Annual and seasonal variation, relative abundance, and effects of managed flows on timing of migration in Brown Trout (*Salmo trutta*) in the upper Trinity River

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We evaluated annual and seasonal patterns of relative abundance and timing of migration from historic trapping data in non-anadromous Brown Trout (*Salmo trutta*) inhabiting the upper Trinity River, California. Results of our analysis failed to support the hypothesis that the population of Brown Trout in the upper Trinity River has increased and continues to proliferate since 2000. Instead, we hypothesize that the peak in Brown Trout catch per unit effort (CPUE) in 2004, was not an indication of an increase in population size, but rather a secondary potamodromous behavioral response by Brown Trout already in the upper Trinity River system, in response to variation in managed flows and altered environmental conditions that ensued. We also tested the hypothesis of no significant difference in timing of migration in response to annually managed flow regimes. Managed hydrographs associated with the Trinity River Restoration Program (TRRP) and United States Bureau of Reclamation (USBR) were categorized into three flow types: 1) baseline Pre-ROD flows (1982-2002); 2) Record of Decision (ROD) flows (2005-2011, 2017); and 3) pulsed augmentation (Pulse) flows (2003, 2004, 2012-2016). Annual variation in CPUE showed cyclic fluctuations approximately every four to eight years and there was a significant positive relationship between CPUE and year (1982-2017). However, for the sampling period 2003 to 2017, the relationship between CPUE and year was significant and negative, indicating that Brown Trout have declined dramatically in relative abundance since peaking in 2004, especially after 2014. This sequence of dates coincides with establishment of the Trinity River Restoration Program in 2002, and subsequent Record of Decision "ROD flows" and periodic augmentation flows ("Pulse flows") beginning in 2003. Additionally, our results failed to support the hypothesis of no significant difference in timing of migration among different flow types. Instead, annually managed flow regimes appear to have significantly affected timing of migration in Brown Trout. Deviation away from the baseline Pre-ROD flow pattern of seasonal migration occurred through reduction in counts of fish early to mid-season begin-

ning in late May (Julian week 21), followed by an increase in counts late in the season (mid-December, Julian week 49); thus displacing the baseline Pre-ROD flow timing of migration to later in the season. Results of our analysis, together with a review of pertinent literature and available data do not support the suggestion that Brown Trout be actively removed from the upper Trinity River, because of increased population growth since 2000, competitive lifestyle, or negative impact to native juvenile anadromous salmonids, relative to other co-occurring adult piscivorous salmonids and fish-eating terrestrial vertebrates. We make several recommendations for future management actions to help resolve issues related to Brown Trout and other salmonids in the Trinity River.

Key words: annual and seasonal variation, Brown Trout, managed flow regimes, migration, piscivorous lifestyle, potamodromous, suppression of population, Trinity River

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Brown Trout (*Salmo trutta*) are a non-native species of salmonid found in the Trinity River, Klamath Basin of northwestern California. Although capable of developing an anadromous life history form in response to localized food limitation as a population expands (O'Neal and Stanford 2011), there are no definitive tagging studies to suggest that the current population of Brown Trout in the upper Trinity River is anadromous (M. Currier, California Department of Fish and Wildlife [CDFW] Reservoir Biologist, personal communication 2017). This species has coexisted with native anadromous salmonids in the Trinity River for over a century. Brown Trout are territorial, predatory, and potentially compete with co-occurring native anadromous salmonids for food, space, and cover (Glova and Field-Dodgson 1995, L'Abee-Lund et al. 2002). Large adult Brown Trout may predominate in areas of suitable habitat within the mainstem Trinity River. Preliminary analysis of count data suggested that the population of Brown Trout in the upper Trinity River has increased and continues to proliferate since 2000 (CDFW 2014, USBR 2014). This hypothesis, in conjunction with the view that Brown Trout adversely affect populations of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*), steelhead (*Oncorhynchus mykiss*), Klamath River Lamprey (*Entosphenus similus*), and potentially impede recovery of listed Coho Salmon (*Oncorhynchus kisutch*) (NOAA Fisheries 2014), resulted in recommendations to specifically and systematically remove Brown Trout in the upper Trinity River (Alvarez 2017).

At issue is whether: 1) "continued proliferation" of Brown Trout undermines efforts to restore native anadromous fish in the upper Trinity River; 2) release of Brown Trout captured during salmonid monitoring is a breach of Tribal Trust Responsibilities (DOI 1993, TRFES 1999) constituting "take" of listed Coho Salmon; and 3) presence of Brown Trout significantly reduces commercial and sport fishing opportunities for native salmonids. However, the same piscivorous lifestyle is also true for resident steelhead, and Coho Salmon in other river systems (Ruggergone 1989, Ruggergone and Rogers 1992, McConnaughey 1999, TRFES 1999, Naman 2008, YTFP 2008). Moreover, numerous other aquatic and terrestrial piscivorous predators also inhabit the upper Trinity River (TRFES 1999). Further, comprehensive comparative studies that document: 1) competition among anadromous salmonids, and 2) the relative impact and importance of predation on juvenile salmonids by any of a suite of anadromous, aquatic, or terrestrial piscivorous taxa inhabiting the upper Trinity

River are lacking. As such, the long-term benefit to populations of juvenile salmonids, by systematically eliminating adult Brown Trout from the upper Trinity River, is lacking critical information and remains entirely unknown, as is the relative impact to the local economy in the context of both current and future opportunities for recreational angling.

Complicating this issue further is a lack of understanding of the potential effects of variable and intensely managed annual flow regimes, which characterizes the upper Trinity River, on the relative abundance estimates and timing of migration in several species of adult salmonids. For example, effects of seasonal variability in relative abundance of salmonid populations associated with annually managed flow regimes and restoration programs can be considerable (Platts and Nelson 1988, Holtby and Scrivener 1989, Bradford et al. 1997, Ham and Pearsons 2000, Bayley 2002, Hasler et al. 2014, Peterson et al. 2017). Such variability may severely constrain estimates of population size and trends, and interpretations of the effects of variable managed flow and temperature regimes on seasonal patterns of migration, local movements, habitat use, and rates of survival in resident non-anadromous and anadromous fish (Crisp 1993, Clark and Rose 1997, Cunjak et al. 1998).

Because Brown Trout in the Trinity River are non-anadromous and do not rely on ocean conditions for their life history requirements, their annual abundance and seasonal migratory responses to changes in flow patterns affected by managed flow regimes are independent of any oceanic influence, unlike anadromous species. As such, we view Brown Trout as an excellent "control" species for evaluating potential effects of managed hydrological variation within the upper Trinity River, compared to anadromous salmonids.

Our specific objectives were fourfold. First, we re-evaluate relative abundance, annual distribution, timing of seasonal migration, and potential impact of Klamath River Lamprey (*Entosphenus similus*) parasitism on Brown Trout, relative to other sympatric salmonids. Second, we test the hypothesis that the population of Brown Trout in the upper Trinity River has increased since 2000. Third, we test the hypothesis of no significant difference in pattern of timing of migration in relation to annually managed flow regimes (hydrographs). Forth, we use results of our analyses to address: 1) competition among sympatric salmonids inhabiting the upper Trinity River, 2) the potential impact to commercial and sport fishing opportunities, and 3) management recommendations advocating systematic removal of Brown Trout from the Trinity River because of its competitive and piscivorous lifestyle.

Background on history of introduction.—The United States Commission of Fish and Fisheries in the late 1800s imported both "Von Behr" trout from the Black Forest of Germany (stream type *S. trutta*), and "Loch Leven" trout from Scotland (lake type *S. trutta*). Von Behr trout eggs were brought to the New York State Hatchery at Cold Springs Harbor and the United States Fish Commission hatchery at Northville, Michigan in 1882. Loch Leven trout eggs were brought to Cold Springs Harbor Hatchery in 1884 (Dill and Cordone 1997). Although Brown Trout are frequently referred to as "German Brown Trout", Von Behr trout were eventually outcrossed with Loch Leven fish.

The US Fish Commission hatchery at Northville Michigan delivered Loch Leven, Von Behr, and hybrid Brown Trout eggs to Fort Gaston in Hoopa and Sisson Hatchery in Mt. Shasta, California (Adkins 2007). There were two introductions from these hatcheries into the Trinity River, one near the mouth at Fort Gaston and a separate effort closer to the headwaters in Stewart's Fork and the upper Trinity River near Lewiston, California (Adkins 2007). The U.S. Fish Commission conducted the first documented introduction of Brown Trout into the Trinity River in July 1883 (USCFF 1895). To promote recreational angling,

24,856 yearling Brown Trout were released into the tributaries in the lower Trinity River from fish reared at Fort Gaston in Hoopa Valley (Dill and Cordone 1997). Re-introductions (stocking) of Brown Trout to the Trinity River and tributaries occurred annually from 1911 to 1932, peaking at 180,000 Brown Trout stocked in 1925 (Wertz 1979). From 1964 to 1976, California Department of Fish and Game (CDFG) implemented a Brown Trout maintenance program at Trinity River Hatchery (TRH) and propagated Brown Trout from adult returns to TRH. Managers stocked Brown Trout from this maintenance program on a near annual basis at various locations in the Trinity River and below Lewiston Dam. There is a series of annual hatchery reports documenting TRH Brown Trout production and stocking from 1961 to 1968 by Murray (1968) and from 1970 to 1977 by Bedell (1977 and 1979), including references therein. We summarize data from these reports in Appendix I.

In 1969, CDFG released TRH-produced yearling Brown Trout into the lower Klamath River at the township of Klamath Glen. This practice ended in 1976, when 12,600 yearling Brown Trout were released into the Trinity River at TRH. In that same year, 29,500 two-year old Brown Trout (2nd brood year 1975 fish) were released into Trinity Lake (Bedell 1977). However, CDFG discontinued the Brown Trout maintenance program because of low returns, small size, and lack of development and retention of anadromous characteristics in the Trinity River population (Bedell 1979).

In 2001, CDFG began stocking reproductively viable Brown Trout into Trinity Lake but this practice stopped in 2008 (M. Currier, personal communication 2017). Also in 2008, CDFG marked (adipose fin clip) and released 64,750 Brown Trout into Trinity Lake to determine if a portion of these fish survive migration through the turbines at Trinity Dam, immigrate into Lewiston Lake, and escape into the upper Trinity River through Lewiston Dam. Such movement could potentially have provided a continuous source of Brown Trout into the Trinity River, particularly during periods of low water levels in Trinity Lake, in combination with pulsed augmentation flows into the Trinity River. However, although this management action potentially could have artificially augmented annual counts of Brown Trout at Junction City Weir (JCW) between 2001 and 2008, no marked Brown Trout have been recorded in the Trinity River (M. Currier, personal communication 2017).

At the terminal end of anadromy in the upper Trinity River at Lewiston Dam, only three "wild" Brown Trout (all unmarked and not weir-tagged) have been recorded captured in annual TRH adult Salmonid returns since 1978 (one each in 1998, 2005, and 2014). Moreover, information on Brown Trout in the Klamath River appears to be extremely uncommon. For example, historically (1997-2017) there have been no Brown Trout verified by creel censuses conducted by CDFW from the mouth of the Klamath River to Weitchpec (S. Borok, Environmental Scientist, CDFW personal communication 2017). Additionally, 1,618 trap-days resulted in only 39 Brown Trout counted from 1989 to 2017 at the Willow Creek Weir, lower Trinity River (M. Kier, CDFW Environmental Scientist, personal communication 2017).

Methods and Materials

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 2.45 million acre-feet of water (USFWS and HVT 1999). Lewiston Lake, formed by Lewiston Dam, is located 11.8 km downstream of
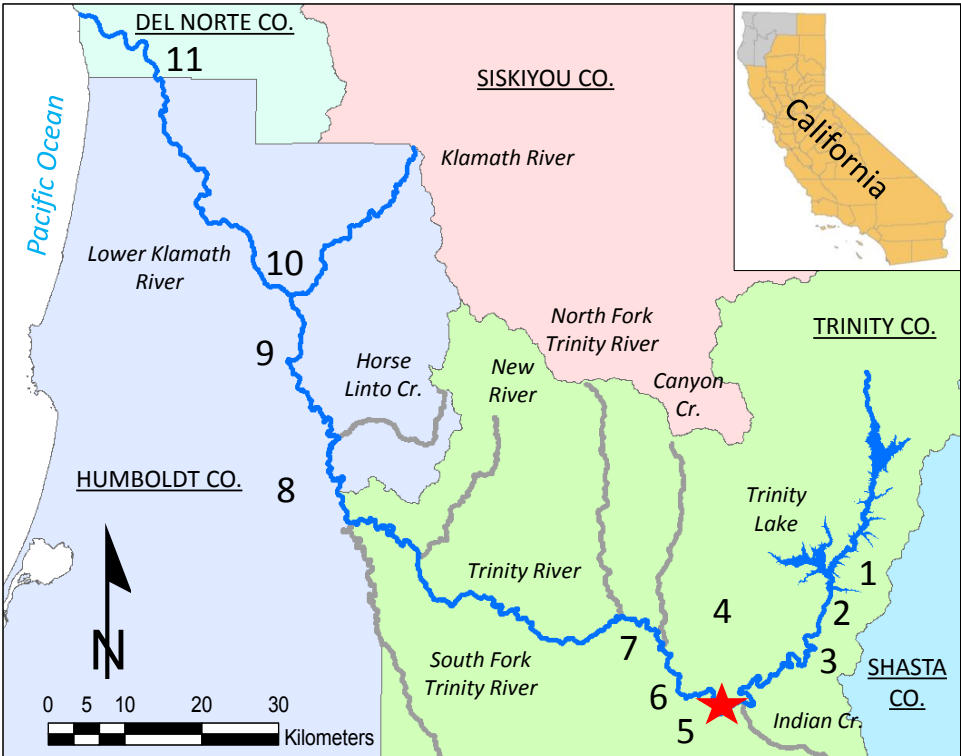
Figure 1.—Map of Lower Klamath River, Klamath River, Trinity River, and major tributaries of the upper Trinity River. Also included various other landmarks, including: 1) Trinity Dam, 2) Lewiston Lake, 3) Lewiston Dam and Trinity River Hatchery, 4) Weaverville, 5) Junction City Weir (red star), 6) Junction City, 7) Pear Tree Gulch, 8) Willow Cr., 9) Fort Gaston/Hoopa, 10) Weitchpec, and 11) Klamath Glen.

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 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 (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. The upper Trinity River is the stretch from the confluence of the North Fork Trinity River to 63.1 km upstream to Lewiston Dam. Trinity River Hatchery (TRH) is located immediately below Lewiston Dam.

Weir sampling.—Data presented herein derive from JCW, which is a Bertoni (Alaskan) style fish-tagging weir located 43.7 km downstream of Lewiston Dam. CDFW has operated JCW on an annual basis since 1978 and in cooperation with the Hoopa Valley Tribe since 1996. JCW functions to mark spring-run Chinook Salmon as part of an annual single mark-recapture estimate for the upper Trinity River above the weir. JCW also traps Coho Salmon, steelhead, Brown Trout, and Klamath Smallscale Sucker (*C. rimiculus*), but these species are considered "by-catch" by CDFW, as the primary target species was spring-run Chinook Salmon. Although annual sampling of Brown Trout began in 1982, lack of funding

and administration mandate prevented data collection in 1983, 1984, 1992, and 1995. Prior to 1996, installation of JCW occurred when spring flows receded in June or July, and the weir was "fished" through December depending upon flow conditions. However, in 1996 a decision was made to truncate annual trapping efforts at the end of September, a procedure that continues to today. There are no trapping efficiency estimates for Brown Trout. Spring-run Chinook Salmon efficiency estimates at JCW vary from 26.6% of the annual run-size in 1992 (n =5,329) to 0.5% in 2012 (n = 35,326). Long-term average trapping efficiency for spring-run Chinook Salmon at JCW was 7.9% of the annual run size estimate. Same-season marked Brown Trout are not common, indicating that multiple captures of individual fish are rare.

Operation of JCW is a passive process, in which the weir is "fished" five days per week (Sunday evening - Friday afternoon). Trap-days start one half hour before sunset and end mid-day the following day, in order to exploit crepuscular behavior of the target species (spring-run Chinook Salmon), and capture both dusk and dawn migrating fish. JCW is open to both boat traffic and passage of migrating fish on a daily basis from mid-day to early evening, and on weekends. Limitations on scheduling are a function of safety, funding, and staffing. The term "fished" refers to blocking river to passage of adult fish except at a small opening at a pair of fyke panels spaced 11.4 cm apart inside a trap box, where the gap is located. The trap box consists of a cage immediately upstream of the weir, with a "V"-shaped opening (fyke) with wide end facing downstream that narrows towards the upstream interior of the trap box, where the gap is located. Upstream migrating fish swim through an 11.4 cm funneled gap in the fyke panels into the trap box, trapping adult fish. Staff check the trap box twice daily, once in the morning and again in the afternoon each trap-day, before opening the 4.9 m wide panel to recreational boat navigation. Unimpeded passage of fish occurs after the second trap check, and on weekends. Beginning in 2005, captured Brown Trout were measured, tagged (serial numbered T-bar [Floy tag]), and all salmonids evaluated for condition (i.e., evidence of predator wounds, gill net scars, and wounds by Klamath River Lamprey, etc.).

Study design.—The Trinity River Restoration Program (TRRP 2018), created by the Record of Decision (ROD) outlined a plan for restoration of the upper 63.1 km (mainstem) of the Trinity River and its fish and wildlife populations (TRFES 1999). The Trinity River Mainstem Fishery Restoration Environmental Impact Statement/Report was the document upon which the ROD was based (USDI 2000). TRRP restoration strategy 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, and volume of restoration flows appear in Appendix II. Information on the intended benefit of each ROD and Pulse flow hydrograph varies on an annual basis depending upon water availability and the particular restoration objective at the time of implementation (TRRP 2018).

To test the hypothesis of no significant difference in the annual pattern of timing of migration associated with managed hydrographs, we designated three flow year-types (henceforth called flow types): 1) baseline Pre-ROD flow (1982-2002), 2) ROD flow (2005-2011, 2017), and 3) Pulse flow (2003, 2004, 2012-2016). Pulsed augmentation flows were designed to cue migration of Chinook Salmon out of the Lower Klamath River to prevent risk of infection due to the ciliate parasite *Ichthyophthirius multifiliis*. Prior to 2003, there

were no annually managed ROD or Pulse flows. Additionally, we note that each Pulse flow event was accompanied by a single ROD flow hydrograph (ROD plus Pulse flows), 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 flows, 2) Tribal Ceremonial Boat Dance flows, and 3) pulsed augmentation flows. Ceremonial Tribal Boat Dance flows occur in odd years just prior to any pulsed flow augmentation. However, because they only amount to 0.6% of the total release into the Trinity River (TRRP 2018), we did not include them in our analysis, even though pulse flows occasionally tier off the trailing ends of ceremonial flows. Shapes of the ascending limbs of the hydrographs were mostly rapid (19/22) with few years in which there were benches (7/22), all of which were associated with managed flows. In contrast, shapes of the descending limbs of the hydrographs were all gradual with numerous benches associated with virtually all managed flows (14/22). Benches in hydrographs included stabilization of water release for approximately one or more 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 were rapid with at least one bench. Spring-summer base flows historically equate to 13 m^3/s.

ROD flows occurred annually from late April to August. Conjoining Pulse flows occurred from August to September. Actual magnitude and duration of ROD and Pulse flows varied in hydrologic characteristics, cubic meters per second (m^3/s), shape of the hydrograph, and duration of the hydrograph depending upon the specific management intent. Average duration of ROD flows was about 89.8 days (range 62.0-112.0 days) from mid-April to early August, and averaged 221.9 m^3/s (range 124.9-328.6 m^3/s) of flow at the top end of the hydrograph. Average duration of Pulse flows was about 28.3 days (range 11.0-40.0 days) from mid-August to late September, and averaged 61.1 m^3/s (range 35.3-97.0 m^3/s) of flow at the top end of the hydrograph. For the same general monthly period, average duration of baseline Pre-ROD flows was about 52.4 days (range 28.0-81.0 days) from late April to late July, and averaged 119.6 m^3/s (range 62.3-192.3 m^3/s) of flow at the top of the hydrograph. Water summary data and a typical flow release diagram (hydrograph) tiered to water-year type are available at the TRRP website (TRRP 2018). We obtained digital and printed hydrographic data from the US Bureau of Reclamation (USBR) Lewiston Water Quality Gauge (LWS) in the upper Trinity River (rkm 178.2 at Lewiston Dam) downloaded from the California Department of Water Resources, California Data Exchange Center (DWR 2017).

Statistical analysis.—We used catch per unit effort (CPUE) in units of adult fish trapped (caught) per trap-day (effort) to estimate relative annual abundance and evaluate "population" trends over time. Brown Trout were considered adults if they were at least 32 centimeters in fork length (one-year-old fish). Although CPUE is not a measure of true abundance, it is an established indicator of relative abundance (Bonar et al. 2009). Estimates of CPUE derive from by-catch data collected at JCW for Brown Trout (1982-2017). A test of the hypothesis that the annual distribution of CPUE was derived from a normally distributed population was rejected (Shapiro-Wilk test (W) = 0.88, P <0.01, n = 32; McDonald 2014). Because annual estimates of CPUE were skewed significantly to the right, they were ranked, visually inspected by use of normalized (0.0, 1.0) quantile-quantile (Q-Q) plots (R Core Team 2013), and found to be normally distributed (W = 0.96, P = 0.23, n = 32). Thus, all subsequent statistical analyses of count data used non-parametric methods (McDonald 2014). Because of small annual sample size, we used the Spearman rank correlation (r_s) to assess evidence

of trends in parasitism (wounding) by Klamath River Lamprey.

We analyzed trends in seasonal 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. The extra day in leap years was included in the ninth week. Wilcoxon signed-rank test, computed from an approximate normal variate (Z) using non-zero data, evaluated the hypothesis that the median difference between pairs of JW was zero among different flows (Hasler et al. 2014). To determine if timing of seasonal migration in ROD and Pulse flows deviated from the baseline Pre-ROD flow, we calculated a Percent Deviation Index (PDI) from total trap counts:

PDI ROD flow = %ROD flow count – %Pre-ROD flow count

PDI Pulse flow = %Pulse flow count – %Pre-ROD flow count

To evaluate the specific timing of migration, we tested the hypothesis that counts of Brown Trout captured during individual JW were not significantly different between Pre-ROD, ROD, or Pulse flow types (years 1982-2017, JW21-JW49). We attempted to standardize sampling effort by including in our analysis only those pairwise comparisons that had a sample size ≥5 for each flow type. Pairwise comparisons of non-zero counts using JW as attributes were then evaluated using the nonparametric Dwass-Steel-Chritchlow-Fligner (*DSCF*) test (Critchlow and Fligner 1991).

We used Robust Regression (ROBREG) analysis to test the hypothesis that the population of Brown Trout in the upper Trinity River has increased and continues to proliferate since 2000 (SYSTAT 2009 and references therein). We conducted all regressions on ranked counts, used the Least Trimmed Squares (LTS) method and FAST-LTS algorithm and the weighted median to compute estimates of regression coefficients in determining adequacy of the model to generate a robust regression estimator (**Rousseeuw and Leroy 1987**, Huber and Ronchetti 2009). This method uses ranks of residuals instead of observed residuals, has few distributional assumptions, and is useful in detecting and deleting outliers in both the *Y*-space and *X*-space prior to performing ordinary least-squares regression on outlier-free data. Robust regression statistics and plots included the least-squares regression correlation coefficient (R) on outlier-free data, adjusted and robust coefficients of determination (R^2) to assess adequacy of the model (Rousseeuw and Van Driessen 2000, Maronna et al. 2006), and 95% confidence intervals surrounding the regression line. We accepted statistical significance at $P \leq 0.05$ (McDonald 2014).

Results

Annual variation in trap counts.—The relationship between: 1) total days the JCW was in place and 2) total days the weir was fished was positive and highly significant (R = 0.98, Robust R^2 = 0.98, Adj. R^2 = 0.96, F = 752.0, P <0.01, $d.f._{1,30}$; Figure 2A). Whereas, the relationship between year and these two variables was both negative and significant from 1982 to 2017 (Figure 2B and 2C). Average days of operation for this period was 72.5 trap days (range = 15 [2012] - 139 [1991], with the largest number of trap days associated with sampling from 1982 to 1994 (average = 104.3 trap days). In contrast, after truncating sampling at the end of September in 1995, the relationship between year and number of days JCW was fished, although negative, was not significant. Thus, except for 2005 when JCW was fished through October, sampling effort was relatively consistent from 1996 to 2017
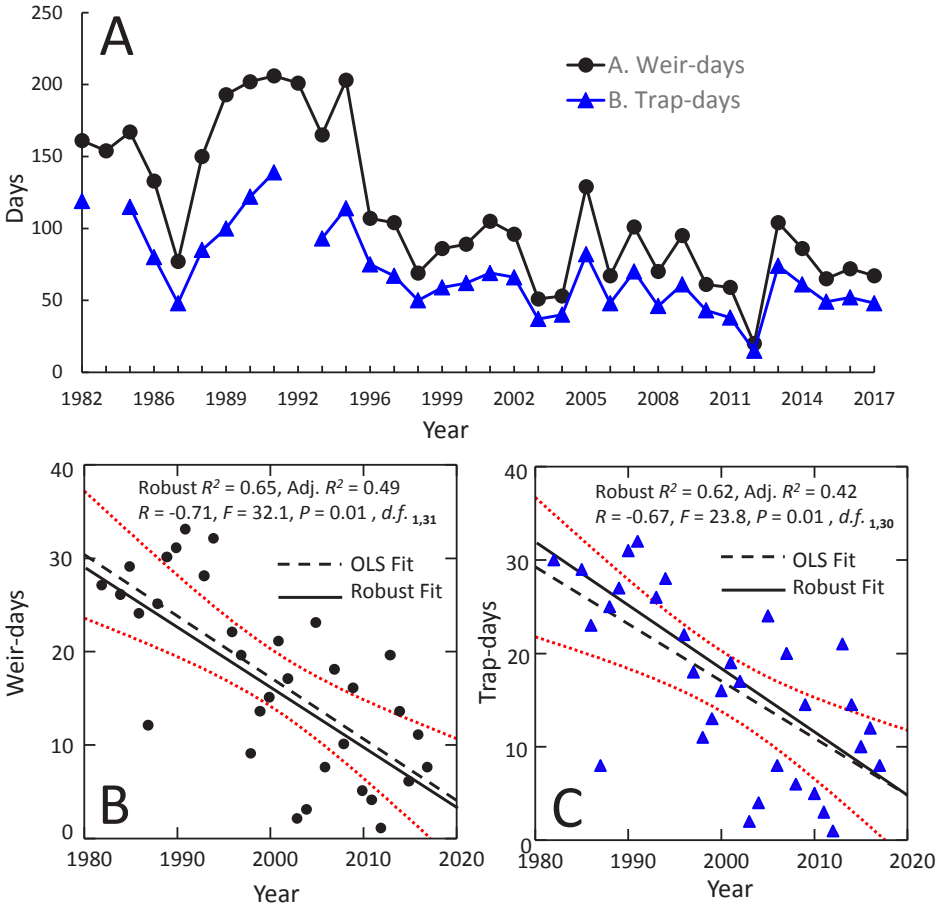
FIGURE 2.—A) Annual variation in total days Junction City Weir was in placed and total days the weir was fished. B) Relationship between total days the weir was in place versus total days weir was fished. OLS Fit = Ordinary Least Squares regression for outlier free data, Robust Fit = Least Trimmed Squares regression, and 95% confidence intervals on regression line.

(average = 55.1 trap days). Beginning in 2003, however, weir operations were temporarily and routinely halted in ROD and Pulse flow years until flows in those years subsided sufficiently to reinstate JCW (average = 50.9 trap days).

   Annual variation in CPUE for Brown Trout exhibited cyclic fluctuations approximately every four to six years (Figure 3A, Table 1). These fluctuations were relatively muted between 1982 and 2002, but CPUE increased beginning in 2003, peaked in 2004, and was followed by a sharp decline through 2017. Regression analysis showed a significant and positive relationship between CPUE and year for the sampling period 1982 to 2017 (Figure 3B). However, for the sampling period 2003 to 2017, the relationship between year and CPUE was significantly negative (Figure 3C), indicating that Brown Trout have declined dramatically in relative abundance since 2003.

   Effects of in-river parasitism by Klamath River Lamprey.—Combined data for all species analyzed herein, showed that the largest number of annual observations of adult fish
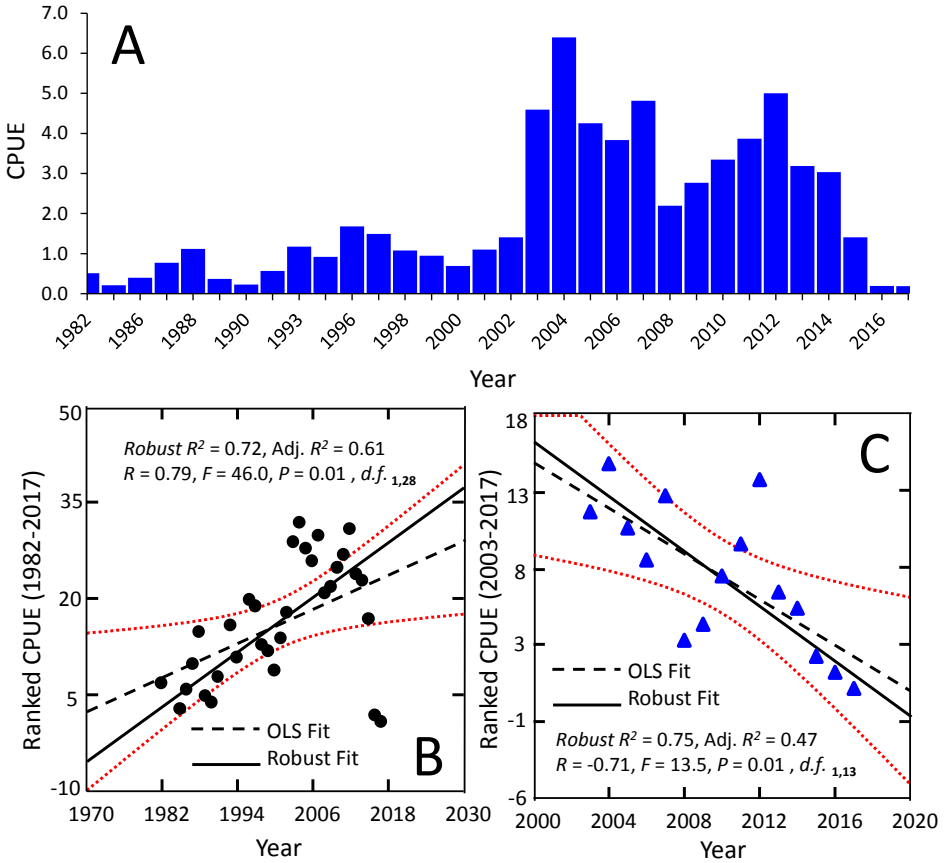
FIGURE 3.—Annual variation in catch per unit effort (CPUE) of total counts of Brown Trout (n = 3,596) from the Junction City Weir for years: A) 1984 to 2017 and B) 2003 to 2017, which included all ROD and Pulse flows over the last 15 years. OLS Fit = Ordinary Least Squares regression for outlier free data, Robust Fit = Least Trimmed Squares regression, and 95% confidence intervals on regression line.

trapped at JCW with fresh circular Klamath River Lamprey wounds (2.0 - 3.0 cm diameter) on their lateral surfaces occurred in 2015, 2016, and 2017 (Table 2). The percentage of all species of live adult fish with fresh lamprey wounds was significant and positively correlated with year (r_s = 0.67, P <0.05, n = 8). This apparent increased trend of visible lamprey wounds on adult fish was significant for Chinook Salmon (r_s = 0.71, P <0.05, n = 8) and Brown Trout (r_s = 0.69, P <0.05, n = 8), but not for steelhead (r_s = 0.61, P > 0.05, n = 8). For Brown Trout and Chinook Salmon the largest percentage of adult fish with lamprey wounds occurred in 2015, 2016, and 2017, and for adult steelhead the largest percentages occurred in 2012, 2015, and 2016. Additionally, we note that adult Coho Salmon generally occur in the upper Trinity River no earlier than late September after wier operations cease for the season, which precludes observations of lamprey wounds for this taxon.

Further, although the percentage of non-weir tagged mortalities that drifted downriver and impinged upon the panels of weir for all adult species combined showed no significantly correlated with year (r_s = -0.14, P >0.05, n = 8); this relationship was significant and positive

TABLE 1.—Annual and Julian week sample data for Brown Trout from 1982 to 2017; and a summary of non-weir tagged mortalities that washed onto the weir from up river. Data for 1983, 1984, 1992, and 1995 are missing (na = no data) because of lack of funding for Junction City Weir; including total days the weir was in place (Weir-days) and total days the weir was fished (Trap-days).

Year	Weir-days	Trap-days	Count	Non-weir tagged mortality	Julian week	Count
1982	161	119	61	na	21	3
1984	154	na	na	na	22	8
1985	167	115	24	na	23	19
1986	133	80	32	na	24	104
1987	77	48	37	na	25	249
1988	150	85	95	na	26	280
1989	193	100	37	na	27	303
1990	202	122	28	na	28	360
1991	206	139	79	na	29	265
1992	201	na	na	na	30	480
1993	165	93	109	na	31	481
1994	203	114	105	na	32	368
1996	107	75	126	0	33	135
1997	104	67	100	0	34	71
1998	69	50	54	0	35	22
1999	86	59	56	0	36	36
2000	89	62	43	0	37	35
2001	105	69	76	0	38	63
2002	96	66	93	0	39	118
2003	51	37	170	0	40	62
2004	53	40	256	0	41	29
2005	129	82	349	4	42	41
2006	67	48	184	1	43	30
2007	101	70	337	na	44	9
2008	70	46	101	0	45	15
2009	95	61	169	0	46	4
2010	61	43	144	0	47	1
2011	59	38	147	0	48	1
2012	20	15	75	0	49	4
2013	104	74	236	5		
2014	86	61	185	9		
2015	65	49	69	48		
2016	72	52	10	4		
2017	67	48	9	1		

for Brown Trout (r_s = -0.88, P <0.01, n = 8). However, the historically elevated counts of non-weir tagged mortalities in adult Brown Trout observed in 2015 were coincident with a tagging study initiated in 2013 (Table 1, CDFW 2014, USBR 2014), and included three individual radio tagged and one anchor-style tagged fish (02 July 2015). As such, the relationship between the percentage of non-weir tagged mortality and wounding by lamprey was significant and positive for Brown Trout (r_s = 0.76, P <0.05, n = 8), but not for any other species ($r_s \leq$ -0.50, P >0.05, n = 8).

Seasonal variation in trap counts.—Relative abundance of Brown Trout fluctuated weekly, beginning in late May (JW21), and continued through mid-December (JW49, Figure 4). Brown Trout occurred most frequently in the upper Trinity River from late June (JW25) through mid-August (JW33), with a primary peak in late July (JW30) and early August (JW31), declining abruptly through early September (JW35), with very few fish lingering in the area through mid-December (JW49). The relationship between percent seasonal trap counts of Brown Trout and JW exhibited a significant negative trend (Figure 4), with the percent count decreasing (negative trend) over the total season but increased in the early part of the season, declining late in the season.

Deviation in timing of migration from baseline flow type.—Total counts for each flow type were: 1) baseline Pre-ROD flow = 1,155; 2) ROD flow = 1,001; and 3) Pulse flow = 1,440 from 1982 to 2017 (n = 3,596; Figure 5A and B). A positive or negative PDI (*Y*-axis) signaled deviation from the baseline Pre-ROD flow pattern in timing of migration, by addition or subtraction of fish along the *X*-axis (JW) in ROD and Pulse flows (Figure 5C and D). Deviation away from the baseline occurred through: 1) reduction in counts of fish at the ascending limb, and 2) addition of fish along the declining central segment and trailing end of migration. A Wilcoxon signed-ranks test showed a significant overall difference between baseline Pre-ROD and ROD flows (Z = 2.0, P = 0.05, n = 29), ROD and Pulse flows (Z = 2.5, P = 0.01, n = 29), but not baseline Pre-ROD and Pulse flows (Z = 0.37, P = 0.71, n = 29).

Further, of 29 JW sampled, 37.9% (n = 11) had sample sizes ≥5 for each flow type (Table 3). Of these, eight showed significant differences among flow groups. For example, 87.5% differed significantly between baseline Pre-ROD and ROD flows; 62.5% differed significantly between baseline Pre-ROD and Pulse flows; but there were no significant differences between ROD and Pulse flows. Total counts of Brown Trout that encompassed all deviations away from the baseline Pre-ROD flow pattern of migration (positive plus negative counts), ranged from 488 fish (ROD flows) to 775 fish (Pulse flows; Table 4). Hence, the combined influence of both ROD and Pulse flow hydrographs post-2003 affected 1,263 Brown Trout relative to the baseline Pre-ROD flow pattern in timing of migration. The relationship between total counts of ROD and Pulse flow-affected fish was both significant and positive (Figure 6). Thus, as the count difference of ROD flows to baseline flows increases so does the count difference of Pulse flows to baseline flows.

Additionally, of all Brown Trout affected by ROD and Pulse flows, 59.1% encompassed JW28 through JW32. As indicated in Appendix II, implementation of ROD flows occurred from early April (JW17) through early August (JW32), whereas Pulse flows occurred from mid-August (JW35) to late September (JW39). Thus, in Brown Trout, alteration in the baseline Pre-ROD flow pattern of migration appeared to be most affected by the descending limbs of ROD flows, especially in wet years with hydrographs that have relatively long descending limbs.

T<small>ABLE</small> 2.—Percent frequency of fish with visible Klamath River Lamprey wounds and number of mortalities counted for Brown Trout and anadromous steelhead and Chinook Salmon, co-occurring in the Trinity River, and trapped at Junction City Weir.

| Year	All species (%)			Chinook Salmon (%)			Steelhead (%)			Brown Trout (%)		
	n	Wounds	Mortality	*n*	Wounds	Mortality	*n*	Wounds	Mortality	*n*	Wounds	Mortality
2010	387	14.2	2.1	222	10.8	3.6	21	0.0	0.0	144	21.5	0.0
2011	449	4.9	5.6	247	2.8	9.7	55	0.0	1.8	147	10.2	0.0
2012	274	11.7	1.8	189	4.8	2.6	10	20.0	0.0	75	28.0	0.0
2013	1155	8.0	1.1	835	4.4	1.0	84	3.6	0.0	236	22.0	2.1
2014	1246	9.0	1.6	1028	7.1	1.1	33	9.1	0.0	185	19.5	4.9
2015	468	35.8	13.9	343	28.9	5.0	56	25.0	0.0	69	78.3	69.6
2016	227	42.9	3.1	154	50.6	1.9	63	19.0	0.0	10	70.0	40.0
2017	269	41.3	1.5	208	48.6	1.4	52	9.6	0.0	9	55.6	11.0
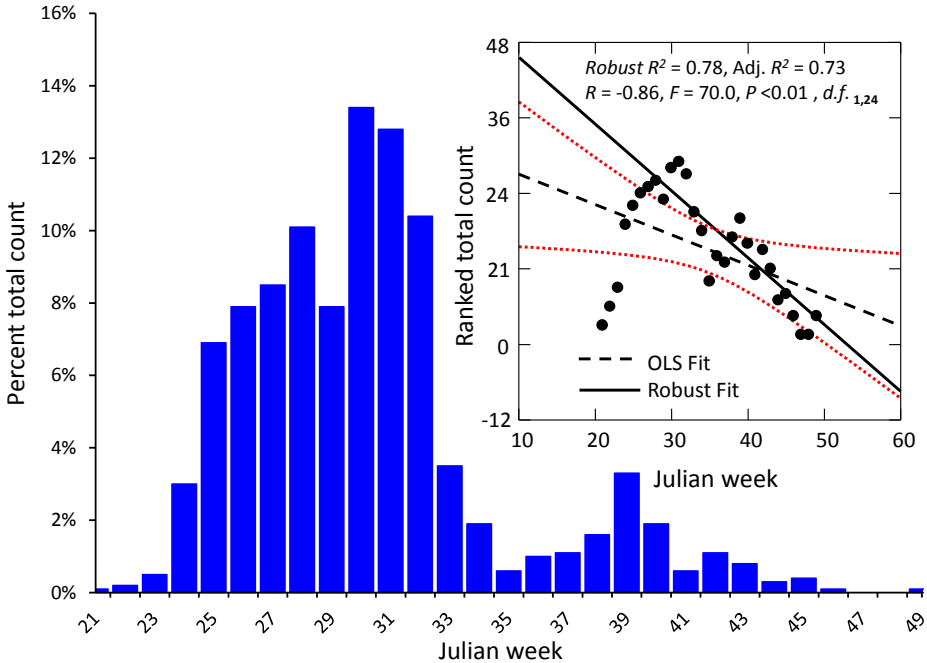
F<small>IGURE</small> 4.—Seasonal variation in percent total counts (*n* = 3,596) by Julian week (JW) of Brown Trout from Junction City Weir (years 1982-2017 and JW21-JW49). OLS Fit = Ordinary Least Squares regression for outlier free data, Robust Fit = Least Trimmed Squares regression, and 95% confidence intervals on regression line.
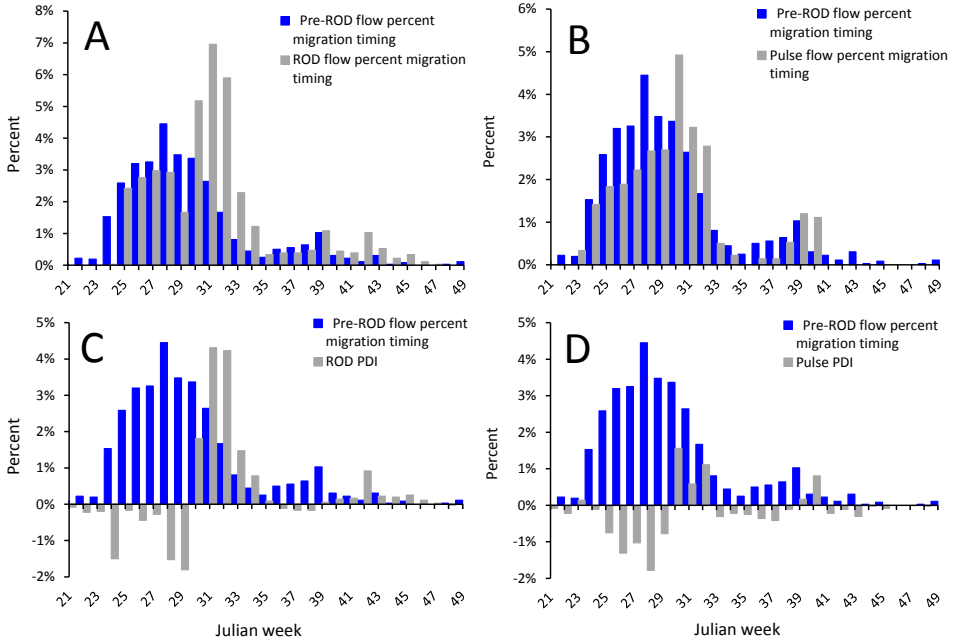
Figure 5.—Percent total count by Julian week (JW) of Brown Trout for baseline Pre-ROD flow (*n* = 1,155) in relation to: A) ROD flow (*n* = 1,001) and B) Pulse flow (*n* = 1,440; years 1982-2017 and JW21-JW49). Percent total count by JW of Brown Trout baseline Pre-ROD flow relative to the Percent Deviation Index (PDI) for: C) ROD and D) Pulse flows.

Discussion

Annual and seasonal variation in estimates of relative abundance.—Although the overall pattern of annual variation in Brown Trout CPUE showed a significant increase in relative abundance from 1982 to 2017, we show that counts of Brown Trout have decreased significantly from 2003 to 2017. These results deviate dramatically from the hypothesis that the population of Brown Trout in the Trinity River has increased in number and continues to proliferate since 2000. This sequence of dates coincides with establishment of the Trinity River Restoration Program in 2002, and subsequent "ROD flows" in combination with periodic Pulse Flows beginning in 2003. As such, we do not interpret any increased "trend" as a reflection of an increase in relative abundance (population size) of Brown Trout in the upper Trinity River in recent times. Not only did the increase in Brown Trout actually start in 2003, but the magnitude of change in CPUE from 1.4 (2002) to 6.4 (2004) is explained more parsimoniously as an extreme migratory response by Brown Trout already in the Trinity River system coincident with managed flow regimes initiated in 2003 by the USBR and TRRP. It is not possible to attribute an increase in "size" of the Brown Trout population based on reproductive output, relative to the baseline Pre-ROD Flow trap count, given the timeline and extent of sampling that occurred between 2002 and 2004. This means that the peak in Brown Trout CPUE at JCW beginning in 2003 was not an indication of an increase in population size, but rather an indication of a secondary behavioral response to managed flows and the altered environmental conditions that ensued.

TABLE 3.—Dwass-Steel-Critchlow-Fligner (*DSCF*) statistical tests for pairwise comparisons of ranked non-zero total counts of Brown Trout by Julian week. Only those non-zero pairwise comparisons that had a sample size ≥5 for each flow type were included in our analysis; and only comparisons that were significant (*P* ≤0.05) were included in the table.

Julian week	Flow group(*i*)	*n*	Flow group(*j*)	*n*	*DSCF* statistic	*P*-value
29	Pre-ROD	15	ROD	5	11.8	0.00
	Pre-ROD	15	Pulse	5	12.6	0.00
30	Pre-ROD	15	ROD	7	6.2	0.00
	Pre-ROD	15	Pulse	6	7.2	0.00
31	Pre-ROD	13	Pulse	9	6.6	0.00
	Pre-ROD	13	Pulse	6	8.3	0.00
32	Pre-ROD	12	Pulse	6	9.1	0.00
	Pre-ROD	12	Pulse	6	12	0.00
33	Pre-ROD	8	Pulse	5	3.3	0.05
34	Pre-ROD	7	ROD	5	5.8	0.00
35	Pre-ROD	9	ROD	7	5.9	0.01
39	Pre-ROD	11	ROD	8	8.1	0.00

Although we focused specifically on the potential effects on a river system subjected to highly managed flow regimes and geomorphological restoration of the mainstem, other covariates besides hydrology and geomorphology affect annual and seasonal patterns of relative abundance and timing of migration in salmonids. For example, factors responsible for decreasing stocks of anadromous salmonids in both Trinity and Klamath rivers reference recent ocean conditions and drought (Dettinger and Cayan 2014, Diffenbaugh et al. 2015, and Mann and Gleick 2015). Since 2001, 38.9% of regional water-years had "dry" or "critically dry" designations, including two periods of three consecutive dry water-years (2007-2009 and 2013-2015.

Moreover, CPUE estimates of Brown Trout relative abundance in 2015, 2016, and 2017 are consistent with estimates of abundance observed pre-2003. This decrease post-2003 also likely reflects in part, the historically unprecedented level of non-weir tagged Brown Trout mortalities observed in 2015 that drifted downriver and impinged upon weir panels beginning in 2015 relative to any other previous year (see Table 1). In our analysis, a potential complicating factor in determining population trends of Brown Trout included documentation of non-weir tagged mortalities, which may be associated with in-river wounding by Klamath River Lamprey that parasitize adult salmonids. Brown Trout in the upper Trinity River spend their entire life cycle in the river, which likely subjects them to a higher risk of in-river Klamath River Lamprey parasitism compared to other sympatric salmonids. Although wounds from Klamath River Lamprey parasitism may contribute to a decline in Brown Trout abundance in the upper Trinity River (Alvarez 2017), we found no evidence to suggest a strong relationship between wounding by Klamath River Lamprey and high

TABLE 4.—Total counts (positive and negative) and total cumulative counts (positive plus negative) by Julian week of Brown Trout affected by ROD and Pulse flows, relative to the pattern in timing of migration representative of the baseline Pre-ROD flow (1982–2017 and JW21-JW49).

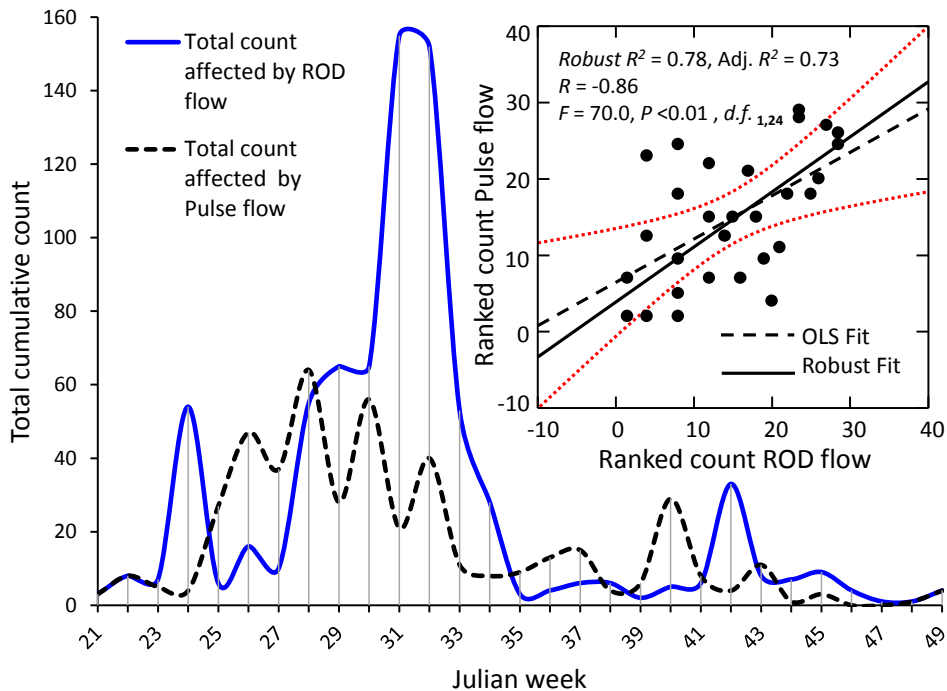| Brood year	Adults	Females spawned	Eggs taken	Date	1st Release group		Date	2nd Release group	
					Number released	Location		Released	Location
1963	34	22	58,100	23-Apr-65	28,500 (UM)	Trinity River Hatchery			
1964	145	64	163,600	18-Apr-66	28,900 (AD)	Trinity River Hatchery			
1965	100	39	109,900	1-Nov-67	35,200 (LV)	Hawkin's Bar			
1966	152	62	75,600	1-Oct-68	41,514 (UM)	Hawkin's Bar			
1967	231	62	158,700	na	na	na			
1968	170	32	76,644	Oct-70/Nov-70	18,967 (RV, LV)	China Slide (LV)	Nov-70	10841 (RV)	Klamath Glen
1969	70	26	53,000	29-Mar-71	23,370 (UM)	Lime Point	Nov-72	2321 (UM)	Trinity River Hatchery
1970	23	2	na	na	na	Trinity River Hatchery			
1971	7	34	140793	17-Apr-73	30,220 (UM)	Trinity River Hatchery			
1972	111	43	73,000	8-Aug-74	23,030 (UM)	Old Lewiston Bridge			
1973	39	26	55,227	14-Apr-75	17,820 (UM)	Old Weir Site			
1974	32	7	13,200	23-Apr-76	73,60 (UM)	Trinity River Hatchery			
1975	24	9	17,272	1-Apr-77	12,600 (AD)	Trinity River Hatchery			
1976	49	28	52,000	5-May-77	29,500 (UM)	Trinity Lake			

FIGURE 6.—Total cumulative count (positive plus negative) and Robust Regression of Brown Trout affected by both ROD and Pulse flows relative to baseline Pre-ROD flow (years 1982-2017 and JW21-JW49). OLS Fit = Ordinary Least Squares regression for outlier free data, Robust Fit = Least Trimmed Squares regression, and 95% confidence intervals on regression line.

levels of mortality in Brown Trout, relative to co-occurring anadromous salmonids. Instead, our data showed that although all three sympatric species of salmonids may exhibit elevated levels of lamprey wounds, mortalities in these species did not increase proportionately. Without additional information demonstrating a significant relationship between wounding by Klamath River Lamprey and subsequent mortality, we are unable to determine if parasitism by Klamath River Lamprey is a major factor contributing to fluctuations in populations of non-anadromous or anadromous species of fish in the upper Trinity River.

Potamodromous migration in Brown Trout.—Anadromy is a life history strategy in which adult fish migrate from saltwater to an upstream body of flowing fresh water (river or stream) to spawn (Moyle 2004). In contrast, a potamodromous life history refers to fish whose migrations occur wholly within fresh water (Maki-Petays et al. 1997). There have been no comprehensive tagging studies of Brown Trout in the Trinity River to suggest that Brown Trout are not anadromous. However, our analysis suggests that Brown Trout in the upper Trinity River are best described as a potamodromous population, born in upstream freshwater habitats, migrating downstream as juveniles (but still in freshwater), and growing into adults before migrating back upstream to spawn. Meyers et al. (1992) found that seasonal movements in Brown Trout may range from 7.2 to 20.1 km during spring and fall,

but were relatively sedentary at other times (Burrell et al. 2000). Rapidly fluctuating flow conditions are critical factors with which spawning Brown Trout below peaking hydroelectric dams must contend. Indeed, Heggenes et al. (2007) found that Brown Trout appeared to move more when high flows continued for longer durations.

From 2012 to 2017, there were five consecutive ROD and Pulse flows in the upper Trinity River. Other studies have hypothesized that varying water flow may induce longer movements when Brown Trout are predisposed to move (e.g. spawning movements). Ovidio et al. (1998) and Young et al. (2010) reported that varying flow, in conjunction with varying temperature, triggered movements to the spawning areas for Brown Trout. Both Clapp and Clark (1990) and Brown et al. (2001) found a correlation between water flow and longer movements in relatively large Brown Trout. In contrast, Bunt et al. (1999) reported no effects of pulsed flows on Brown Trout movements within their study site; however, pulsed flows were regular on a diurnal basis, which may have allowed fish to adapt or acclimate behaviorally to recurrent pulsed flow augmentation.

Our hypothesis that Brown Trout populations are responding behaviorally to managed flow regimes is consistent with the recent suggestion that the magnitude and duration of flows are more important than quality of additional pulsed cold water intended to stimulate fish to move for prevention of disease (Strange 2010, USBR 2016). For example, we show that timing of migration in the baseline Pre-ROD Flow of Brown Trout from 1994 to 2017 has changed in response to both ROD and Pulse flows, both separately and in combination, since 2003. If variation in Brown Trout CPUE is a behavioral response to ROD and Pulse flows, this likely implies that these flows enable Brown Trout to occupy downriver habitats for a longer period relative to baseline conditions. Potentially well beyond the duration that juvenile salmon and steelhead out-migrate. Salmon fry typically emerge from the gravel around mid-February and out-migrate from March through June.

Additionally, ROD flows in conjunction with Pulse flows may facilitate prolonged opportunities for feeding on out-migrating juvenile salmonids. This condition would constitute "prey switching" by Brown Trout as a function of frequency-dependent predation associated with release of approximately 3- to 5-million fingerlings annually by the TRH (Larry Glenn, CDFW TRH Manager, personal communication 2016). Further, anecdotal information from local anglers suggest that Brown Trout follow spawning Klamath Smallscale Suckers to feed on sucker roe during the early summer in the upper Trinity River. Empirical evidence does suggest that Klamath Smallscale Suckers do spawn in the early summer in the upper Trinity River as exemplified by capture of gravid female suckers on June 30, 2009 (JW26) at JCW.

Seasonal variation in migration in relation to flow type.—Seasonal variation in trap counts of Brown Trout showed significant differences in the timing of migration between baseline Pre-ROD, ROD, and Pulse flows. There also was a significant difference between ROD and Pulse flows, suggesting that pulsed augmentation flows may represent an important additional and independent factor affecting the timing of migration, relative to a ROD Flow hydrograph. Deviation away from the baseline Pre-ROD migration pattern occurred through reduction in counts of fish early to mid-season and an increase in counts late in the season, which displaced the actual timing of migration in post-2003 flows to later in the season. That both ROD and Pulse flows have altered the timing of migration, relative to the baseline Pre-ROD condition, fails to support the hypothesis of no significant difference in the timing of migration of Brown Trout in relation to annually managed flow regimes.

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 observed at a weir on 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 flow hydrographs as opposed to short-term pulsed flow augmentations. The effects of managed flow on the timing of adult migration clearly needs further investigation in relation to the potential measured impacts of flow management, as well as other physical and biological covariates, prior to implementing any actions that actively suppress adult Brown Trout in the upper Trinity River.

Although we show that Brown Trout responded behaviorally on an annual and seasonal basis to flow augmentation, we lack reproductive data for Brown Trout to test an additional hypothesis that managed flow regimes likely affect multiple brood-year cycles post-2003 if ROD and Pulse flows continue. Flow-related impacts to multiple brood-year cycles likely have even greater implications for co-occurring anadromous species of salmonids inhabiting the Trinity River, particularly those that overlap in the pattern of run-timing, most notably spring-run and fall-run Chinook Salmon. Currently these issues have not been part of the 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 salmonid in the upper Trinity River or as part of any proposed environmental impact assessment (Mary Paasch, USBR, personal communication 25 July 2016).

How viable is the competition scenario?—Brown Trout predation on native populations of salmonids and use of suitable habitat within the upper Trinity River, has resulted in criticism that there is significant competition between Brown Trout and native anadromous salmonids for limited food, space, and cover (McHugh and Budy 2006, Naman 2008, Waters 1983, Wang and White 1994, Alvarez 2017). However, documenting interspecific competition in nature is equivocal at best and only potentially possible where the combined demand for a resource is in excess of the supply (Larson and Moore 1985, Fausch 1988, Lohr and West 1992, Brewer 1994, Meffe and Carroll 1994, Blanchet et al. 2007). Additionally, documenting competition is particularly problematic in a large riverine system continuously subjected to variation in hydrology, temperature of water, and in-river restoration associated with floodplain reconstruction.

Several studies show that adult steelhead and Coho Salmon consume hatchery and naturally produced salmonid fry or smolts (Ruggergone 1989, Ruggergone and Rogers 1992, McConnaughey 1999, Pearsons and Fritts 1999, Naman and Sharpe 2012). Naman (2008) stated that release of large numbers of hatchery steelhead from the TRH could result in substantial counts of Chinook Salmon and Coho Salmon fry being consumed even with relatively low predation rates (i.e., 25,000 fry per day equating to approximately 9.0% of all Chinook Salmon and Coho Salmon fry produced). Studies in other river systems concluded that Brown Trout were superior competitors to sympatric Brook Trout (*Salvelinus fontinalis,* Fausch and White 1981, Blanchet et al. 2007, Korsu et al. 2010). Whereas, several investigations suggest that co-occurring piscivorous species were a superior pairwise competitor relative to Brown Trout (Fausch and White 1986, Magoulick and Wilzbach 1998, Strange

and Habera 1998). Additionally, McKenna et al. (2013) found evidence for a decline of Brook Trout in the presence of Brown Trout across many watersheds. Yet a model of the relationship between Brook Trout and Brown Trout abundance explained less than 1% of the variation documented; and ordination showed extensive overlap in habitat used by these two taxa, with only small components of the "hypervolume" (multidimensional space) being distinctive (McKenna et al. 2013).

The relative importance of competition and predation also changes with life stage and seasonal availability of different prey items (Jonsson et al. 1999, L'abee-Lund et al. 2002, Browne and Rasmussen 2009). In controlled laboratory stream experiments, Coho Salmon dominated Brook Trout and Brown Trout of equal size, and Brook Trout dominated equal-size Brown Trout. However, when released from competition, subordinate species shifted to positions that were more resource profitable (Fausch and White 1986). Further, laboratory growth rates of Coho Salmon equaled rates measured in tributaries, whereas both Brook Trout and Brown Trout grew more slowly in the laboratory than in the field as a result of intraspecific competition due to lack of cover affording visual isolation (Fausch and White 1986). These results suggest that larger size and competitive superiority of Coho Salmon give them an advantage over juvenile Brook Trout and Brown Trout in tributaries when resources are limiting.

Based on recent dietary and bioenergetics analyses, Alvarez (2017) concluded that predation by Brown Trout poses a potential impediment to recovery of native salmonids in the Trinity River. However, the comparative impact of predation by co-occurring anadromous salmonids, as well as terrestrial *piscivorous* predators, on juvenile salmonids in the Trinity River is unknown relative to Brown Trout. Without comparative and simultaneous equal sampling effort, co-occurring species of adult salmonids, individually or in combination, could be a far bigger problem that Brown Trout, in relation to the overall impacts to survival of juvenile fish. Therefore, we maintain that, without such comparative information on both aquatic and terrestrial fish predators, it is premature to advocate or implement any comprehensive management strategy that would systematically remove Brown Trout from the Trinity River.

Economic impact of the Trinity River Brown Trout sport fishery.—Flow regimes managed annually in combination with massive programs of habitat restoration in the upper Trinity River have contributed to a substantial recreational fishery for Brown Trout, particularly among fly anglers. This industry brings intrinsic value and economic stimulus to the local community. The Trinity River Brown Trout fishery is unique in that, unlike fisheries in other regions of California, and on the West Coast, the Trinity River offers an opportunity to catch both trophy steelhead and Brown Trout. Commercial sport fishing guides operate under special recreation permits issued by the US Bureau of Land Management, which issue 100 guide permits for the Trinity River on a first-come, first-serve basis. Commercial fishing guides charge upward of $450 per day to fish steelhead and Brown Trout on the upper Trinity River. They typically book clients 4 days per week for 15 weeks (October-January), yielding an estimated $27,000 generated per guide annually (Bill Dickens, former President of the Trinity River Guides Association, personal communication 2017). If half of the commercial fly-fishing guides book clients at this rate, the conservative estimated income generated from commercial guide fees is approximately $1,350,000 annually, which does not include revenues benefitting local hotels, restaurants, businesses, and the community as a whole through tax-generated revenues. In theory, any financial loss from a managed

fishery that seeks to remove Brown Trout could potentially benefit by economic opportunities derived from increased numbers of native salmonids. However, the validity of this premise remains untested in practice for the upper Trinity River.

Management recommendations.—Several factors are important in determining whether programmatic removal of Brown Trout from the Trinity River is necessary and has the potential to be successful. First, is the consideration of whether removal of Brown Trout is required for enhancing populations of target species. Fetherman et al. (2015) found that Brown Trout removal did not dramatically affect survival or emigration from the study site of sympatric salmonids. Second, it is important to consider whether removal will be successful after one removal effort, or are multiple removal efforts needed to overcome biotic resistance. A single removal of 66% of the Brown Trout population in the Au Sable River in Michigan did not result in population or size at age increases within sympatric Brook Trout populations (Shetter and Alexander 1970). Third, focus should be placed on whether environmental resistance factors, such as temperature, flow, and abiotic resources, may prevent successful removal (Moyle and Light 1996). Williams et al. (2009) showed that lower flows resulted in higher summer water temperatures and lower dissolved oxygen levels; both variables directly affect salmonid survival (Hicks et al. 1991, Fetherman et al. 2015). Fourth, the logistical and economic constraints of conducting large-scale removals in large river systems are substantially unattractive as a viable management option.

For example, although nearly $4.4 million was spent to remove 1.5 million nonnative predatory fish from the Colorado River, 86% of published reports (as of 2005) suggested that native species do not benefit from removal efforts (Mueller 2005). Fetherman et al. (2015) also found that Brown Trout removal had only a short-term positive benefit on Rainbow Trout (*O. mykiss*). However, the overall benefit of removal was equivocal, which led these authors to conclude that removal of adult Brown Trout was not a viable management option to pursue in future conservation efforts of Rainbow Trout, and certainly not in perpetuity. As such, resource managers and policy makers must weigh the logistical constraints, economic costs, and achievable measures of success associated with removal efforts against benefit(s) of the action. This is the only approach by which a resource agency responsible for the stewardship of fish and wildlife, can reasonably determine whether removal of adult Brown Trout from a large hydrologically influenced, temperature and water variable, and habitat managed riverine system is a viable long-term management option, pursuant to future species, conservation, and economic needs.

Facilitating completion of the adaptive management loop is often disconnected from reality by the politics of resource management (Murphy and Weiland 2014). Attributes of effective and comprehensive species-focused management for the upper Trinity River must rely upon implementation of the best available science, which includes relevant aspects of species life history requirements (TRFES 1999, Sullivan et al. 2006). CDFW does not currently have a management policy that mandates systematic removal of Brown Trout captured through any sampling effort or caught by anglers. We believe that advocating destruction of captured Brown Trout and development of recommendations for suppression to population levels that do not "significantly" impede the Endangered Species Act (ESA), Tribal-trust species recovery goals and objectives (Alvarez 2017), or programmatic restoration efforts within the upper Trinity River are premature, and the possible outcomes of such actions are likely not knowable. Our view is particularly relevant given the lack of: 1) information on comparative predatory impacts of other fish and terrestrial species on juvenile salmonid

survival, 2) a thorough economic analysis of the long-term consequences of any proposed management actions, and 3) an analysis of the relative impact to the local commercial sport fishing industry focused on the upper Trinity River.

Instead, we maintain that progressive actions derive from *a priori* assessment of the: 1) comparative impacts of managed flow regimes on timing of migration in adult Brown Trout, as well as anadromous salmonids (Peterson et al. 2017); 2) population size and age structure of sympatric co-occurring salmonids; and, 3) metric-driven prey-base and dietary requirements of co-occurring riverine salmonid communities. We also suggest that studies be implemented that focus on age-specific habitat use within both aquatic and terrestrial piscivorous communities inhabiting the upper Trinity River, in conjunction with experimental and in-river studies focused on specific species; including non-salmonid fish taxa. Such actions would allow a better understanding of the potential for managed flows in facilitating conservation in all connected co-varying segments of this highly regulated river system (Hasler et al. 2014, Peterson et al. 2017), which constitute essential and integral elements of any coordinated science-based adaptive management program.

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APPENDIX I.—History of annual Trinity River Hatchery spawning and juvenile release dates for Brown Trout in the upper Trinity River; na = no data, blank = not applicable, UM = unmarked release, AD = adipose fin clipped release, LV = left ventral fin clipped release, RV= right ventral fin clipped release.

Brood year	Adults	Females spawned	Eggs taken	Date	Number released	Location	Date	Released	Location
					1st Release group		2nd Release group		
1963	34	22	58,100	23-Apr-65	28,500 (UM)	Trinity River Hatchery			
1964	145	64	163,600	18-Apr-66	28,900 (AD)	Trinity River Hatchery			
1965	100	39	109,900	1-Nov-67	35,200 (LV)	Hawkin's Bar			
1966	152	62	75,600	1-Oct-68	41,514 (UM)	Hawkin's Bar			
1967	231	62	158,700	na	na	na			
1968	170	32	76,644	Oct-70/Nov-70	18,967 (RV, LV)	China Slide (LV)	Nov-70	10841 (RV)	Klamath Glen
1969	70	26	53,000	29-Mar-71	23,370 (UM)	Lime Point	Nov-72	2321 (UM)	Trinity River Hatchery
1970	23	2	na	na	na	Trinity River Hatchery			
1971	7	34	140793	17-Apr-73	30,220 (UM)	Trinity River Hatchery			
1972	111	43	73,000	8-Aug-74	23,030 (UM)	Old Lewiston Bridge			
1973	39	26	55,227	14-Apr-75	17,820 (UM)	Old Weir Site			
1974	32	7	13,200	23-Apr-76	73,60 (UM)	Trinity River Hatchery			
1975	24	9	17,272	1-Apr-77	12,600 (AD)	Trinity River Hatchery			
1976	49	28	52,000	5-May-77	29,500 (UM)	Trinity Lake			

Appendix II.—Annual attributes of ascending and descending limbs of hydrographs that characterized baseline Pre-ROD, ROD, and Pulse flows for the years (1995-2000 and 2002-2017). Rate of flow measured in cubic meters per second (m³/s) and flow release in hector meters. For each hydrograph, a bench indicated a temporary holding steady of flow release volume and flattening of the hydrograph. 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, 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 California Department of Water Resources, California Data Exchange Center website for the time-period encompassing all 3-flow types.

Year	Water Year	Flow	Low release magnitude (m³/s)	Shape ascending	Ascending and descending limbs of hydrograph								Pulse flow ascending-descending limbs of hydrograph					
					Peak release magnitude (m³/s)	Restoration release (hector m)	Shape descending	Low release magnitude (m³/s)	Date and duration flow to base-flow	Total days	Low (m³/s)	Shape ascending	Peak release magnitude (m³/s)	Pulse restoration release (hector m)	Shape descending	Low release magnitude (m³/s)	Date and duration flow to base-flow	Total days
1995	na	Pre-ROD	14	R	131	na	G	27	25 Apr-22 May	28								
1996	na	Pre-ROD	9	R	144	na	G, 1B	14	10 May-9 Jun	31								
1997	na	Pre-ROD	10	R	62	na	G, 3B	13	2 May-2 Jul	62								
1998	na	Pre-ROD	47	R	192	na	G	13	24 May-27 Jul	65								
1999	na	Pre-ROD	15	G	71	na	G	13	8 May-18 Jul	72								
2000	na	Pre-ROD	9	R	66	na	G	13	8 May-27 Jul	81								
2002	normal	Pre-ROD	9	R	171	59,540	G	13	27 Apr-25 Jun	28								
2003	wet	Pulse	9	R	74	55,272	G, 2B	12	29 Apr-22 Jul	85	13	R	51	4,194	G	12	23 Aug-18 Sep	27
2004	wet	Pulse	9	R	176	80,300	G, 4B	12	4 May-22 Jul	80	16	R	48	4,465	G	14	21 Aug-14 Sep	25
2005	wet	ROD	8	R, 2 B	197	79,880	G, 1B	13	27 Apr-22 Jul	87								
2006	extra wet	ROD	8	G, 5B	286	99,900	G, 2B	13	16 Apr-22 Jul	98								
2007	dry	ROD	8	R	135	55,963	G	13	25 Apr-25 Jun	62								
2008	dry	ROD	9	R, 1B	183	80,016	G, 3B	20	22 Apr-15 Jul	85								
2009	dry	ROD	8	R	125	54,952	G, 4B	12	24 Apr-6 Jul	74								
2010	wet	ROD	9	R	194	81,003	G, 3B	12	22 Apr-2 Aug	102								
2011	wet	ROD	7	R, 2B	329	89,033	G, 2B	13	26 Apr-1 Aug	98								
2012	normal	Pulse	9	R, 2B	172	79,819	G, 4B	13	4 Apr-26 Jul	114	13	R, 1B	39	4,811	R, 1B	13	12 Aug-20 Sep	40
2013	dry	Pulse	8	R, 1B	125	55,741	G, 2B	13	13 Apr-25 Jun	74	13	R	74	2,294	R, 1B	13	24 Aug-20 Sep	28
2014	critically dry	Pulse	9	R, 1B	97	45,701	G, 1B	13	21 Apr-26 Jun	67	12	R, 1B	97	7,993	R, 1B	13	15-25 Sep	11
2015	dry	Pulse	9	R	241	55,593	G, 3B	13	21 Apr-1 Jul	72	19	R, 1B	83	5,908	R, 1B	13	20 Aug-21 Sep	31
2016	wet	Pulse	9	R, 2P	283	87,429	G	13	20 Apr-2 Aug	105	14	R, 1B	35	4,835	R, 2B	13	24 Aug-28 Sep	36
2017	extra wet	ROD	9	R, 2P	326	101,536	G	13	22 Apr-11 Aug	112								