Hatchery practices may result in replacement of wild salmonids: adult trends in the Klamath basin, California

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Abstract Appraisal of hatchery-related effects on Pacific salmonids (*Oncorhynchus* spp.) is a necessary component of species conservation. For example, hatchery supplementation can influence species viability by changing genetic, phenotypic and life-history diversity. We analyzed time series data for seven salmonid taxa from the Klamath River basin, California, to investigate trajectories of wild and hatchery adult populations. Linear regression coupled with randomized permutations ($n=99,999$), two- tailed t tests, and Bayesian change point analysis were used to detect trends over time. Cross correlation was also used to evaluate relationships between wild and hatchery populations. The taxa of interest were spring, fall, and late-fall Chinook Salmon (*O. tshawytscha*); Coho Salmon (*O. kisutch*); Coastal Cutthroat Trout (*O. clarki clarki*); and summer and hybrid Steelhead Trout (*O. mykiss*). Significant decreases were detected for summer and hybrid Steelhead Trout. The proportion of wild fall Chinook has also significantly decreased concurrently with increases in hatchery returns. In comparison, returns of most Chinook and coho runs to the hatcheries, and fall Chinook strays to wild spawning areas from Iron Gate Hatchery have significantly increased since the 1970s. Increases were also detected for wild late-fall Chinook and spring Chinook adults. However, both of these were significantly correlated with Chinook Salmon returns to Trinity River Hatchery, suggesting augmentation by hatchery strays. Changes in abundances appeared related to changing ocean habitat conditions and hatchery practices. Our results suggest that anadromous salmonid populations in the Klamath River basin are becoming increasingly dependent on hatchery propagation, a pattern that can threaten population persistence.

Keywords Hatchery effects · Chinook Salmon · Coho Salmon · Steelhead trout · Salmon conservation · Bayesian change point analysis

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Introduction

Persistence of wild fish populations can be significantly affected by management operations, including captive breeding in hatcheries. Captive breeding of Pacific salmonids (*Oncorhynchus* spp.) can augment commercial fisheries and mitigate loss of salmonid production when fresh water habitats become inaccessible or degraded (Lichatowich 1999; Brannon et al. 2004). In declining populations where native broodstock is used, hatchery fish may increase population sizes so that threat of

inbreeding and loss of genetic diversity are minimized (Eldridge and Killebrew 2008; McClure et al. 2008; Van Doornik et al. 2010). In systems where habitat is in good condition and few threats are present, captive breeding can also enhance reestablishment of dwindling populations (Carmona-Catot et al. 2012). Large-scale hatchery supplementation, however, can result in detrimental effects to naturally spawning populations (Bisson et al. 2002; Buhle et al. 2009; Kostow 2009). Consequently, resource managers must evaluate the impact of hatchery operations when making decisions about wild species conservation.

Hatchery-produced salmonids can differ from wild conspecifics in phenotype (Hjort and Schreck 1982; Kostow 2004; Knudsen et al. 2006), fitness (Reisenbichler and Rubin 1999; Araki et al. 2008), reproductive success (Berejikian et al. 2001; McLean et al. 2003; Araki et al. 2007), physiology (Brauner et al. 1994; Shrimpton et al. 1994; Chittenden et al. 2008), and behavior (Chittenden et al. 2010; Dittman et al. 2010; Melnychuk et al. 2010). Consequently, natural spawning populations that interbreed extensively with hatchery strays may become maladapted to conditions in the wild (Kostow et al. 2003; Tymchuk et al. 2007; Araki et al. 2009). Maladaptation of wild populations coupled with ecological and behavioral interactions with hatchery fish may hinder recovery of imperiled salmonid species (Hilborn 1992; NMFS 2010) by increasing competition (Heard 1998; Levin et al. 2001; Kaeriyama 2004), predation (Nickelson 2003), and/or fishing pressure (Hard et al. 2008). Wild populations are increasingly being replaced by their hatchery-reared counterparts or by hybrids of wild-hatchery descent (Noakes et al. 2000; Sweeting et al. 2003; Zaporozhets and Zaporozhets 2004). Subsequent generations of wild populations become more vulnerable to extirpation and extinction as a result (Myers et al. 1998; Levin et al. 2001; Moore et al. 2010).

In California, replacement of commercially important runs for some species (e.g., Coho Salmon, *O. kisutch*, and Chinook Salmon, *O. tshawytscha*) by hatchery fish has already been documented (Weitkamp et al. 1995; Williams 2006). In the Sacramento River, historically the largest salmon producer in the state, decades of hatchery supplementation of fall Central Valley Chinook and related straying of adults have resulted in hatchery and wild populations that are genetically indistinguishable (Lindley et al. 2009). An estimated 90 % of the catch in the ocean fishery for fall Central Valley Chinook has been attributed to hatchery stock (Barnett-

Johnson et al. 2007). As dominance of hatchery fish has increased, vulnerability of fall Central Valley Chinook Salmon to changing environmental conditions, such as adverse ocean conditions, has also increased, likely contributing to years of dismally low adult spawner abundance and closure of fisheries (Lindley et al. 2009). Populations of Coho Salmon in the state also are largely dependent on artificial propagation (Brown et al. 1994). Wild coho populations throughout much of the state are believed to have low viability (CDFG 2002; NMFS 2010), sustainable only through hatchery supplementation (Brown et al. 1994; Weitkamp et al. 1995). Given the problems in the Sacramento River and the level of hatchery production in the Klamath basin, we sought to evaluate whether Klamath River salmonids are also at risk from hatchery practices. Here, we evaluate whether hatchery fishes are replacing wild salmonids in the Klamath River, where both imperiled (e.g., Coho Salmon) and apparently stable (e.g., Chinook Salmon) wild populations interact with hatchery conspecifics.

The Klamath River drainage is approximately 30,000 km^2, located in southern Oregon and northern California (Fig. 1). Estimates of historical abundance of all runs of salmon in the Klamath basin range from 650,000 to 1 million fish per year (Gresh et al. 2000), making it the second largest producer of salmon in California. The Klamath River once supported 55 separate stocks of salmonids but runs of Chum Salmon (*O. keta*) and Pink Salmon (*O. gorbuscha*) are now nearly extinct (Nehlsen et al. 1991; NRC 2004; Katz et al. 2012). Klamath River Coho Salmon [Southern Oregon and Northern California Coasts Evolutionarily Significant Unit] were listed under Endangered Species Acts as threatened in 1997 (62 FR 24588; Federal listing) and 2005 (state listing). Nevertheless, the Klamath River basin may represent the best opportunity for the rebuilding wild salmon populations in California because of extensive restoration being proposed (e.g., removal of four large dams), combined with tributaries with habitat still in good condition (e.g., Blue Creek).

Salmonids in the Klamath River face many natural and anthropogenic stressors, including impacts from hatchery supplementation (Moyle 2002; Moyle et al. 2008). Hatchery supplementation of salmonids in the basin began in 1890 with opening of a hatchery on Minor Creek (Trinity River; Kirk 1994 in Myers et al. 1998). Interbasin egg transfers, common before the mid-1990s, introduced broodstock from the Sacramento (Chinook Salmon), Eel (Coho Salmon), Noyo (Coho
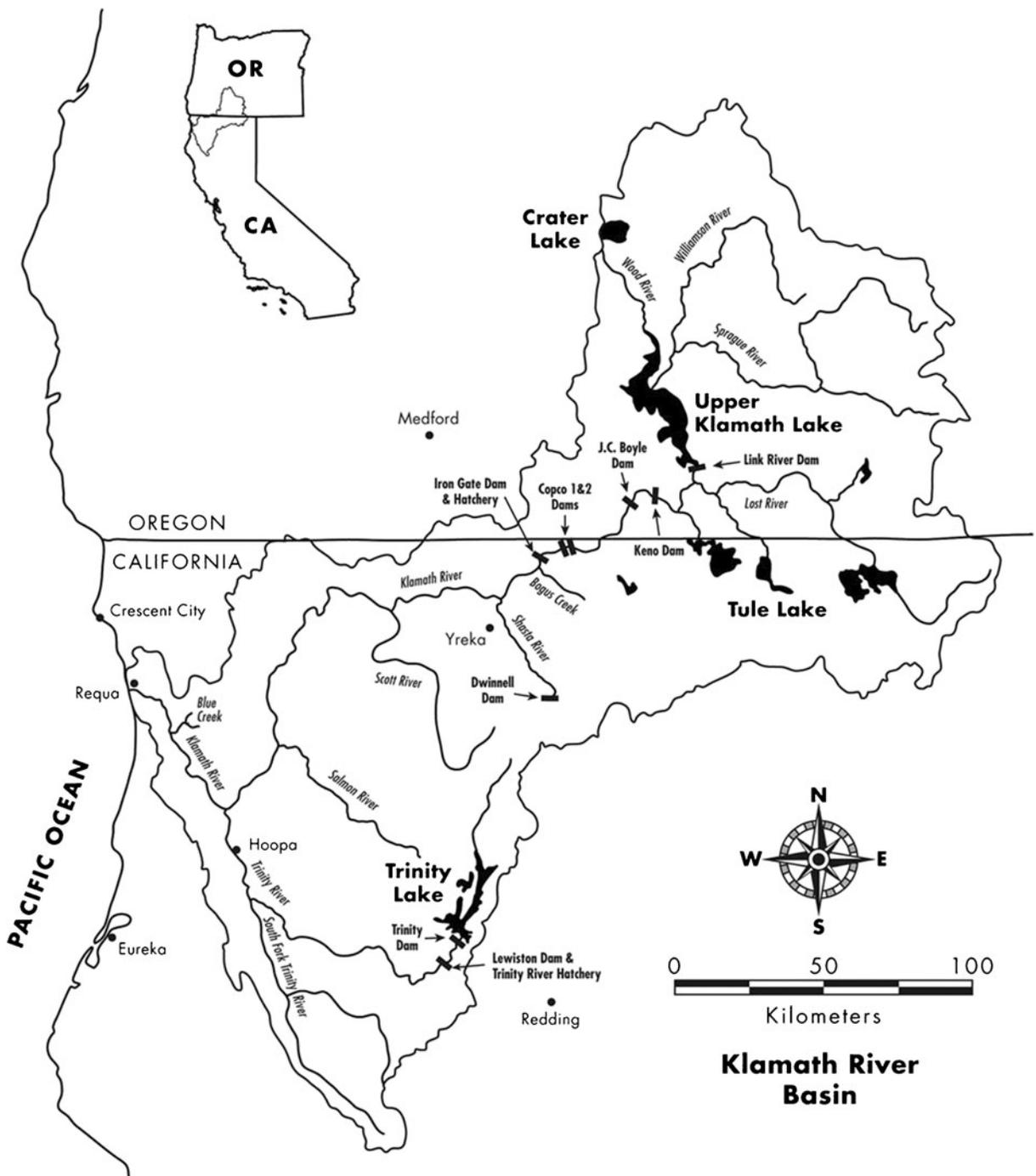
Fig. 1 Klamath River basin, California and Oregon, USA

Salmon), Alsea (Coho Salmon), Cascade (Oregon; Coho Salmon), Willamette (Oregon; Steelhead Trout), Washougal (Washington; Steelhead Trout) and Cowlitz (Washington; Steelhead Trout) rivers as well as Redwood Creek (Chinook Salmon) (Brown et al.

1994; Myers et al. 1998). From 1981 to 1998, up to 10 separate "major" artificial propagation efforts operated simultaneously in the basin (Myers et al. 1998).

Two hatcheries currently supplement Klamath River salmonid fisheries (Chinook Salmon, Coho Salmon,

Steelhead Trout): Iron Gate Hatchery (IGH, Klamath River) and Trinity River Hatchery (TRH). Together the hatcheries release approximately 12 million juvenile Chinook Salmon, Coho Salmon and Steelhead Trout each year (Hamilton et al. 2011). Hatchery-reared adults now contribute significant numbers to spawning adults. From 1978 to 2009, 11–52 % of total adult fall-run Chinook Salmon spawners were fish returning to the hatcheries (CDFG, unpublished data). Furthermore, based on coded wire tag expansions specific to brood year, up to 13 % of adults reared in IGH strayed into streams (CDFG, unpublished data), primarily into Bogus Creek and Shasta River which are located near the hatchery (S. Borok, California Department of Fish and Game, pers. comm. 2010). Coho Salmon in the basin are likely derived from hatchery sources, with little natural production (reviewed in Weitkamp et al. 1995). In 2001, an estimated 73 % of juvenile coho captured in the Klamath River estuary were classified as hatchery releases, an increase from 61 % in 2000 and 34 % in 1997 (CDFG 2004). Hatchery Steelhead Trout represent 20–34 % of Trinity River runs but less than 8 % in other parts of the basins (Busby et al. 1994).

Analyses of adult spawner abundance are used to set harvest quotas (Kope 2006) as well as to track demographic trends (Routledge and Irvine 1999). However, analyses that do not separate trends in naturally spawning fish from trends in fish returning to hatcheries may mask declining trends in wild populations (Wainwright and Kope 1999; Myers et al. 2004; Murdoch et al. 2010), the target of most conservation programs. We looked at trends in wild and hatchery spawners separately to determine status and trajectory of anadromous salmonid runs in the Klamath River. We recognize that wild spawners likely include progeny of hatchery descent but estimates of hatchery contributions specific to each taxon are not available. Here, we address the following questions for seven salmonid taxa:

1. Are adult spawner numbers increasing or decreasing?
2. Do trends in wild spawners differ from trends of spawners returning to hatcheries (a.k.a. hatchery returns)?
3. To what extent are wild-spawning fish being replaced and/or supplemented by fish of hatchery origin?
4. Do trends in populations show significant changes in overall abundance or rates of change as a response, immediate or delayed, to multiple stressors?

To our knowledge, this is the most comprehensive analysis of spawner trends for Klamath River salmonids. Our study is designed to establish a baseline for the status of salmonids in the basin in order to evaluate effectiveness of future restoration and salmon recovery efforts. The results of this study provide further evidence of large-scale negative impacts of hatchery programs on wild salmonid populations, demonstrating the need for reform in hatchery practices.

Methods

Data were collected from multiple existing sources in order to build time series for each of the seven taxon (Table 1): spring-, fall-, and late fall-run Chinook Salmon; Coho Salmon; summer and hybrid (mixed run) Steelhead Trout; and Coastal Cutthroat Trout (O. clarki clarki). We refer to Steelhead Trout returning to IGH as "hybrids" because the hatchery does not segregate spawners with different migration patterns (IGH, unpublished data). Compiled data is available at www.watershed.ucdavis.edu.

Only years with consistent sampling methods were evaluated in each time series. Therefore, not all available data were used, as reflected by the different number of years analyzed for each taxon. Adult spawner numbers were standardized by survey length (river kilometers) and type of survey when necessary in order for data to be directly comparable between years (Hill and Irvine 2001). For example, counts of Salmon River spring Chinook Salmon and summer Steelhead Trout adults were divided by the number of river kilometers surveyed per year after removing years (e.g., 2006, 2008) with differing methods from the time series. Only summer Steelhead Trout adult numbers were included in our analysis due to the common misidentification of large resident trout as half-pounders (Quiñones, unpublished observations). Half-pounders are young Steelhead Trout that return to fresh water after spending one summer in the ocean. Numbers of fall Chinook wild spawners of hatchery origin (hatchery strays) were estimated by expanding coded wire tag recoveries with production multipliers specific to brood year and tag number (CDFG, unpublished data). However,

Table 1 Data used for trend analysis of salmonid spawner abundance in the Klamath River, California

Run/Species	Location	Years	No. years	Collection method/survey	Data	Source
Fall Chinook Salmon	Klamath basin	78-09	32	Carcass, redd, video weir, hatchery returns	ln(x)	CDFG
	Klamath basin	78-09	32	Carcass, redd, video weir	ln(x)	CDFG
	Bogus Creek	78-09	32	Carcass, redd	ln(x)	CDFG
	Salmon River	78-09	32	Carcass, redd	ln(x)	CDFG
	Scott River	78-09	32	Carcass, redd, video weir	ln(x)	CDFG
	Shasta River	78-09	32	Carcass, redd, weir	ln(x)	CDFG
	Trinity River	78-09	32	Carcass, redd	ln(x)	CDFG
	Klamath basin	78-09	32	Carcass, redd, video weir	% wild	CDFG
	Klamath basin	80-04	23	Coded wire tag recoveries of hatchery strays	ln(x)	CDFG[a]
	Iron Gate Hatchery	67-09	43	Hatchery returns	ln(x)	CDFG
	Trinity River Hatchery	78-05	28	Hatchery returns	ln(x)	CDFG
Late-fall Chinook Salmon	Blue Creek	88-09	20	Snorkel surveys	ln(x)	YTF
Spring Chinook Salmon	Salmon River	68-09	34	Snorkel surveys	ln(x/km)	KNF
	Trinity River Hatchery	80-05	26	Hatchery returns	ln(x)	USFWS
	Trinity River	78-07	28	Carcass, redd	ln(x)	CDFG[b]
Coho Salmon	Iron Gate Hatchery	67-09	43	Hatchery returns	ln(x)	IGH
	Trinity River Hatchery	58-08	44	Hatchery returns	ln(x)	TRH
Steelhead Trout	Iron Gate Hatchery	63-08	44	Hatchery returns	ln(x)	IGH
	Trinity River Hatchery	58-08	44	Hatchery returns	ln(x)	TRH
Summer Steelhead Trout	Clear Creek	85-09	25	Snorkel surveys	ln(x/km)	KNF
	Elk Creek	87-09	23	Snorkel surveys	ln(x/km)	KNF
	Salmon River	68-09	34	Snorkel surveys	ln(x/km)	KNF
Coastal Cutthroat Trout	Blue Creek	99-09	9	Snorkel surveys	ln(x)	YTF

CDFG California Department of Fish and Game's "megatable"; CDFG[a] = unpublished data; CDFG[b] = Sinnen et al. 2010; *YTF* Yurok Tribe Fisheries; *KNF* Klamath National Forest; *USFWS* United States Fish and Wildlife Service; *IGH* Iron Gate Hatchery; *TRH* Trinity River Hatchery

information on tag recoveries was only available up to 2000 so the proportion of hatchery strays may be underestimated for years 2002 to 2009. Estimates of fall Chinook were taken directly from California Department of Fish and Game's annual estimates of Chinook harvest and escapement (nrm.dfg.ca.gov/FileHandler.ashx?DocumentVersionID = 48064). Although IGH has been spawning salmonids since 1962, we only incorporated data from 1967 to 2009 for Chinook and coho due to uncertainty as to whether hatchery gates were kept open throughout the entire run (K. Rushton, Iron Gate Hatchery, pers. comm. 2007). We assumed that the bias of stream surveys was the same among years and acknowledged that estimates of hatchery returns are likely more precise than those obtained through visual surveys. Nonetheless, we used the data as the only available to describe patterns of adult spawner abundance at different spatial and temporal scales.

Trend analysis

We used trend analysis to determine if adult spawner numbers are increasing or decreasing. Trends were built using data that met the following criteria as set by Biological Review Teams conducting status reviews for National Marine Fisheries Service: [1] abundance numbers were collected using the same methods for at least eight consecutive years, and [2] data sets did not contain more than 35 % zero values (Spence et al. 2005). Data sets were tested for autocorrelation and transformed (ln) before analysis in order to reduce the

influence of outliers and increase the ability to meet distributional and variance assumptions required for linear models (Quinn and Keough 2002). The ratio of fall Chinook abundance made up of wild spawners vs. hatchery returns was not transformed since it was a relative rather than nominal measure. Data were analyzed through linear regression of (ln) spawner numbers vs. year. We used NCSS (v. 2004) statistical software to run all data diagnostics and fit linear regression models. Our null hypothesis was that trends did not exist (slope of trend line = 0) at a 0.05 level of significance.

Although we recognize trends in wild spawners may not represent trends in the population as a whole, spawner abundance data allows monitoring of patterns that can alter genetic, phenotypic and life history (e.g., migration timing, reproductive success) diversity of the species as a whole. One drawback to using this analysis on spawner abundance is that it assumes that harvest rate and stock productivity remain constant throughout the period of analysis (Korman and Higgins 1997), an unrealistic assumption. Therefore, we used permutation tests to determine whether detected trends resulted from pattern in the data rather than from random chance. The nature of abundance trends over time is better discerned by coupling the use of linear regression (e.g., increasing/decreasing trend) with permutations tests (i.e. presence/absence of trend).

Permutation tests

Permutation tests allow for analysis of non-parametric data and have greater power than normal t tests when errors are not normal (Anderson and Legendre 1999; Anderson and Robinson 2001). Permutation tests assume exchangeability between observations as ensured by a priori random allocation of observations. "A permutation test calculates the probability of getting a value equal to or more extreme than an observed value of a test statistic under a specified null hypothesis by recalculating the test statistic after random reordering (shuffling) of the data" (pg. 626, Anderson 2001). Manly (1997) recommended at least 1,000 permutations for tests with a significance level of 0.05 (in Anderson 2001). In our case, data were shuffled 99,999 times and the p value was interpreted as the probability that an observed trend resulted from chance alone. Detailed descriptions and notations of permutation methods can be found in Anderson and

Robinson (2001), and Anderson (2001). We used software developed by Legendre (1999) to conduct permutation tests (http://www.bio.umontreal.ca/casgrain/en/labo/regression.html).

Cross correlations

We used cross correlation of trends between adults spawning in the wild vs. hatcheries to evaluate the possible occurrence of hatchery supplementation or replacement of wild populations. Cross correlation is useful in evaluating the relationship between two time series (Box et al. 2008). Because we wanted to further investigate the relationship between wild spawning and hatchery supplementation, we conducted cross correlation between pairs of time series where both wild spawner and hatchery return estimates were available for the same taxa. The pairs evaluated were:

- Total numbers of fall Chinook Salmon spawners (wild spawners + hatchery returns) in the basin vs. fall Chinook Salmon returns to both hatcheries,
- spring Chinook Salmon wild spawner numbers to the Salmon River vs. spring Chinook Salmon returns to TRH,
- spring Chinook Salmon wild spawner numbers to the Trinity River vs. spring Chinook Salmon returns to TRH,
- late-fall Chinook Salmon wild spawner numbers to Blue Creek vs. fall Chinook Salmon returns to TRH, and
- summer Steelhead Trout wild spawner numbers to Salmon River vs. Steelhead Trout returns to IGH.

We also wanted to investigate whether relationships between wild spawners and hatchery returns differed by location. Therefore, cross correlations were also completed separately for fall Chinook Salmon wild spawner numbers to Trinity, Salmon, Scott, Shasta rivers and Bogus Creek vs. fall Chinook Salmon returns to IGH and TRH. Cross correlations were completed in NCSS 2004. Pearson Correlation Coefficients were used to determine statistical significance between time series at $\alpha = 0.05$ and df$= n - 2$.

Bayesian change point analysis

We used Bayesian change point analysis to evaluate significant changes in overall abundance and or rates

of change within time series. Time series found to have statistically significant trends ($n=8$) were further analyzed to determine epochs with abrupt changes in abundance (step change) or with a significant rate of change (trend change). Epochs describe time periods during which abundance trends behaved similarly (e.g., increasing; as in Chu and Zhao 2004; Thomson et al. 2010). We completed Bayesian change point analysis using WinBUGS and R software as outlined in Thomson et al. (2010). First, step and trend changes between data points were assessed through piecewise linear regression models (Denison et al. 1998). Second, posterior probabilities for all possible models were calculated using a Bayesian approach in reversible jump Markov chain Monte Carlo (MCMC) simulation. Our methods differed from Thomson et al. (2010) in that we allowed one change point for every 10 (rounded) years of data. Consequently, the necessary prior distributions were defined as Binomial (number of years/10, 0.5). Third, we calculated odds ratios based on a three-fold increase from prior odds to underscore specific years of substantial step or trend changes (Thomson et al. 2010). A prior odd is the probability of a change point occurring in any given year.

Results

Time series trends and permutation tests

Eight of the 23 time series analyzed were found to have statistically significant trends based on per-mutations tests (p<0.05; Table 2). For fall Chinook Salmon, returns to Iron Gate Hatchery ($p=<0.001$, $r^2=0.39$; Fig. 2a) significantly increased as did the number of hatchery strays throughout the basin ($p=0.013$, $r^2=0.26$; Fig. 2b). Although no trend was detected for basinwide adult fall Chinook spawner abundance (wild spawners + hatchery returns), the ratio of wild spawners to hatchery returns has significantly decreased ($p=0.001$, $r^2=0.31$; Fig. 3). Populations trended upwards for spring Chinook Salmon returning to Salmon River ($p=0.0015$, $r^2=0.28$; Fig. 2c), spring Chinook Salmon returning to Trinity River Hatchery ($p=0.0009$, $r^2=0.35$, power; Fig. 2d), late-fall Chinook Salmon returning to Blue Creek ($p=0.032$, $r^2=0.23$; Fig. 4a), and Coho Salmon returning to Trinity River

Hatchery ($p=<0.0001$, $r^2=0.47$; Fig. 4b). Decreasing trends were detected for Steelhead Trout returning to Iron Gate Hatchery ($p=0.0004$, $r^2=0.30$; Fig. 4c) and summer Steelhead Trout wild spawners in Salmon River ($p=0.0007$, $r^2=0.32$; Fig. 4d).

Cross correlations

Several wild spawner time series were significantly corre-lated to hatchery returns (Table 3). Basinwide fall Chinook Salmon adult spawner abundance was significantly corre-lated to returns to both hatcheries ($r=0.53$, $p=<0.05$). Fall Chinook Salmon wild spawner numbers to Bogus Creek were significantly correlated to returns to both IGH ($r=0.60$, $p=<0.05$) and TRH ($r=0.58$, $p=<0.05$). Fall Chinook Salmon wild spawner numbers to Salmon River were significantly correlated to returns to IGH ($r=0.36$, $p=<0.05$). Fall Chinook Salmon wild spawner num-bers to Trinity River were significantly correlated to returns to both IGH ($r=0.41$, $p=<0.05$) and TRH ($r=0.72$, $p=<0.05$). Spring Chinook Salmon wild spawner numbers to the Salmon River were significantly correlated to spring Chinook Salmon returns to TRH ($r=0.50$, $p=<0.05$). Spring Chinook Salmon wild spawner numbers to the Trinity River were significantly correlated to spring Chinook Salmon returns to TRH ($r=0.83$, $p=<0.05$). Late-fall Chinook Salmon wild spawner numbers to Blue Creek were significantly correlated to fall Chinook Salmon returning to TRH ($r=0.57$, $p=<0.05$). Summer Steelhead Trout wild spawner numbers to Salmon River were significantly correlated to Steelhead Trout returning to IGH ($r=0.75$, $p=<0.05$).

Bayesian change point analysis

Significant changes to abundance (step changes) were exhibited by six of the eight time series with signifi-cant trends. Fall Chinook Salmon returns to IGH ex-perienced increases from the late 1960s to mid-1970s, decreases in the late 1970s, increases from ca.1982 to 2000, and decreases to 2009 (Fig. 2a). Spring Chinook Salmon returns to TRH experienced decreases from 1978 to ca. 1985, increases to the late 1980s, decreases in the early 1990s, and increases to 2009 (Fig. 2d). Late-fall Chinook Salmon wild spawner numbers in Blue Creek experienced decreases in the late 1980s and early 1990s, increases to ca. 2002, and decreases to 2004 (Fig. 4a). Coho Salmon returns to TRH expe-rienced decreases in the early and mid-1960s,

Table 2 Time series data tested (permutations) for trends in spawner abundance

Run/Species	Location	p reg[a]	r^2	slope	Intercept	p perm[b]
Fall Chinook Salmon	Klamath basin	0.30	0.036	0.012	−12.63	0.30
	Klamath basin	0.84	0.0013	0.0024	6.0	0.84
	Klamath basin (hatchery only)	0.013*	0.26	0.12	−227.35	0.013*
	Iron Gate Hatchery	<0.001*	0.39	0.04	−67.36	<0.001*
	Trinity River Hatchery	0.064	0.13	0.036	−63.66	0.065
	Trinity River	0.83	0.0016	−0.51	1998.63	0.83
	Salmon River	0.71	0.0046	−0.90	2000.37	0.71
	Scott River	0.29	0.037	−2.41	2013.61	0.29
	Shasta River	0.25	0.04	−2.08	2010.48	0.25
	Bogus Creek	0.25	0.04	2.23	1974.11	0.25
Late-fall Chinook Salmon	Blue Creek	0.032*	0.23	0.070	−135.21	0.032*
Spring Chinook Salmon	Salmon River	0.0013*	0.28	0.055	−108.47	0.0015*
	Trinity River Hatchery	0.0009*	0.35	0.054	−98.88	0.001*
	Trinity River	0.27	0.047	0.023	−37.21	0.27
Coho Salmon	Iron Gate Hatchery	0.26	0.030	0.013	−19.51	0.27
	Trinity River Hatchery	<0.001*	0.47	0.09	−169.46	<0.001*
Steelhead Trout	Iron Gate Hatchery	0.0004*	0.30	−0.054	112.94	0.0004*
	Trinity River Hatchery	0.51	0.010	0.010	−64.09	0.51
Summer Steelhead Trout	Clear Creek	0.19	0.072	−0.03	66.98	0.19
	Elk Creek	0.68	0.0084	−0.01	21.80	0.68
	Salmon River	0.0006*	0.32	−0.063	125.62	0.0007*
	Wooley Creek	0.66	0.010	−0.015	31.00	0.65
Coastal Cutthroat Trout	Blue Creek	0.10	0.33	0.11	−213.25	0.10

[a] p values of original time series, [b] p values of permutated data, *p values significant at $\alpha=0.05$

increases to the late 1980s, decreases in the early 1990s, and increases to 2009 (Fig. 4b). Steelhead Trout returns to IGH experienced decreases in the late 1960s, increases to the late 1980s, decreases to late 1990s, increases in the early 2000s, and decreases to 2009 (Fig. 4c). Summer Steelhead Trout wild spawner numbers in Salmon River experienced increases in the late 1960s and early 1970s and decreases to 2009 (Fig. 4d). We interpreted the lack of significant step or trend changes as the result of steady increases in the abundance of IGH fall Chinook Salmon strays (Fig. 2b) and Salmon River spring Chinook Salmon wild spawners (Fig. 2c).

Discussion

Since the 1990s, researchers have identified hatchery practices as contributing to the overall decline of some wild salmonid populations (Levin et al. 2001; Levin and Williams 2002; Sweeting et al. 2003). Because wild populations exposed to long-term hatchery supplementation can become incapable of sustaining themselves (Lynch and O'Hely 2001), we sought to understand how trends in salmonid wild spawners and hatchery returns have changed through time in the Klamath River basin.

We found a general pattern of increasing hatchery returns with simultaneous decreasing wild spawner abundance for most runs (Figs. 2, 3 and 4). Hatchery returns of fall Chinook to IGH, and spring Chinook and coho to TRH have increased significantly in the last 40+ years. Furthermore, the number of fall Chinook IGH strays spawning in rivers has also increased. In contrast, the ratio of wild spawners to hatchery returns of fall Chinook Salmon returning to the entire basin and of summer Steelhead Trout returning to the Salmon River have significantly
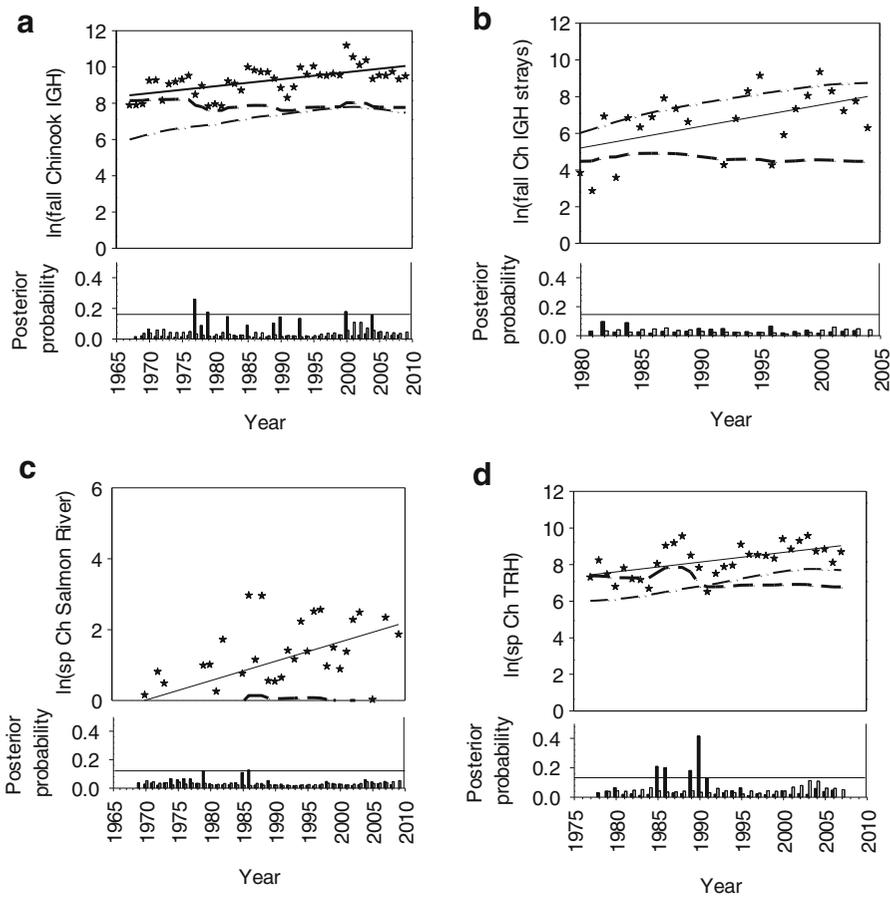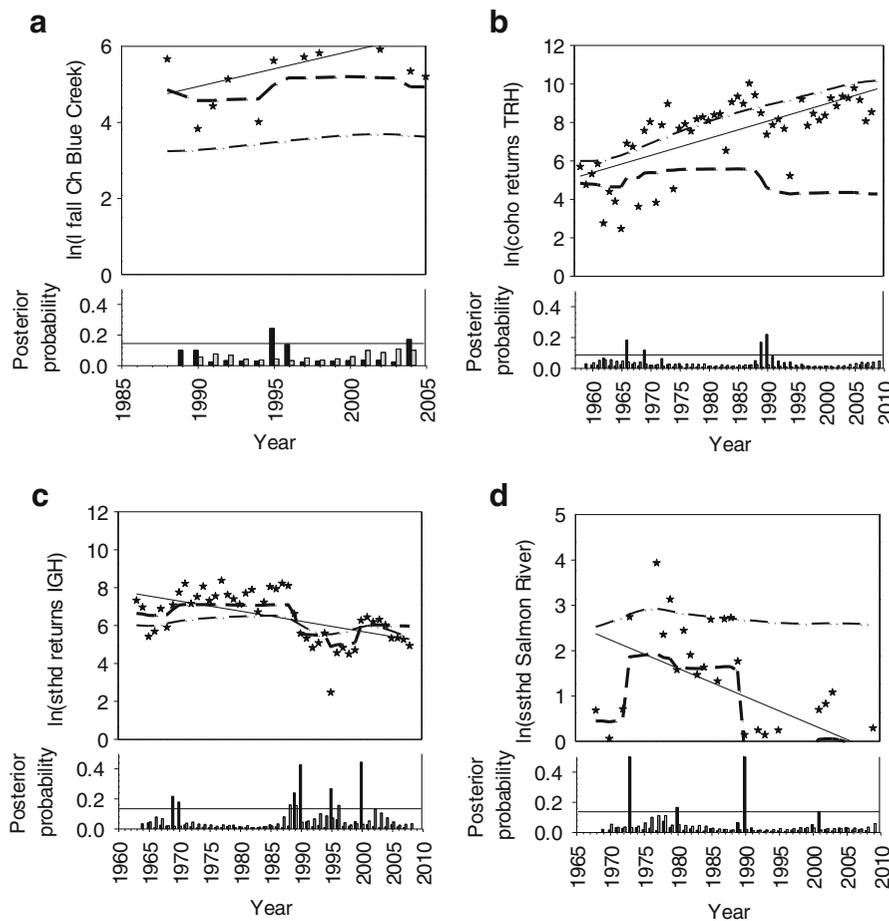
Fig. 2 Trends in salmonid adult spawner abundance for fall and spring Chinook Salmon in the Klamath River, California, USA. In the upper graph, *black stars* represent time series data, *black lines* represent linear trend lines (from permutations), *dot-dash lines* represent trend output, and *broken lines* represent intercept parameters. In the lower graphs, *black bars* represent posterior probabilites of step changes, *gray bars* represent posterior probabilites of trend changes, and the *lines* represent the odds ratio significant to each time series. *Ch* Chinook Salmon, *IGH* Iron Gate Hatchery, *Sp Ch* spring Chinook Salmon, *TRH* Trinity River Hatchery

Fig. 3 Ratio of fall Chinook Salmon spawning in the wild (wild spawners) vs. hatcheries (hatchery returns), Klamath River, California, USA, 1978–2009

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$R^2 = 0.3269$
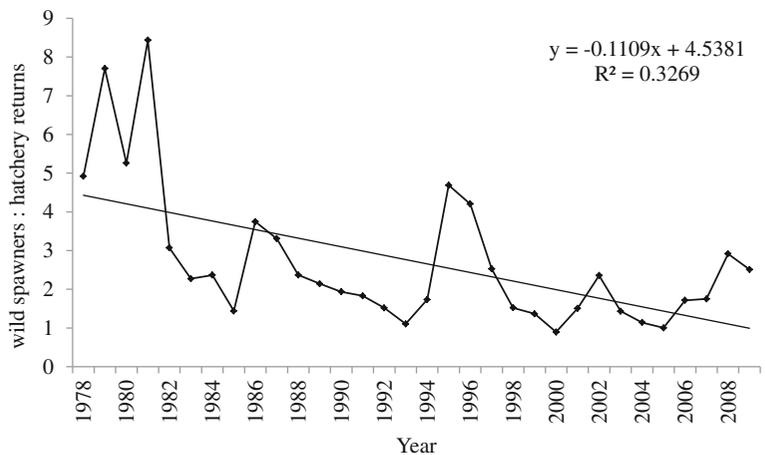
Fig. 4 Trends in salmonid adult spawner abundance for fall and spring Chinook Salmon in the Klamath River, California, USA. In the upper graph, *black stars* represent time series data, *black lines* represent linear trend lines (from permutations), *dot-dash lines* represent trend output, and *broken lines* represent intercept parameters. In the lower graphs, *black bars* represent posterior probabilites of step changes, *gray bars* represent posterior probabilites of trend changes, and the *lines* represent the odds ratio significant to each time series. *IGH* Iron Gate Hatchery, *l fall Ch* late-fall Chinook Salmon, *sthd* Steelhead Trout, *s sthd* summer Steelhead Trout, *TRH* Trinity River Hatchery

decreased. Of particular concern are trends in Steelhead Trout populations where both returns of hatchery fish to IGH and of wild summer Steelhead Trout to the Salmon River have declined. Interestingly, both wild taxa with increasing trends (Salmon River spring Chinook and Blue Creek late-fall Chinook) were significantly correlated to hatchery returns (Table 3), suggesting that these trends are supplemented by hatchery strays.

Because we dealt with adult numbers in rivers (a.k.a. escapement), we considered the potential impact of commercial fishing on IGH fall Chinook Salmon abundance. Escapement by definition is the sum of fish that "escaped" being harvested and arrived into rivers and streams to spawn (www.psc.org). The

Pacific Coast Salmon Fishery Management Plan established a minimum escapement of 35,000 fall Chinook Salmon wild spawners as a conservation goal (Gutierrez 2006). Yet, less than 35,000 natural spawners (adults and grilse) returned to spawn in 1983 (33,310), 1984 (21,349), 1990 (16,946), 1991 (12,367), 1992 (17,171), 1993 (25,683), 1999 (28,904), 2004 (29,053) and 2005 (28,388). We expected that years when minimum escapement goals were not met would decrease basinwide spawner abundance in subsequent years. This appeared not to be the case as indicated by IGH fall Chinook abundance, which only significantly decreased in the late 1970s. This may reflect that hatcheries are relatively immune to total escapement effects because they can

Table 3 Taxa and locations of abundance time series paired for cross correlation analysis

Taxa	Location of wild spawning	Location of hatchery returns	Minimum Pearson coefficient	r(df − 2)
Fall Chinook Salmon	Klamath River basin	IGH and TRH	0.35	0.53*
	Bogus Creek	IGH	0.35	0.60*
		TRH	0.35	0.58*
	Salmon River	IGH	0.35	0.36*
		TRH	0.35	0.08
	Scott River	IGH	0.35	0.27
		TRH	0.35	0.21
	Shasta River	IGH	0.35	0.11
		TRH	0.35	0.32
	Trinity River	IGH	0.35	0.41*
		TRH	0.35	0.72*
Spring Chinook Salmon	Salmon River	TRH	0.37	0.50*
	Trinity River	TRH	0.40	0.83*
Late-fall Chinook Salmon	Blue Creek	TRH	0.55	0.57*
Summer Steelhead Trout	Salmon River	IGH[a]	0.35	0.75*

[a] hybrids; *Correlations significant at $\alpha = 0.05$

usually fill hatchery-rearing capacity with even a small number of spawners.

Regardless of the factors influencing trends, hatchery returns are likely replacing spawners in at least some wild populations in the Klamath basin. This pattern is most obvious for fall Chinook Salmon where the lack of a significant trend in total spawner abundance (wild spawners + hatchery returns) masks the inverse relationship of wild spawners and hatchery returns (Fig. 3). Cross correlation results also suggest that hatchery supplementation and/or replacement may be occurring in the Salmon River, Trinity River, Bogus Creek, and Blue Creek (Table 3). However, we recognize that significant cross correlations between hatchery and wild fish may reflect changes in abundances as affected by environmental conditions, rather than intraspecific interaction, if both groups respond similarly.

Bayesian change point analysis underscored epochs with significant changes to abundance and/or trend for each taxon. Our interpretations cover general patterns but recognize the complexity of interactions between factors and the likelihood of time lags in the response of adult abundances. Abundances for fall Chinook Salmon (IGH; early 1980s to ca. 2000) appeared to increase in accordance with sharp decreases of IGH Chinook Salmon smolt releases [from ~10 million (1985–1988) to 5 million (1989–2009) per year; IGH, unpublished data] and favorable ocean conditions in the early 2000s. The

inverse relationship between hatchery releases and adult abundance likely signaled a relaxation of density dependent mortality which was high when ocean productivity was low (Beamish and Mahnken 2001; Levin et al. 2001). In the 1980s and early 1990s, climatic patterns (e.g., PDO warm phase) resulted in unfavorable ocean conditions and poor salmon returns (Mantua et al. 1997; Mantua and Hare 2002). Favorable ocean conditions, in contrast, may explain increases of coho (TRH) and Steelhead Trout (IGH, Salmon River) abundances during the mid-1960s to early 1970s and ca. 2000, years during cold PDO phases (Mantua and Hare 2002). Like IGH fall Chinook Salmon, decreases of Coho Salmon and Steelhead Trout reflect unfavorable ocean conditions (warm PDO phase) in the late 1970s, mid to late 1980s and early 1990s. Steelhead Trout IGH returns were the only group with trend changes showing decreased abundance. Decreases in Salmon River summer Steelhead Trout may be amplified by interbreeding with IGH Steelhead Trout as suggested by cross correlation ($r = 0.75$) since hatchery salmonids have been shown to reproduce less successfully than their wild counterparts (Berejikian et al. 2001; McLean et al. 2003; Buhle et al. 2009). Genetic analysis suggested that IGH Steelhead Trout have already interbred with Steelhead Trout in the Shasta and Scott rivers (Pearse et al. 2007).

Spring (TRH) and late-fall (Blue Creek) Chinook Salmon abundances also seemed to reflect influences

from ocean conditions and hatchery practices. Spring Chinook Salmon returns to TRH exhibited a decrease (1980s) and an increase (1990s) that is best explained by ocean conditions. However, other increases (mid-1980s) likely reflected the switch by the hatchery from earthen to cement raceways in the 1980s (N. Hemphill, Trinity River Restoration Program, pers. comm. 2010), improving hatchery production (CDFG 2010) and increasing adult returns in the short term. The increase (mid-1990s) in Blue Creek late-fall Chinook Salmon likely reflected the same release from density dependent factors as was seen in IGH fall Chinook Salmon due to decreases in hatchery releases.

Although we think the Bayesian change point analysis provides worthwhile insights into the complexity of factors affecting salmon trends, we also recognize several problems with our analysis. First, we were limited by the available data. Little standardized data specific to the Klamath River were available prior to 1960 and most of these were of hatchery returns. Second, our interpretation focused on large scale factors (e.g., ocean conditions) that can mask changes at the local scale (e.g., habitat degradation/restoration) which are also important in determining salmonid survival (Ebersole et al. 2001; Lackey et al. 2006; Battin et al. 2007). Finally, the most realistic scenario is that all factors (e.g., hatchery supplementation, habitat degradation and ocean conditions) acted synergistically to influence the trends we described.

Hatchery supplementation is just one stressor acting on Klamath River salmonids. However, we focused our discussion on the impacts of hatchery supplementation in order to challenge the notion that hatcheries can effectively rebuild imperiled wild populations (as in Brannon et al. 2004). Here, we propose that hatchery supplementation may be facilitating the extirpation of wild populations in parts of the Klamath River basin.

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