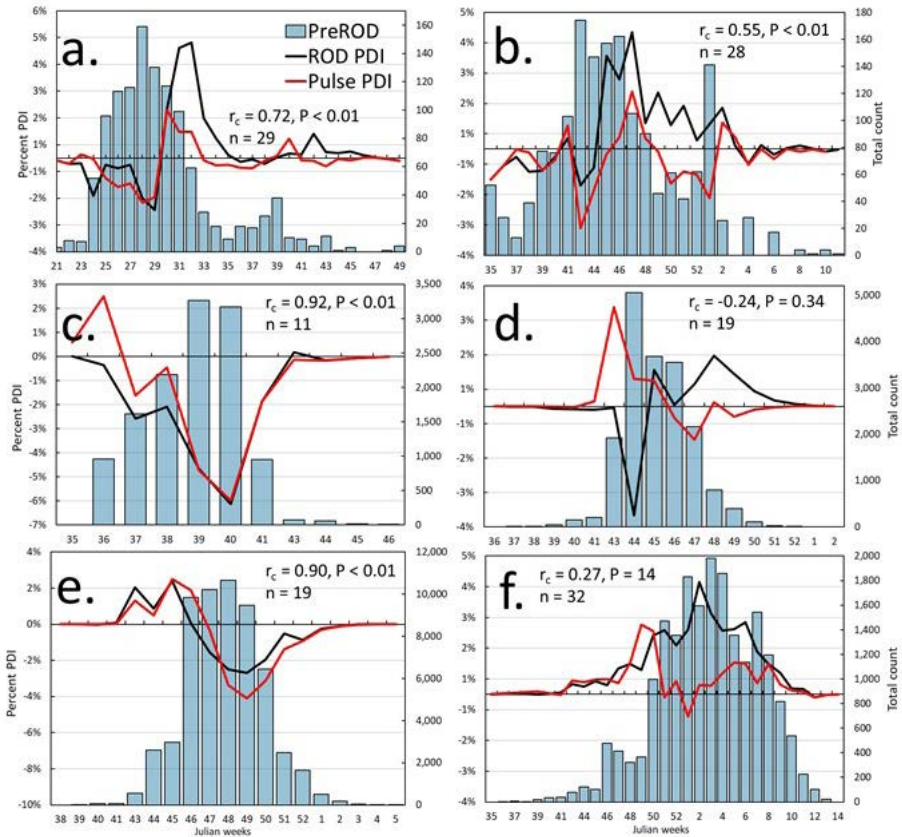
Figure 6. Line graphs showing seasonal fluctuations in total counts (positive + and negative) by Julian week for each species that deviated from the baseline PreROD flow pattern of migration (bar graphs), as a function of the Percent Deviation Index (PDI) in response to ROD and Pulse flows. Lines above or below the dashed black zero line on the y-axis added or subtracted fish from the baseline PreROD flow pattern in timing of migration or run-timing specific to each Julian week (x-axis). Pearson correlations (rc) and sample sizes are between each species-specific ROD and Pulse PDI; a = Brown Trout, b = Klamath Smallscale Sucker, c = spring-run Chinook Salmon, d = fall-run Chinook Salmon, e = Coho Salmon, and f = steelhead

DISCUSSION

Annual fluctuations in estimates of relative abundance

Natural flow regimes reflect inter-annual climate variability, as larger peak flows, longer duration recessions, and higher base-flows occur in wet years, and smaller, shorter, lower flows occur in dry years. Thus, inter-annual variation is a key attribute of functional riverine ecosystems for all life forms (Yarnell et al. 2015). Similarly, duration and magnitude of dry-season low flows are important drivers of lotic ecosystems and most native species adapt to these biologically stressful periods. Whereas, episodic disturbances from climatically driven high-flow events tend to reset successional stages in riverscapes and regulate aquatic food webs by decreasing abundance of predator-resistant primary consumers that support diverse food chains (Ward 1998; Power et al. 2013). Consequently, the magnitude, timing, and duration of natural flow events vary seasonally, depending upon regional climatic conditions, and between years depending upon fluctuation in patterns of global climate. When combined with spatial heterogeneity throughout the channel and floodplain, this inter-annual variability supports diversity in habitat conditions, recruitment, and refugia from competition, thus facilitating subsequent diversity in native species (Naiman et al. 2008; Viers and Rheinheimer 2011; Petts and Gurnell 2013).

In contrast, altered natural streamflow and highly variable flow regimes associated with dams and other anthropogenic activities exhibit reduced flow seasonality and variability (Poff et al. 2007; Carlisle et al. 2011), which generally increase short-term minimum flows while decreasing short-term maximum flows (Magilligan and Nislow 2005). Moreover, highly managed flows may alter the historical disturbance regime, rendering some biotic adaptations to these regimes obsolete while potentially favoring others. Reduced flow variability by dams has been associated with significant losses of native fish species while concurrently creating new niche opportunities often occupied by non-native species with life histories novel to the system or basin (Bunn and Arthington 2002; Olden et al. 2006). In our study, although fluctuations in counts of anadromous and non-anadromous species of fish fluctuated considerably on an annual basis, we show that all taxa decreased significantly and strongly from 2003 to 2017, more so than in any other sequence of years sampled. This sequence of dates coincides with establishment of the Trinity River Restoration Program in 2002 and subsequent "ROD flows" in combination with periodic pulse flow augmentations beginning in 2003. Additionally, since 2001, 38.9% of regional water-years had "dry" or "critically dry" designations, including two periods of three consecutive dry water-years associated with regional drought (Table 1; TRRP 2019). Yet the relative abundance of populations of anadromous and non-anadromous taxa we studied began declining prior to 2007 and continue to do so (Figure 3 and Figure 4).

Albeit some watersheds and associated streams in the upper Trinity River basin suffered from the effects of regional drought over the last several years (CDFW 2019), the mainstem Trinity River and its associated major tributaries did not (Canyon Creek, North Fork Trinity River, South Fork Trinity River, and New River; Figure 1). 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 from this segment of the watershed was less relative to inflow from the major tributaries mostly below the mainstem Trinity River. Additionally, although a recent assessment of the effects of drought on critical habitat for nine
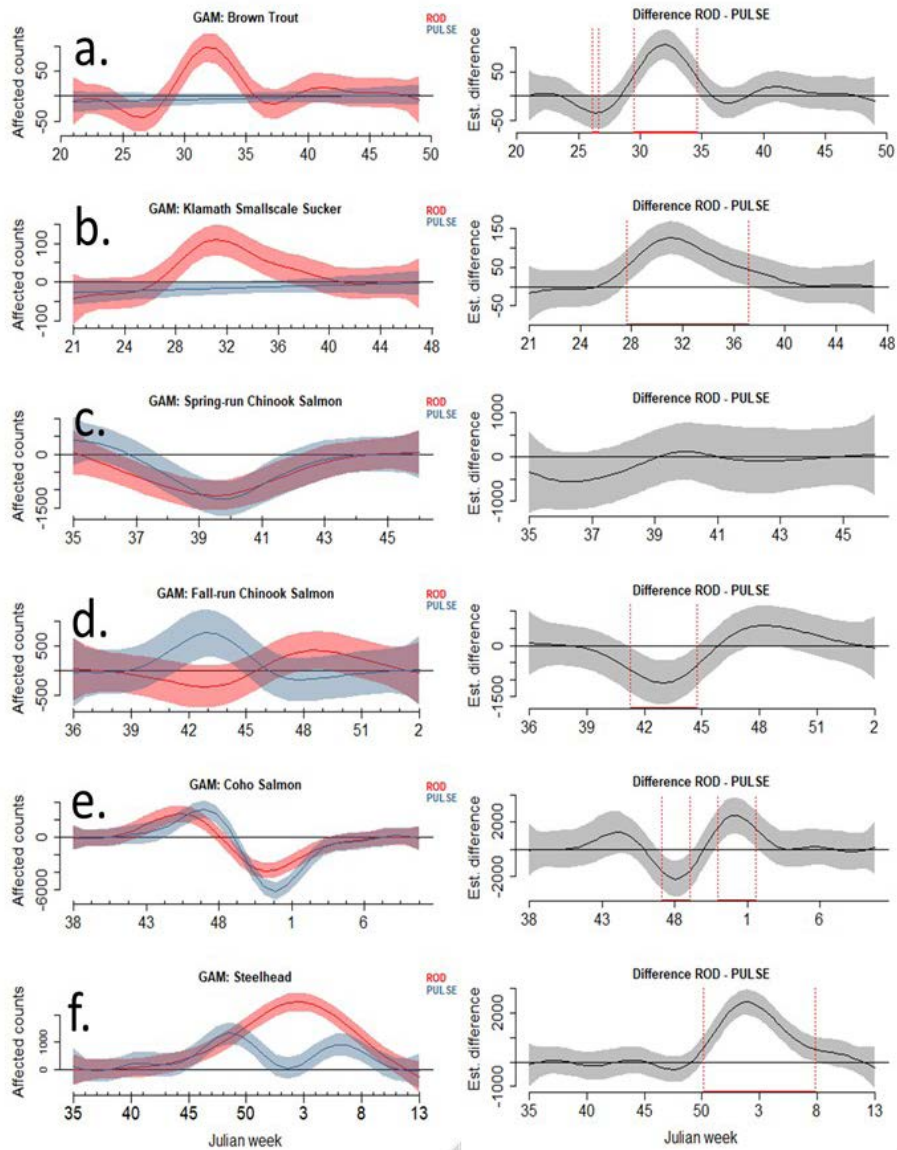
Figure 7. Species-specific GAM plots and their companion differenced plots showing differences between ROD and Pulse flow-types based on the number of counts (positive + negative) that deviated from the baseline PreROD flow-type. Red colored dashed vertical (y-axes) and solid horizontal lines (x-axes) identified Julian weeks that were significantly different (P < 0.05) between GAMs of each species-specific pair of ROD and Pulse flow-types, including approximate 95% point-wise standard error bands for each curve of the factor level. X-axes (independent variable/predictor) labeled with the covariate name. Scale of the y-axis in the difference smooth is the same as the link function (link = "identity") of the model because affected data included both positive and negative counts.

streams in watersheds within the upper Trinity River basin found significant reductions in streamflow, water temperatures remained suitable for survival of Coho Salmon and steelhead in four of the nine streams monitored, including Canyon Creek the northernmost and only major tributary of the mainstem upstream of the North Fork Trinity River (CDFW 2019). Yet this report provided no assessment of 1) the three larger tributaries of the Trinity River below Canyon Creek, 2) the effect on the mainstem Trinity River, or 3) the potential impact of in-basin regional drought on productivity derived from natural-origin spawning for any species of salmonid in the streams studied or in major tributaries of the mainstem Trinity River (CDFW 2019).

Similarly, whereas several environmental documents have determined no significant impact to populations of salmonids in the Trinity River from implementation of ROD flows or Pulse flows (USBR 2016 and references therein), there has been no quantified assessment of the potential effects of altered flow regimes on run-timing or impacts to female reproduction performance, relative to Pre-ROD baseline conditions, for any species of salmonid, whether hatchery- or natural-origin spawning. Moreover, whereas factors responsible for decreasing stocks of anadromous salmonids in both the Trinity and Klamath rivers frequently reference recent ocean conditions and regional drought (Dettinger and Cayan 2014; Diffenbaugh et al. 2015; Mann and Gleick 2015; Michel et al. 2015; Adams et al. 2017), yet to be fully documented is the degree to which these conditions pose threats to inland fisheries, as a function of changing climate (Sullivan and Hileman 2019). Importantly, Lawson et al (2004) and Michel (2018) emphasize that climatic dynamics that led to increases or decreases in precipitation over inland portions of the geographic range of anadromous salmonids may also influenced marine conditions in a manner not captured by marine productivity indices. For example, contrary to the popular belief that "the ocean did it," recent telemetry-based information on hatchery-origin fish suggests that marine mortality may not be the primary source of variability in cohort size, and that out-migrant survival (freshwater seaward migration) associated with flow is likely more important (Michel 2018). The hypothesis that fisheries managers potentially have control over as much as 35% of the annual variability in production of hatchery populations of salmon, thus potentially buffering populations from negative effects of poor marine conditions, provides significant incentive to do a better job of monitoring flow dynamics during out-migration (Michel 2018). However, declines in the quality of the marine food web, which support anadromous salmonid life histories, could not have affected relative abundance in Brown Trout or Klamath Smallscale Suckers, because neither taxon exhibits anadromous migratory behavior, yet both species exhibited concordant patterns of annual decline in relative "synchrony" with all anadromous species described herein.

Seasonal fluctuations in migration in relation to flow type

Our study showed that seasonal variation in Julian week counts of all anadromous and non-anadromous species 1) appeared more attuned to timing of managed flows and water temperature than to flow volume, and 2) all species-specific baseline PreROD flow patterns were affected by managed flow-types in both addition or deletion of counts at some point in their seasonal Julian week migration or runtime schedules since 2003. Additionally, whereas several studies have yet to demonstrate a clear relationship between pulse flows and fish movement (Thorstad and Heggberget 1998; Thorstad et al. 2003; Hasler et al. 2014; Peter-

son et al. 2017), we found significant differences between ROD and Pulse flows in several taxa (Table 3, Figure 8). These findings suggest to us that pulsed flows likely represent an important additional and independent factor affecting the pattern and timing of migration, irrespective of their accompanying ROD flow segment, relative to a "purely" ROD flow hydrograph, which dominated most patterns we described.

Notably, not all taxa exhibited deviation away from their species-specific baseline PreROD flow pattern through reduction in counts early to mid-season and increasing counts late in the season, which resulted in displacement of the actual timing of migration in post-2003 flows to later in migration or run-timing. Instead, several species, including spring-run Chinook Salmon, Coho salmon, and steelhead demonstrated variations on this run-time theme. That both ROD and Pulse flows have altered the pattern and timing of migration, relative to the baseline PreROD flow condition, in both anadromous and non-anadromous species, which exhibit very divergent life histories and in a significant and concordant way, provides evidence in support of our hypothesis of significant difference in timing of local migration or run-timing in response to annually altered flow schedules. The observation that both anadromous and anadromous species respond behaviorally to altered flow regimes, is consistent with the recent suggestion that velocities and higher turnover rates of water associated with the magnitude and duration of additional water provided by pulse flows are likely more important than quality of additional cold water from the Trinity River intended to stimulate fish to move for prevention of potential disease outbreaks in the lower Klamath River (Strange 2010; Peterson et al. 2017). Likewise, Peterson et al. (2017) used a variety of environmental attributes to assess the relative influence of pulsed flow augmentation to explain the magnitude of daily trap-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. As relates to the upper Trinity River, we interpret these observations to be more reflective of the effects of implementing annual ROD flows as opposed to short-term pulsed flow augmentations. However, pulsed augmentations may be very influential in stimulating declining stocks of spring-run Chinook Salmon to migrate from the estuary at the mouth of the Klamath River into the upper Trinity.

Management implications

Although we show that both non-anadromous and anadromous species responded behaviorally to flow augmentation, a test of the hypothesis that managed flow regimes also effect reproductive performance post-2003 in anadromous salmonids necessarily requires information on adult female reproductive performance for both hatchery-spawning and natural-area spawning fish, particularly if ROD and Pulse flow augmentations continue indefinitely. As in iteroparous (multiple reproductive cycle life histories), Brown Tout, Klamath Smallscale Suckers, and steelhead flow-related impacts to multiple brood-year cohorts likely have significant implications for co-occurring semelparous (single reproductive cycle life history) salmonids, particularly those that overlap in run timing, most notably spring- and fall-run Chinook Salmon. Currently, none of the issues discussed above have been part of any long-term effects analysis to protect adult anadromous salmon in the lower Klamath River, even though flows designed to facilitate such protection originate in the upper Trinity

River (USBR 2016). As of 25 July 2016, there was no plan to address these issues for any species of adult salmonid in the upper Trinity River or as part of proposed environmental impact assessments (M. Paasch, personal communication, 2016).

Scientific and policy communities increasingly acknowledge the need for maintaining or restoring natural flow variability to sustain the ecological health of fluvial ecosystems (Rytwinski et al. 2017). Maintaining or "mimicking" features of a natural flow regime is paramount to any successful management strategy designed to conserve freshwater biodiversity (Marchetti and Moyle 2001; Viers and Rheinhemir 2011). To accomplish this goal requires an understanding of the mechanisms that structure riverine communities using a multiscale approach that recognizes the nested physical hierarchy of natural river systems (Fausch et al. 2002; Lowe et al. 2006). Our study suggests that further investigations into the effects of flow management on migration and life history strategies and requirements in sympatric multispecies assemblages of non-anadromous and anadromous species of fish inhabiting the Trinity River are warranted and necessary. For these reasons, we recommend the following management strategies:

1. Because life history differences among taxa are important for assessing responses to flow manipulations (Konrad et al 2011), it is necessary to implement long-term and carefully designed field studies using controls that test species-specific hypotheses in relation to life history requirements potentially influenced by physical elements of the riverine environment. This approach, combined with long-term data sets, modeling, and monitoring of the effects of flow management on lotic environs is essential in identifying the underlying mechanistic links that inform environmental flow standards specific to regional riverscapes (Konrad et al. 2011; Mims and Olden 2012).

2. Develop an integrated management strategy that includes comparative analyses and synthesis of potential impacts of managed flow regimes on timing of migration, population size, age structure, individual performance, composite reproductive output, and recruitment of both hatchery production and in-river spawning in populations of adult anadromous salmonids (Peterson et al. 2017; Rytwinski et al. 2017).

3. Initiate annual comparative monitoring of production in juvenile and adult age classes, annual and seasonal frequency distributions, and migration patterns before, during, and after flow augmentation. This action will help determine if a change in flow regimes acts either as a temporary stimulus or as a retardant to both upstream and downstream movements, and run-timing, particularly as it applies to survival through flow management and other associated beneficial riverine conditions during the out-migration season in populations of hatchery-origin salmonids.

4. Assemble and initiate inspection, coordination, and integration of historical flow related information with covering physical riverine attributes, and hatchery records, procedures, and production mandates with agency flow and operational mandates, in tandem with in-river restoration activities and collection of long-term biological data to provide insight into potential effects of planned management of flow augmentation on all fisheries resources.

5. As part of the overall coverage of the fluvial ecosystem and the fisheries resources supported, we recommend integrating non-anadromous species into monitoring and modeling analyses, as these taxa have historically not been a management priority for the upper Trinity River. Because these resident species are not affected by marine conditions, they potentially are better suited as potential "control" or "indicator" taxa for assessing year-round effects of

managed flows, restoration actions, and variation in other intrinsic environmental co-variates concurrently with studies on commercially valuable anadromous salmonids.

Adoption of such recommendations will allow a better understanding of the potential for managed flows in facilitating conservation of fisheries resources in connected and co-varying segments of regulated river systems (Hasler et al. 2014; Peterson et al. 2017); thus enabling practical flow management based on hypotheses-driven study designs applied to priority issues (Watts et al. 2010; Viers and Rheinhemir 2011). Such actions are an integral part of any coordinated science-based adaptive management program, which was in large measure the original vision of the Record of Decision outlining a plan for restoration of the Trinity River and its populations of fish and wildlife (USBR 2000). Recommendations developed herein are particularly relevant given: 1) fluctuations in influential ocean conditions, 2) climate change and associated regional drought (Rupert et al. 2017a,b), and 3) increased environmental degradation and pollution of watersheds from illegal growing of marijuana throughout the Trinity River basin (Welsh 2011; Kilduff et al. 2015; Murad et al. 2018). Immediate, however, are the social, political, and scientific pressures to 'legitimize' rivers as water users continue to aggressively focus on compromises in water-flow management and policy in California and elsewhere, to meet both human and ecosystem water needs through provisioning of "environmental flows" (Arthington et al. 2006; Arthington et al. 2010; Konrad et al. 2011). Given the growing momentum in recognition of the need for ecologically sustainable water management, lack of scientific information often cited by resource agencies, is no longer a valid excuse for failure to endorse application of such approaches to ensure maintenance of healthy and productive aquatic ecosystems, and sustainability of resident riverine fisheries (Viers and Rheinhemir 2011; Mims and Olden 2013). Inevitably, these issues will become more problematic as climate change predictably progresses in step with the insatiable anthropocentric demand for water (Tockner et al. 2010).

ACKNOWLEDGEMENTS

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Appendix I. Normal quantiles plots and histograms of the frequency distributions catch per unit effort (CPUE) and counts of annual data for all species of fish. Dashed black lines represent 95% confidence limits for the fitted normal quantile plots for each count variable. Relative normality is assumed if all red points fall approximately along the reference solid black line.
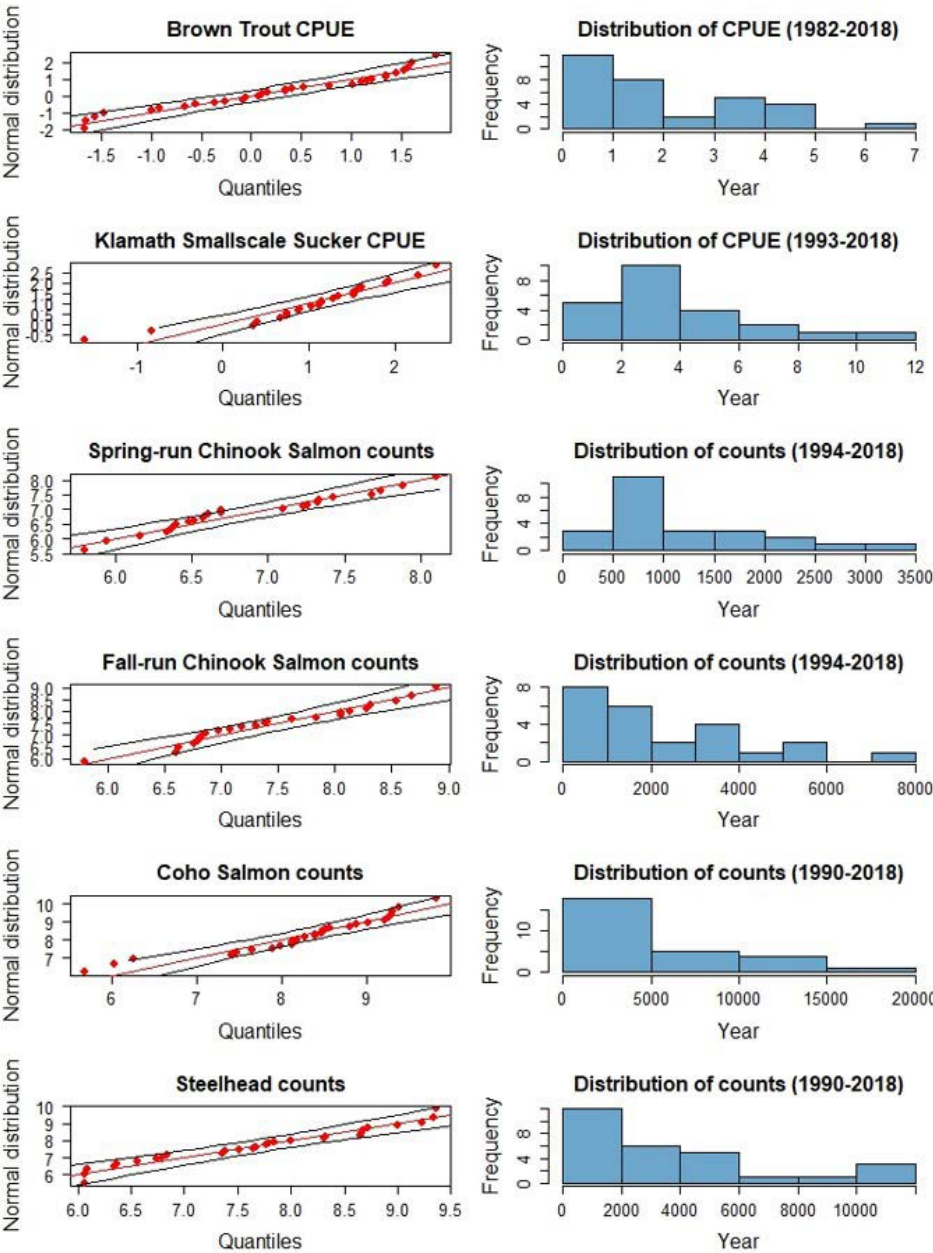
Appendix II. Results of the autocorrelation analyses of residuals derived from generalized linear model (GAM) analyses of annual catch per unit effort (CPUE) and counts of all species of fish, including follow-on Box-Pierce ($\chi 2$) and augmented Dickey-Fuller tests (SDF).

Series: residuals(gam_BT1)
Brown Trout
ADF = 5.7, P = 0.01
χ^2 = 1.3, P = 0.26

Series: residuals(gam_KS1)
Klamath Smallscale Sucker
ADF = 3.5, P = 0.07
χ^2 = 1.3, P = 0.25

Series: residuals(gam_SC1)
Spring-run Chinook Salmon
ADF = 4.7, P = 0.01
χ^2 = 1.6, P = 0.20

Series: residuals(gam_FC1)
Fall-run Chinook Salmon
ADF = 3.5, P = 0.06
χ^2 = 0.24, P = 0.62

Series: residuals(gam_CS1)
Coho Salmon
ADF = 4.3, P = 0.01
χ^2 = 0.1, P = 0.83

Series: residuals(gam_SH1)
Steelhead
ADF = 5.0, P = 0.01
χ^2 = 0.5, P = 0.48