ARTICLE

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Effects of hatchery supplementation on abundance and productivity of natural-origin Chinook salmon: two decades of evaluation and implications for conservation programs

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Abstract: Hatchery supplementation has been developed to conserve salmonid populations and provide fisheries. We evaluated supplemented and reference Chinook salmon (*Oncorhynchus tshawytscha*) populations prior to, during, and after supplementation ceased for 22 years in two major drainages in Idaho, USA. Basin-level analyses showed supplementation increased abundance at some life stages, but effects did not persist into the postsupplementation phase and had no apparent influence on productivity. Natural-origin juvenile abundance increased during supplementation but results for adults were ambiguous. After supplementation ceased, abundance and productivity in supplemented and reference populations returned to their presupplementation relationships. Intensive analyses of supplemented populations with weirs showed abundance increased at some life stages with the addition of female spawners. However, the rate of increase varied with female origin (natural > supplementation ≥ nontreatment hatchery), and effects diminished through the life cycle. Based on these findings, we provide guidance for conservation programs. Supplementation alone is not a panacea because it does not correct limiting factors, which must be addressed to achieve population levels capable of sustaining ecological function and harvest.

Résumé : Le renforcement de populations naturelles par des lâchers de poissons d'élevage est utilisé pour la conservation de populations de salmonidés et pour accroître les ressources halieutiques. Nous avons évalué des populations de saumons quinnats (*Oncorhynchus tshawytscha*) ainsi renforcées et des populations de référence avant et durant des lâchers de poissons d'élevage et après la cessation de ces lâchers pendant 22 ans, dans deux grands bassins versants de l'Idaho (États-Unis). Les analyses à l'échelle du bassin montrent que les lâchers accroissent l'abondance à certaines étapes du cycle de vie, mais que les effets ne persistent pas durant la phase post-lâchers et n'ont pas d'influence apparente sur la productivité. Si l'abondance des poissons juvéniles d'origine naturelle augmente durant le renforcement, pour les poissons adultes, les résultats sont ambigus. Après la cessation des lâchers, l'abondance et la productivité dans les populations renforcées et de référence sont revenues aux relations qu'elles présentaient avant leur renforcement. Des analyses intensives de populations renforcées à l'aide de fascines montrent que l'abondance augmente à certaines étapes du cycle de vie avec l'ajout de femelles reproductrices. Cependant, le taux d'augmentation varie selon l'origine des femelles (naturelle > lâchers ≥ élevage sans traitement) et les effets diminuent au fil du cycle biologique. À la lumière de ces constatations, nous formulons des recommandations pour les programmes de conservation. Le renforcement par des lâchers ne constitue pas à lui seul une panacée parce qu'il ne corrige pas certains facteurs limitants dont il faut tenir compte pour pouvoir produire des populations capables de soutenir des fonctions écologiques, ainsi que la pêche. [Traduit par la Rédaction]

Introduction

There have been widespread declines in Atlantic and Pacific salmon populations in recent decades (Parrish et al. 1998; Lichatowich 1999; McClure et al. 2003; Chaput 2012). Hatchery supplementation programs have been developed as one means to address declines and conserve natural-origin (natural hereinafter) populations (Naish et al. 2008). Supplementation is defined as the use of artificial propagation to maintain or increase natural abundance while maintaining the long-term productivity of the target population (RASP 1992). However, debate remains on whether or not supplementation can achieve that goal (ISAB 2003; Fraser 2008).

Typically, hatchery fish do not perform as well as natural fish when spawning in natural habitats, which may affect response of the natural population to supplementation (Araki et al. 2008; Buhle et al. 2009). There may be genetic effects such as reduced reproductive fitness (Araki et al. 2009; Chilcote et al. 2011) due to domestication selection in hatcheries (Hindar et al. 1991; Kostow 2004), as well as ecological effects (Flagg et al. 1995; Nickelson 2003). Competition and behavioral differences between hatchery and natural salmonids have also been observed (Berejikian et al. 1997, 1999, 2000; Weber and Fausch 2003). The key question is whether the increased abundance of spawners provided by sup-

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Fig. 1. Location of supplemented and reference populations and associated sampling infrastructure within the Clearwater River and Salmon River basins. Supplemented populations with weirs included in the intensive analyses are indicated by a black dot within an open circle. Map created by Paul Bunn using ArcMap version 10.0 and ESRI redistributable data.
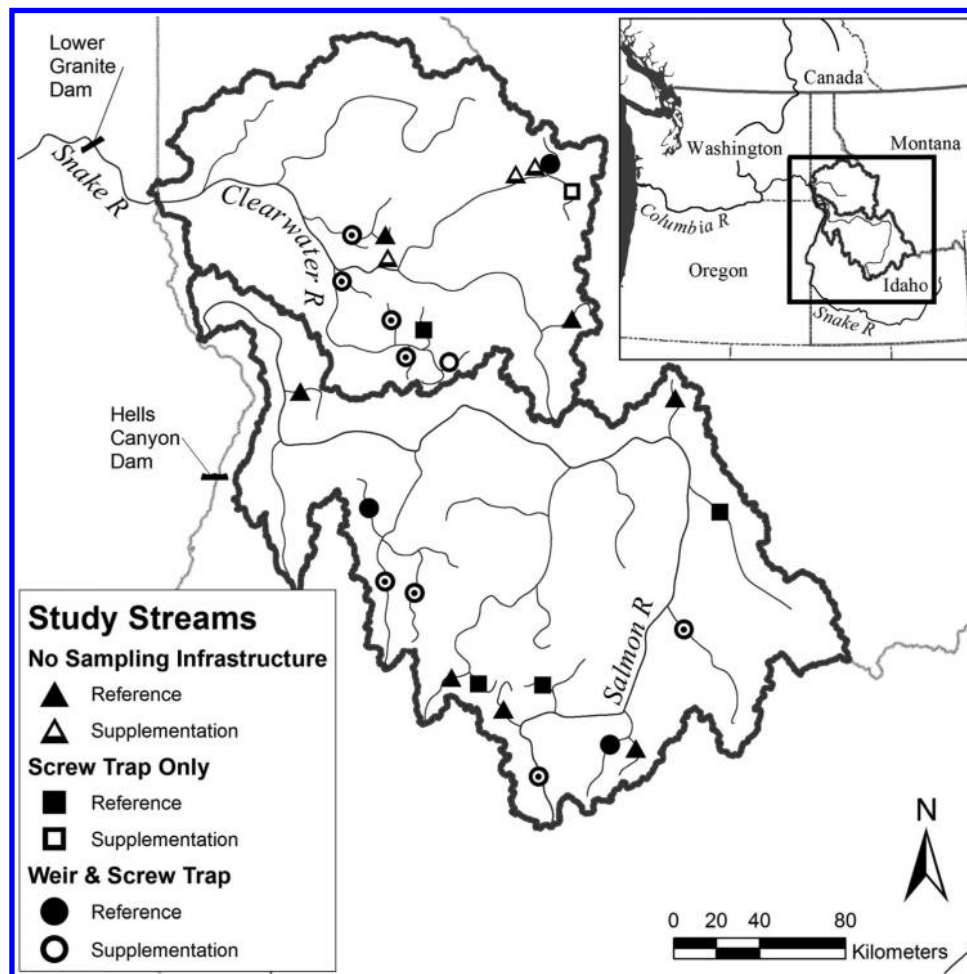
plementation offsets the costs to productivity (i.e., the rate at which the population replaces itself) incurred by adding hatchery fish into the population.

There is a pressing need for a broad evaluation of supplementation as a population-level management technique (ISAB 2003; Fraser 2008). Most published evaluations of supplementation are on a single population and often do not include reference populations to establish a proper standard for measuring supplementation effects (but see Scheuerell et al. 2015). Further, the long-term effects of a supplementation program cannot be assessed as long as the program is operational; effects on population productivity can best be determined after supplementation ceased. Therefore, it remains unclear if the anticipated abundance benefits of supplementation are sufficient to surmount the potential reduction in productivity and if these changes persist after supplementation is stopped.

To address critical uncertainties regarding the long-term demographic effects of supplementation, we evaluated the results of a multigenerational study with multiple supplemented and reference populations prior to, during, and after supplementation. Our objectives were to (1) evaluate the effects of supplementation on natural juvenile and adult abundance, (2) evaluate the effects of supplementation on natural productivity, and (3) evaluate the abundance response to the addition of supplementation and non-treatment hatchery (NTH) females relative to natural females to develop guidance for managers. The first two objectives were analyzed using all supplemented and reference populations within a

basin. The third objective was evaluated using a subset of supplemented populations where weirs provided more precise estimates of the number of spawning females by origin.

Methods

Study area

The study area encompassed the Clearwater River and Salmon River basins (hereinafter Clearwater basin and Salmon basin), which includes all currently accessible stream-type Chinook salmon (*Oncorhynchus tshawytscha*) spawning habitats in Idaho. The basins include portions of the Idaho Batholith, the Middle Rockies, and the Northern Rockies ecoregions (McGrath et al. 2002; Kohler et al. 2013). Water quality is high and substrates range from sand and small gravels to cobbles and large boulders. Winters are harsh and growing seasons are short (45–100 days). The area is relatively dry, with mean annual precipitation (primarily snowfall) ranging from 31 to 203 cm. Locations where data were collected for the study encompassed a variety of conditions and were widely distributed throughout anadromous salmonid habitat in Idaho (Fig. 1). The lower extent of the study area was Lower Granite Dam (LGR), which is the first hydroelectric facility encountered by seaward emigrating smolts. Smolt passage at LGR was used to represent their exit from freshwater rearing areas.

There are two types of hatchery brood stocks within the study area: local and localized. In most of the Salmon basin (including all hatcheries used in this study), hatchery brood stocks were

Fig. 2. Mean annual supplementation ratios (supplementation:natural females) in supplemented populations in the Clearwater River and Salmon River basins.
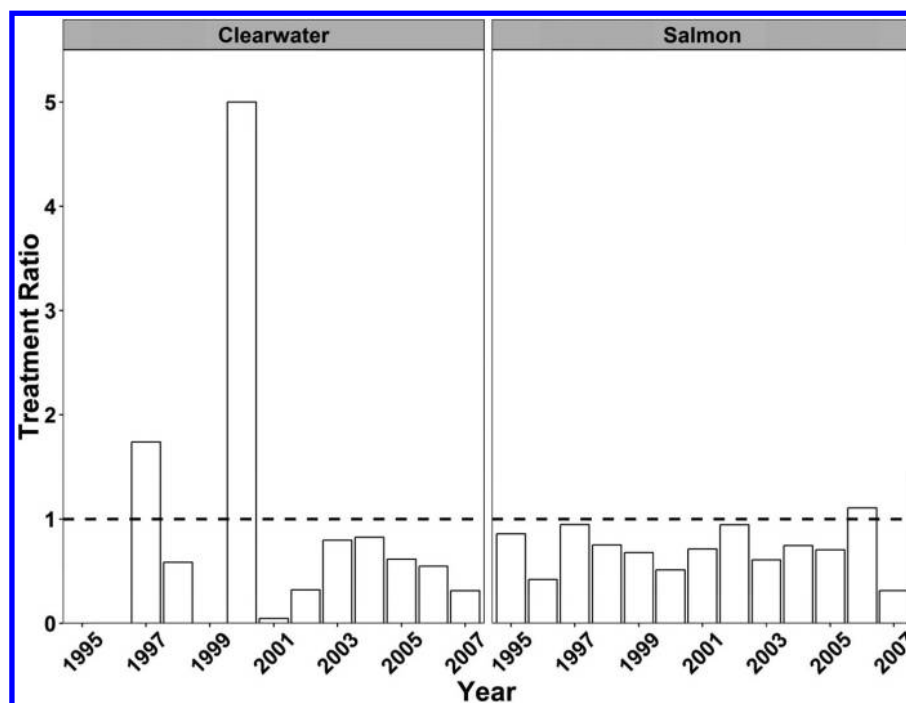
founded with local fish. In the Clearwater basin, Chinook salmon were functionally extirpated following the construction of Lewiston Dam in 1929. Naturally reproducing Chinook salmon populations were re-established there after the dam was removed in 1973. After this time, localized Clearwater basin hatchery stocks were founded from a nearby hatchery in the Snake River basin (Howell et al. 1985; Bowles and Leitzinger 1991). Shortfalls in localized brood stock collections in Clearwater basin hatchery programs are still occasionally addressed with eyed-egg transfers from this facility.

Study design

The study was designed as a three-phase evaluation including supplemented and reference populations. Phase 1 (1992–1995) provided baseline data on the abundance and productivity of all study populations in the absence of supplementation. The first supplementation brood stocks were also spawned in the hatcheries during this phase. The return of their progeny (i.e., supplementation adults) marked the end of Phase 1. Phase 2 (1996–2007) was the supplementation phase of the program. During 1996–2002, returning supplementation adults were passed upstream of weirs to spawn along with natural adults or incorporated into the next generation of supplementation brood stocks. From 2003 to 2007, supplementation continued but brood stock creation was discontinued. In Phase 3 (2008–2014), supplementation was halted, which provided an opportunity to quantify the abundance and freshwater productivity of supplemented and reference populations to determine the legacy of supplementation on natural populations (see online Supplementary material Fig. S1[1] for a detailed timeline).

There were 13 supplemented and 14 reference populations included in the study, which encompassed the stream reaches thought to be most productive and hence most important to overall production in Idaho (Fig. 1). The Clearwater basin contained nine supplemented and four reference populations, and the

Salmon basin included four supplemented and 10 reference populations. Population designation (i.e., supplemented or reference) was not randomly assigned. Populations selected to receive supplementation were typically in close proximity to existing hatcheries for ease of access to facilities, brood stock collection, juvenile rearing, and juvenile releases. While this may have some bearing on our findings, this was a necessary compromise to maintain the integrity of our reference populations and reflects the reality that supplementation will often operate concurrently with harvest mitigation programs. For a complete account of the study design and data collection methodologies, see Bowles and Leitzinger (1991), Lutch et al. (2005), and Venditti et al. (2015a).

The goal for creating supplementation brood stocks was to spawn adults from local (Salmon basin) or localized (Clearwater basin) hatchery stocks with natural adults from local populations within the basins (i.e., create integrated brood stocks). We achieved this goal in the Salmon basin, where endemic stocks remained. Extremely low natural escapement in the Clearwater basin during Phase 1 precluded the use of natural adults in the brood stocks, so we used a dedicated portion of the existing hatchery stocks for supplementation. When differentially marked supplementation adults began returning in 1996, a portion was brought into the hatcheries and crossed as above to create the next generation of supplementation brood stock, and a portion was released to spawn naturally.

A supplementation target was set to avoid swamping the natural population with potentially maladapted hatchery fish (Bowles and Leitzinger 1991; RASP 1992), which was a novel innovation at the time. Supplementation adults were not to exceed the number of natural adults; thus a 1:1 target ratio of supplementation to natural spawners was set, which would double the spawning population. Overall, the mean achieved female ratio was 0.72:1, although supplementation rates were more variable in the Clearwater basin than in the Salmon basin (Fig. 2). Estimated numbers

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Table 1. Notation and descriptions of variables and fixed effect coefficients used in statistical analyses.

Variable	Coefficient	Description
y_{ijt}		Abundance or productivity of the jth population in the ith geographic group[a] for cohort t
	μ	Mean y_{ijt} for reference populations in Phase 2 in eq. 1; mean y_{ijt} for all populations in eq. 2
Phase 1	β_1	Indicator variable for Phase 1; coefficient is mean intercept adjustment for all populations between Phase 2 and Phase 1
T_{jt}	β_2	No. of female supplementation fish spawning naturally during Phase 2; coefficient is mean effect on cohort t in population j
Phase 3	β_3	Indicator variable for Phase 3; coefficient is mean intercept adjustment for all streams between Phase 2 and Phase 3
S	β_4	Indicator variable for supplemented populations in Phase 3; coefficient is mean intercept adjustment for supplemented compared with reference populations
H_{jt}	β_5	Proportion of spawners that were nontreatment hatchery adults; coefficient is mean intercept adjustment for cohort t in population j
N_{jt}^{F}	β_1	No. of natural females spawning; coefficient is mean effect on cohort t in population j
T_{jt}^{Ratio}	β_2	Ratio of supplementation females to natural females spawning; coefficient is mean effect on cohort t in population j
H_{jt}^{Ratio}	β_3	Ratio of nontreatment hatchery females to natural females spawning; coefficient is mean effect on cohort t in population j

[a]Grouping of populations within a basin is based on proximity and similar geology used to account for additional variance (see online Supplementary material, Table S1[1]).

of fish by sex and origin spawning in study streams can be found in Venditti et al. (2015a) and the reports cited therein.

NTH adults included harvest mitigation stock adults that escaped into study reaches in all populations as well as supplementation adults that strayed into reference populations. Adults from mitigation brood stock programs in both basins were not intentionally released into study reaches but were readily distinguishable by an adipose fin clip. These fish can produce offspring, so it was necessary to distinguish the effect of this unintentional de facto supplementation from that of the dedicated supplementation program. We surveyed for NTH fish in all streams because weirs were either not present or were not 100% efficient. In the Clearwater basin, NTH adults averaged 37.4% (standard deviation (SD) = 35.4%) and in the Salmon basin 5.5% (SD = 14.4%).

Spawning ground surveys were conducted annually in all study populations to measure spawning escapement (i.e., redd counts) and to collect biological data from carcasses. In streams where weirs were present, all adults passed were marked to allow escapement estimates from recovered carcasses. Detailed methodologies are presented in Venditti et al. (2015a). Surveys were assumed to include all available spawning habitat in all streams. Most reaches were surveyed three or more times with ground counts. Exceptions to multiple pass surveys included remote streams or those too large to survey effectively on foot. We surveyed these populations with a single pass ground count, aerial count, or combination that coincided with peak spawning activity along with targeted carcass collections. Biological data from Chinook salmon carcasses provided estimates of hatchery fraction (i.e., supplementation and NTH adults), age structure, and sex ratio. Spawning ground surveys for this study were completed through 2014.

We estimated the number of juveniles emigrating from spawning reaches and survival to LGR using data from rotary screw traps (RSTs) on 18 streams during Phase 1 and Phase 2 and on 15 streams during Phase 3. A subsample of juveniles captured at RSTs were implanted with passive integrated transponder (PIT; Prentice et al. 1990) tags systematically by cohort over the tagging season (see Copeland et al. 2014) and released upstream from the trap. Recaptured fish were used to estimate cohort abundance at the trap (Steinhorst et al. 2004), and tag detections at Snake and Columbia river hydroelectric facilities were used to estimate survival to LGR using a Cormack–Jolly–Seber model and SURPH software (Lady et al. 2013). Juvenile monitoring for this study ended in July 2014, with the final emigrants of the 2012 cohort.

Our index of the abundance of juveniles from spawning reaches and smolts at LGR included only fall and spring emigrants at the traps. We used this index because traps were not operated during the summer prior to 1998. We excluded the summer period in this analysis to maintain consistency over time and between populations. For smolts at LGR, this index was the sum of the products of the emigration and survival estimates for emigrants passing the traps during these two time periods. Omitting summer emigrants likely had little effect on the number of smolts at LGR, because survival of this group was consistently lower than the other groups (see Venditti et al. 2015b).

Analytical methods

We performed two sets of complementary analyses: a basin-level analysis and an intensive analysis of supplemented populations with weirs. Data from the Clearwater and Salmon basins were analyzed separately in both sets of analyses. Each set encompassed the entire life cycle from eggs (indexed by redd count) to returning adults (i.e., the cohort was the experimental unit). We used model selection methods for inference on each life stage and took a weight of evidence approach to compare across life stages. Basin-level analyses were completed using data from all streams within a basin to establish the effects of supplementation with respect to the reference populations. Intensive analyses allowed us to take advantage of the greater precision provided by weirs to better estimate the population response to supplementation and develop guidance for supplementation programs. Notations for variables and coefficients of interest used in the analyses are defined in Table 1.

## Basin-level analyses of abundance and productivity

We developed six a priori hypotheses implemented as alternative models (Table 2) to infer the effect of supplementation and NTH adults (both sexes, including jacks) on abundance and productivity measures. Analyses of abundance and productivity use the same model set with appropriate changes in the response variable. Abundance was examined at four different life stages: redds (an index of egg production), naturally produced emigrants at RST, naturally produced smolts at LGR, and natural progeny redds. Point estimates for emigrants at RST and smolts at LGR were used without incorporating associated error. Progeny redds are those produced by natural females in the generation following supplementation. Productivity was examined at three stages: emigrants at RST per redd, smolts at LGR per redd, and natural

Table 2. Six a priori hypotheses used in basin-level analyses to evaluate changes in abundance and productivity across the three study phases.

Model	Hypotheses	Fixed effects
1	Immediate and persistent supplementation effect, NTH adult effect	$\mu + \beta_1\text{Phase1} + \beta_2T_{jt} + \beta_3\text{Phase3} + \beta_4S + \beta_5H_{jt}$
2	Immediate supplementation effect, NTH adult effect	$\mu + \beta_1\text{Phase1} + \beta_2T_{jt} + \beta_3\text{Phase3} + \beta_5H_{jt}$
3	No supplementation effect, NTH adult effect	$\mu + \beta_1\text{Phase1} + \beta_3\text{Phase3} + \beta_5H_{jt}$
4	Immediate and persistent supplementation effect, no NTH adult effect	$\mu + \beta_1\text{Phase1} + \beta_2T_{jt} + \beta_3\text{Phase3} + \beta_4S$
5	Immediate supplementation effect, no NTH adult effect	$\mu + \beta_1\text{Phase1} + \beta_2T_{jt} + \beta_3\text{Phase3}$
6	No supplementation effect, no NTH adult effect	$\mu + \beta_1\text{Phase1} + \beta_3\text{Phase3}$

Note: NTH, nontreatment hatchery fish.

Fig. 3. Hypothetical figure to illustrate interpretation of fixed effects in basin-level analyses. In this example, mean values of all populations in Phase 1 (when all populations were operating in the absence of supplementation) were lower than those in Phase 2 and β_1 is negative. A positive response to supplementation (β_2) was observed in Phase 2 compared with the mean values in reference populations (μ). In Phase 3, mean values of reference populations were higher than those in Phase 2 and β_3 is positive. Furthermore, mean values of supplemented populations were higher than reference populations in Phase 3, so β_4 is positive and a persistent effect of supplementation is inferred. For this example, there were no nontreatment hatchery adults present; therefore, $\beta_5 = 0$.
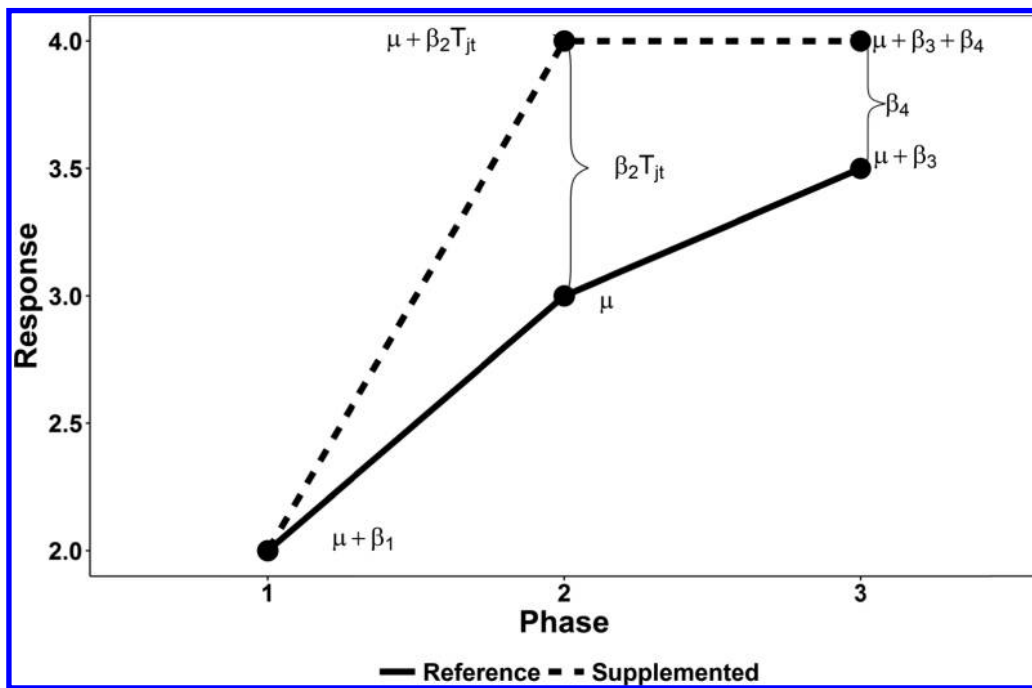
adult progeny per parent redd. In the productivity analyses, redds are used as a surrogate for number of female parents. The basin-level models used the expected value for reference streams as the evaluation point to judge supplementation effects during Phases 2 and 3 (Fig. 3).

The global model contains all the hypothesized fixed terms required to estimate mean expected changes in supplemented populations across the three study phases while accounting for natural changes in response variables using reference populations. We adapted Piepho and Ogutu's (2002) method, which allows the inclusion of indicator and continuous variables in a unified analysis. We used indicator variables to map observations from reference and supplemented populations to the appropriate study phases and continuous variables to account for differing levels of supplementation and the effect of NTH adults. The model that includes all potential variables is

$$
(1) \quad \ln(y_{ijt} + 1) = \mu + \beta_1\text{Phase1} + \beta_2 \ln(T_{jt} + 1) + \beta_3\text{Phase3} \\
+ \beta_4S + \beta_5 \sin^{-1}\sqrt{H_{jt}} + g_i + r_{j(i)} + a_t + \epsilon_{ijt}
$$

Note that eq. 1 is the global model and all other models examined were nested within it and that the effects of T_{jt} and H_{jt} can be positive or negative. The NTH adult variable (H_{jt}) was included in the model as a nuisance variable to control for de facto supplementation, and inference on the effect of NTH fish should be based on the intensive analysis.

To statistically block and account for known variation contained within the data and random noise ($\epsilon_{ijt} \sim N(0, \sigma^2)$), additional error terms were included in all candidate models as random effects:

$$g_i \sim N\left(0, \sigma_g^2\right)$$

$$r_{j(i)} \sim N\left(0, \sigma_r^2\right)$$

$$a_t \sim N\left(0, \sigma_a^2\right)$$

where g_i is a random term for geographic group i based on proximity and geology within basins (see online Supplementary material, Table S1[1]), $r_{j(i)}$ is a random term for population j within geographic group i, and a_t is a random term for cohort t. The $r_{j(i)}$ term also statistically blocks for differences across populations, allowing for a valid assessment of supplementation on an average

Table 3. Four a priori hypotheses used in intensive analyses of supplemented streams with weirs to evaluate changes in abundance due to the origin of female spawners: natural, supplementation, and nontreatment hatchery.

Model	Hypotheses	Fixed effects
1	Abundance change detected from all three female origins	$\mu + \beta_1 N_{jt}^F + \beta_2 T_{jt}^{\text{Ratio}} + \beta_3 H_{jt}^{\text{Ratio}}$
2	Abundance change detected from natural and supplementation females	$\mu + \beta_1 N_{jt}^F + \beta_2 T_{jt}^{\text{Ratio}}$
3	Abundance change detected from natural and nontreatment hatchery females	$\mu + \beta_1 N_{jt}^F + \beta_3 H_{jt}^{\text{Ratio}}$
4	Abundance change detected only from natural females	$\mu + \beta_1 N_{jt}^F$

stream. Estimated variation across geographic groups, populations within geographic groups, year, and unexplained noise equal σ_g^2, σ_r^2, σ_a^2, and σ^2, respectively.

We fit each a priori model using maximum likelihood (ML) estimation in R (R Core Team 2014) using "lme4" (Bates et al. 2014) and ranked them with a modified Akaike information criterion (AIC$_c$; Akaike 1973; Burnham and Anderson 2002). After each model was ranked from the lowest to highest AIC$_c$, the difference in AIC$_c$ values (ΔAIC$_c$) from the top ranked model was calculated (see online Supplementary material, Tables S2–S45[1]), along with model probabilities to assess model selection uncertainty (Burnham and Anderson 2002). After models were ranked with ML methods, each model was then refit using restricted maximum likelihood to estimate coefficients and account for the biased ML variance estimates (Burnham and Anderson 2002; Symonds and Moussalli 2011; Littell et al. 2006).

Multimodel inference was performed by averaging across the full model set using ML-based model probabilities and the restricted maximum likelihood coefficients. Including all models in the set shrank averaged coefficients towards zero, providing a conservative coefficient estimate that includes model uncertainty in the confidence intervals (Burnham and Anderson 2002; Grueber et al. 2011). Parameter (point) estimates were used to estimate the direction of the effect (positive or negative), and 95% confidence intervals (CIs) determined the strength of inference (strong or weak). The CIs are used as a guide to how reliable the point estimates are, not as an accept or reject criterion. We define strong inference when 95% CIs do not overlap zero and weak inference when they do (Burnham and Anderson 2002; Bolker et al. 2009).

Model results are in log space, so for ease of interpretation and to provide managers an estimated change in population demographics from supplementation, it was necessary to back-transform averaged coefficients. A proportional change in a Phase 2 population response variable is given by X^{β_2}, where X is the proportional change in the number of supplementation females passed. Although different values of X can be used, for our purposes we arbitrarily selected $X = 1.25$ to represent a 25% increase in the mean number of supplementation females passed (Clearwater basin = 39 females, Salmon basin = 76 females). To examine the Phase 3 shifts caused by supplementation, a proportional difference between average supplemented and reference streams is given by e^{β_4}.

We assessed model performance in two ways. First, for each ranked model, the proportion of variance explained by the fixed and random terms (conditional R^2) was calculated along with the proportion explained by just the fixed effects (marginal R^2) to decompose the variation (Nakagawa and Schielzeth 2013). We report conditional and marginal R^2 values for the top ranking model. Second, we examined model fit and assumption violations for independence, homogeneity, serial correlation, and normality by visually inspecting residuals from global models using diagnostic plots (Burnham and Anderson 2002).

Intensive analyses of supplemented populations with weirs

To develop guidance for supplementation programs, the abundance response to the addition of supplementation and NTH females relative to natural females was evaluated. For this analysis, we used data collected during Phase 2 in supplemented populations with weirs ($N = 8$; see Fig. 1). These studies were completed at the same four life stages examined with the basin-level analyses. Weir control allowed for a more accurate and precise comparison of female origins with respect to their effect on population response at each life stage; because reference populations were not a consideration here, we were able to use a better metric of abundance for this analysis. Similar to Objectives 1 and 2, a common model set was fit to estimate female spawner contribution to abundance at each life stage by switching the response variable. Evidence of assumption violations were not observed in the residual plots including serial correlation or multicollinearity.

To estimate the rate of change in abundance attributed to spawners of different origin, we began with the global model (eq. 2) written as

$$(2) \quad \ln(y_{jt} + 1) = \mu + \beta_1 \ln\left(N_{jt}^F + 1\right) + \beta_2 \ln\left(T_{jt}^{\text{Ratio}} + 1\right) \\ + \beta_3 \ln\left(H_{jt}^{\text{Ratio}} + 1\right) + r_j + a_t + \epsilon_{jt}$$

where y_{jt} is the response variable of redds, naturally produced emigrants at RST, naturally produced smolts at LGR, or natural progeny returns to the weir for population j in cohort t. The term β_1 is the proportional increase in the response variable due to a proportional increase in natural females spawning. Change in abundance due to an increase in supplementation and NTH females was estimated with β_2 and β_3, respectively. Estimating the change in abundance attributed to different supplementation ratios provides a tool for future weir management, because populations are supplemented with respect to natural abundance rather than fixed amounts. Hence, we use a ratio here, so please note the change from the basin-level analysis. Also note that β_1 is not directly comparable with β_2 or β_3.

We formed four a priori hypotheses and implemented them as alternative models to explain the variation in the data (Table 3). The second and third hypotheses include natural and either supplementation or NTH female terms, respectively, indicating only two origins contribute to abundance changes. The fourth hypothesis predicts that the variation in abundance is explained solely by natural females.

To understand the connection between the related parameter estimates expressed in different scales (i.e., β_1 versus β_2), we modeled the effect of varying supplementation ratios at different female abundance levels using model-averaged coefficients from the intensive analyses. We allowed total female abundance to range from 10 to 660 individuals, which was approximately the observed range of the data. We set supplementation ratio inputs (T_{jt}^{Ratio}) at 0.0, 0.5, 1.0, 1.5, and 2.0, which encompassed the majority of achieved rates (Fig. 2). Then, after applying the fixed supplementation ratios to total females, our natural female inputs (N_{jt}^F) ranged from 3 to 660 individuals. We set the NTH female ratio (H_{jt}^{Ratio}) to zero to focus interpretation on the effect of supplementation. Comparison of β_2 and β_3 is straightforward and is not incorporated into this visualization. Expected model results were then back-transformed from the log-scale and plotted to visualize the average predicted response in real values.

Fig. 4. Mean expected abundance during each study phase at four life stages assuming an average number of adult supplementation females passed into supplemented populations relative to reference populations as estimated from model-averaged coefficients. Bold lines indicate overall basin means, and thin lines are each population's mean abundance by study phase.
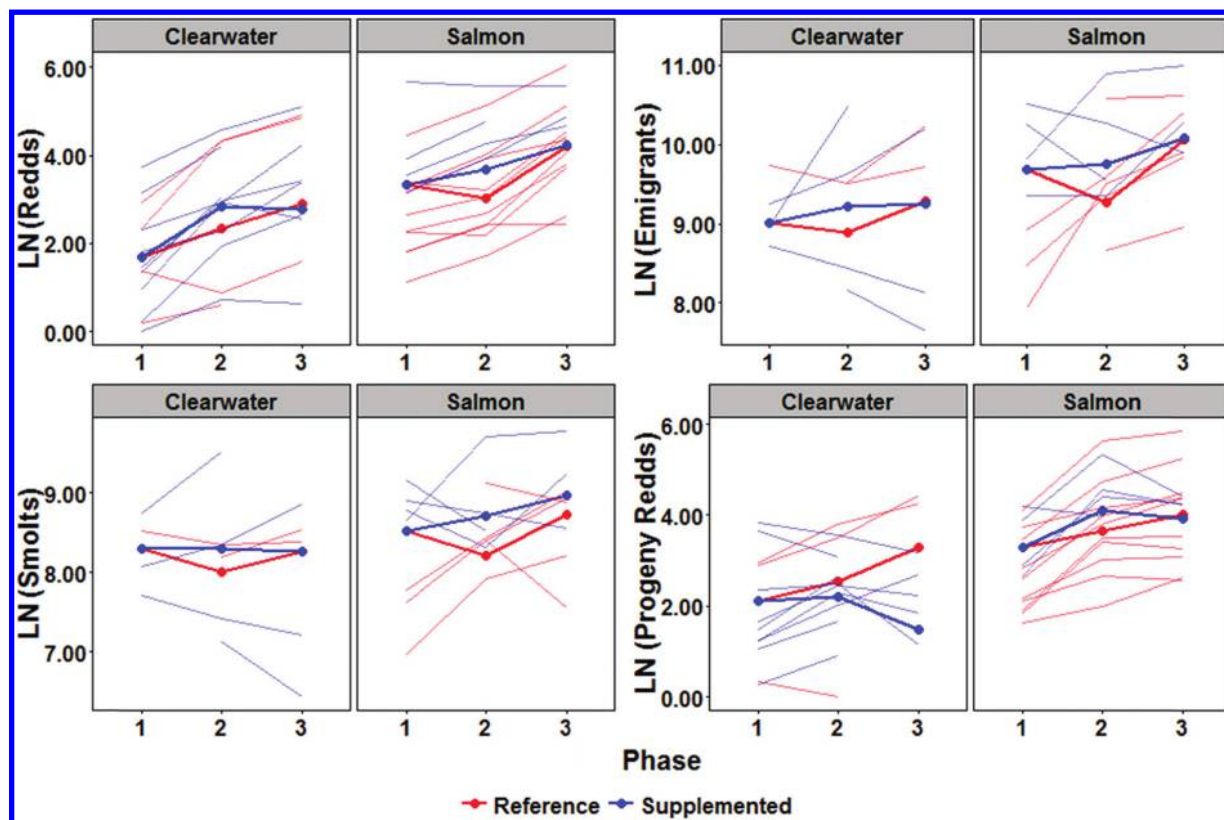
Results

Basin-level analyses of abundance and productivity

Mean expected abundance at all four life stages in both basins generally increased across study phases for both reference and supplemented populations (Fig. 4). Abundance increases were typically larger in supplemented populations during Phase 2. During Phase 3, mean expected abundance in reference and supplemented populations returned to approximately their Phase 1 relationship (i.e., $\beta_4 \approx 0$; Fig. 4). However, in the Clearwater basin, mean expected smolt abundance did not change among study phases and adult progeny declined in supplemented populations from Phase 2 to Phase 3. In the Salmon basin, increases with study phase were more consistent. However, variability around the mean expected abundances was high, much of which was due to stable differences among the study populations (Fig. 4).

In the Clearwater basin during Phase 2, estimates of the supplementation effect on abundance decreased across the four life stages (Fig. 5). There was strong inference for a positive supplementation effect in total redds, although the effect was small. This was the only life stage where the CI did not overlap zero. Increasing mean adult female supplementation by 25.0% would increase redds by 3.9% on average. Point estimates also indicated increases in emigrants at RST and smolts at LGR, although the inference was weak. With a 25% increase in supplementation rate, emigrants at RST would increase by 2.5% and smolts at LGR would increase by 2.3%, slightly less than the mean expected increase for redds. The point estimate for adult progeny return indicated a negative effect with weak inference, which would result in a 2.4% decrease if female supplementation increased by 25.0%.

In the Clearwater basin during Phase 3, abundance estimates were similar between supplemented and reference populations, except for abundance of adult progeny. However, the width of the

CI about the adult progeny abundance estimate shows it is imprecise. This effect was estimated to reduce adult progeny by 83.5% relative to the Clearwater basin reference populations.

In the Salmon basin during Phase 2, estimates of the supplementation effect and CIs at all life stages indicate positive effects with strong inference (Fig. 5). All point estimates again decreased through the life cycle. Increasing adult female supplementation by 25.0% would increase redds by 3.9%. For the same increase in adult female supplementation rates, mean expected abundance increase was slightly lower at the emigrant stage at RST, smolt stage at LGR, and adult progeny life stage with 2.9%, 3.2%, and 2.7% increases, respectively. The smallest supplementation effect occurred at the life-cycle evaluation point furthest in time from the supplementation action: natural adult progeny returns.

During Phase 3 in the Salmon basin, estimated postsupplementation effects were similar across all life stages. Parameter estimates for redds, emigrants at RST, and smolts at LGR were positive with weak inference and negative with weak inference for adult progeny (Fig. 5).

Mean expected productivity estimates predominantly decreased during the study in supplemented and reference populations, although there was much variability among populations (Fig. 6). The mean expected number of emigrants at RST per redd in both basins and population types declined sharply from Phase 1 to Phase 2 and remained similar between Phase 2 and Phase 3. Mean expected number of smolts at LGR per redd followed the same pattern, except reference populations in the Salmon basin declined linearly from Phase 1 to Phase 3. In the Clearwater basin, adult progeny per redd declined from Phase 1 to Phase 3 in both supplemented and reference populations. In the Salmon basin, adult progeny per redd increased from Phase 1 to Phase 2 and then declined in Phase 3 for both population types (Fig. 6). In general,

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Fig. 5. Model-averaged coefficient estimates and 95% confidence intervals for supplementation effects on abundance during Phase 2 and Phase 3 by life stage (β_2 and β_4 from eq. 1).
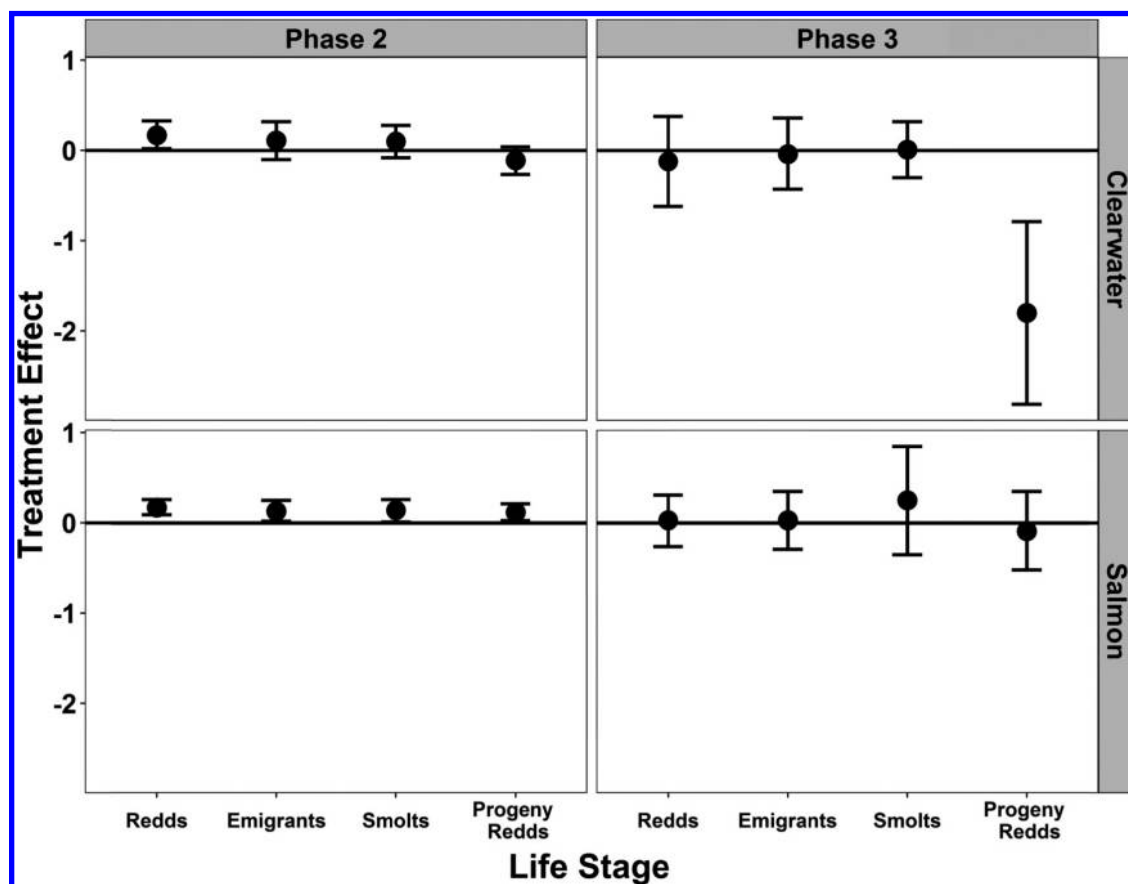
populations in Phase 3 experienced the lowest productivity for all life stages in both Clearwater and Salmon basins during the course of the study.

In the Clearwater basin during Phases 2 and 3, estimates of the supplementation effect on productivity were close to zero. During both phases, point estimates were positive with weak inference for emigrants per redd and smolts per redd and negative with weak inference for adult progeny per redd (Fig. 7). During Phase 2, increasing the mean supplementation rate by 25% resulted in less than a 1.0% increase in productivity measured as emigrants per redd and smolts per redd and a 1.3% reduction measured as adult progeny per redd. In Phase 3, a 25% increase in supplementation rate increased emigrants per redd and smolts per redd by 1.0% and 4.1%, respectively, and reduced adult progeny per redd by 9.5% relative to reference populations.

In the Salmon basin, the supplementation effects on productivity were negative in Phases 2 and 3 at all life stages. All inferences were weak except for the Phase 2 adult progeny per redd estimate (Fig. 7). In Phase 2, increasing adult female supplementation by 25% would reduce productivity by 0.4%, 1.1%, and 1.5% for emigrants at RST per redd, smolts at LGR per redd, and adult progeny per redd, respectively. Estimated Phase 3 supplementation effects on emigrants at RST per redd, smolts at LGR per redd, and adult progeny per redd suggest productivity would decrease by 3.0%, 1.0%, and 9.5%, respectively.

The point estimates for the effect of NTH adults spawning in study populations were positive for abundance measures and negative for productivity measures in both basins. Interpretation of CIs yields strong inference for increases in redd abundance with additional NTH adults in both basins and reductions in smolts at LGR per redd productivity in the Clearwater basin and adult prog-

eny per redd productivity in the Salmon basin (Fig. 8). All other inferences are weak.

The top model explained a large proportion of the variance in abundance and productivity (Table 4). Conditional R^2 averaged 0.577 for the Clearwater basin and 0.661 for the Salmon basin data sets and ranged from 0.169 to 0.832 and 0.531 to 0.837, respectively. However, the amount of variation explained by fixed effects (marginal R^2) was small compared with the total variance explained (conditional R^2) for each model. Examining the Clearwater basin data sets, we found that marginal R^2 averaged 0.118 and ranged from a low of 0.035 for smolts at LGR to a high of 0.327 for smolts at LGR per redd data. Marginal R^2 values in the Salmon basin averaged 0.076 and ranged from a low of 0.018 for smolts per redd to a high of 0.127 for smolts at LGR. Using the average variation explained across all response variables, we found that fixed effects accounted for a small proportion of all explained variation: 0.205 (0.118/0.577) for the Clearwater basin and 0.115 (0.076/0.661) for the Salmon basin.

Intensive analyses of supplemented populations with weirs

Abundance estimates at all life stages increased with the addition of female spawners in both basins, but effects tended to diminish through the life cycle (Fig. 9). Point estimates for natural females indicated positive effects with strong inference on the abundance of redds, emigrants at RST, and smolts at LGR and positive effects with weak inference on adult progeny in both basins. Point estimates for supplementation females suggested positive effects on all life-history stages in the Salmon basin but only for redds in the Clearwater basin, with strong inference for redd abundance in the Salmon basin and weak at all other life stages in both basins. NTH females had point estimates indicating

Fig. 6. Mean expected productivity during each study phase at four life stages assuming an average number of adult supplementation females passed into supplemented populations relative to reference populations as estimated from model-averaged coefficients. Bold lines indicate overall basin means, and the thin lines are each population's mean productivity by study phase.
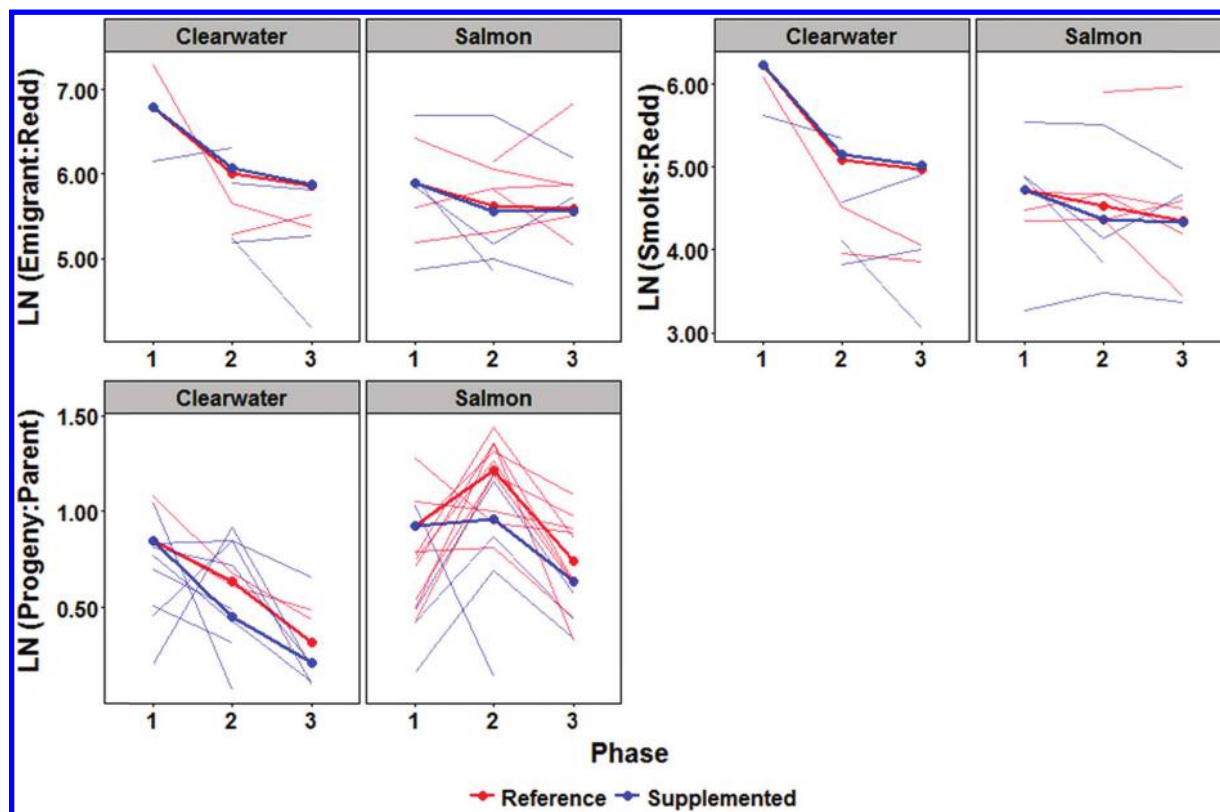
small positive effects on all life stages, except for emigrants at RST in the Clearwater basin, which was negative. Confidence intervals for all NTH female estimates indicated weak inference (Fig. 9). The point estimates of NTH females were smaller in the Clearwater basin compared with the Salmon basin.

Supplementation ratio influenced predicted abundance measures, assuming no NTH females escaped (Fig. 10). For example, supplementing the average population in the Salmon basin at a 1:1 ratio at a natural abundance of 200 females spawners (thus 400 total females spawning) would produce more emigrants than the unsupplemented population but not as many as that population with 400 natural females spawning. At a particular female escapement, the number of progeny produced was predicted to be smaller as the supplementation ratio increased, although adding supplementation females did have a benefit. As total female escapement increased, the abundance of redds, emigrants at RST, and smolts at LGR continued to increase, but the rate of increase declined as the supplementation ratio became larger. There was one exception; there was little or no relationship between natural adult progeny and supplementation ratio in either basin (Fig. 10, bottom right panel). In the Clearwater basin, estimated increases were less than 1.0% for a 25.0% increase in either natural females or supplementation ratio. Estimates for the Salmon basin were slightly larger, with the largest effect of a 5.3% increase in adult progeny for a 25.0% increase in the supplementation ratio.

The models used in the intensive analyses of supplemented populations with weirs again explained a large proportion of the variance in the data, particularly for the freshwater life stages, but here the fixed effects (marginal R^2) were more important. This was likely due to the increased accuracy and precision of adult escapement estimates provided by the weirs. In the Clearwater basin, marginal R^2 values averaged 0.515 and ranged from 0.693 for emigrants at RST to 0.001 for adult progeny. Marginal R^2 values for

the Salmon basin data sets averaged 0.492 and ranged from 0.904 for redds to 0.065 for adult progeny (Table 5). This indicates that fixed effects are important predictors of abundance during the freshwater portion of the life cycle, but random effects drive adult returns.

Discussion

Supplementation resulted in increased abundance in Phase 2 that did not persist into Phase 3, and productivity costs were low. Redd counts increased across both basins from Phase 1 to Phase 2, but they increased more in supplemented than in reference populations. This observed abundance effect diminished through the life cycle, and the trend was consistent across basins. We observed similar effects of NTH adults on redd abundance (i.e., egg production), but positive effects were not observed in juvenile life stages or in adult progeny. After supplementation ceased, abundance and productivity at each life stage in supplemented and reference populations returned to their Phase 1 relationships with one exception (discussed below), suggesting supplementation did not have lasting effects on abundance or productivity. Random effects (population, geographic group, and year) explained the majority of the variation in all models, suggesting factors outside the study design (e.g., hydroelectric development, ocean conditions, local habitat conditions) have a much greater influence on abundances and productivity than factors under the control of supplementation programs (e.g., number of juveniles or adult females released, supplementation ratio, or brood stock type).

The study design was robust enough to allow inference on small supplementation and postsupplementation effects. The target was to double the number of female spawners, but the range of supplementation ratios achieved provided statistical power to estimate population response as supplementation ratio changed.

Fig. 7. Model-averaged coefficient estimates and 95% confidence intervals for supplementation effects on productivity during Phase 2 and Phase 3 by life stage (β_2 and β_4 from eq. 1).
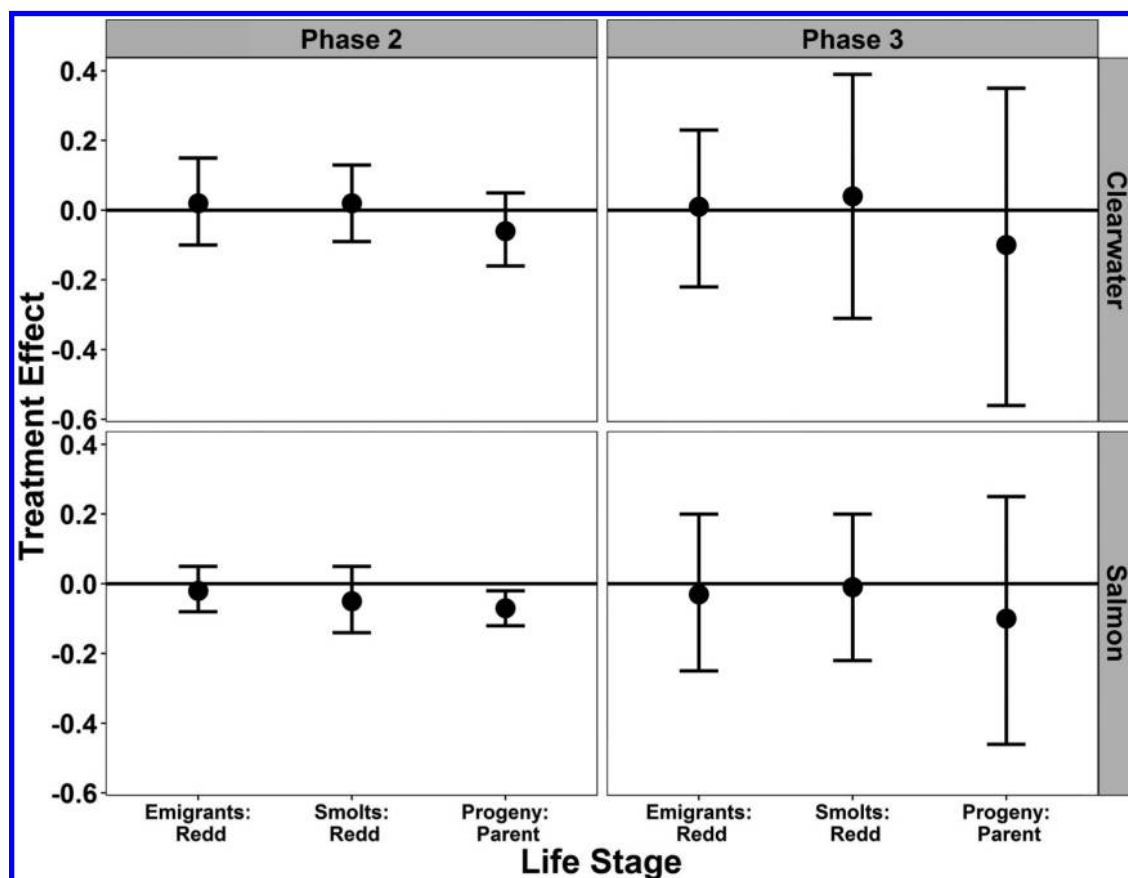
Finally, the phases were of sufficient duration to detect supplementation effects and the return to their original relationships. The inferences made here are conservative and general, but interpopulation variability shows supplementation should be customized to the target population.

Evaluation at multiple points throughout the life cycle is important to understand or explain mechanisms (Dorner et al. 2013). Natural adult progeny represent the ultimate response desired, but estimates of supplementation effects on other life stages provide important insight into the mechanisms behind what was observed. For example, supplementation did not increase the abundance of natural adults, but natural juvenile abundances were increased along with minimal productivity costs. The life cycle evaluation suggests the failure of supplementation to increase adult abundance in the Clearwater basin occurred after smolt emigration.

Likewise, addressing supplementation across two large basins allows for greater generality of inference. We observed common results across basins and life stages, suggesting our results have applicability to other systems where supplementation occurs. The Clearwater and Salmon basins represent contrasting examples of how supplementation programs operate in the Pacific Northwest. The Clearwater basin represents how supplementation was viewed at the inception of this project (early 1990s), whereas the deliberate incorporation of natural adults as done in the Salmon basin was an innovation. Over the course of the study, the state of the science has evolved from the Clearwater example towards the Salmon basin example.

Basin-level analyses of abundance and productivity

The strongest response to supplementation observed here was the immediate production of eggs (as indexed by redds) resulting

from passage of females into spawning reaches. During supplementation, we observed positive effects on abundance across all life stages in the Salmon basin but only on redd production in the Clearwater basin. Response of the reference populations showed that abundance increased in all study populations across phases but, on average, the increase was greater in supplemented populations during Phase 2.

During Phase 3, the persistent effects of supplementation were generally small with weak inference with one notable exception. We observed a negative effect with strong inference on the abundance of adult progeny in the Clearwater basin, even though the effects at other life stages were negligible. We attribute this finding to a large increase in redd abundance in the two reference populations with the highest abundances and a low proportion of NTH adults in these two populations during 2013 and 2014. Concurrently, we had to exclude two low-productivity reference populations during Phase 3 because we lacked age data to assign adult progeny to a cohort. Regardless, this result is inconsistent with other responses observed across phases, basins, and life stages and is not supported by the productivity results.

Abundance increases in response to supplementation are commonly observed. Sharma et al. (2006) found that supplementation of a coho salmon (*Oncorhynchus kisutch*) population on the Washington (USA) coast increased total adult return and was necessary to maximize adult production unless freshwater and ocean conditions were optimal. The authors concluded that supplementation could slow declines and provide increased capacity for recovery. Chum salmon (*Oncorhynchus keta*) populations in the Strait of Juan de Fuca and Hood Canal increased in abundance since supplementation programs were initiated in the 1990s (PNPTT and WDFW 2014). Supplementation of steelhead trout

Fig. 8. Model-averaged coefficient estimates and 95% confidence intervals for effects of nontreatment hatchery adults on abundance and productivity by life stage (β_5 from eq. 1). Note that the coefficient values here are on different scales than in Figs. 5, 7, and 9 and cannot be directly compared.
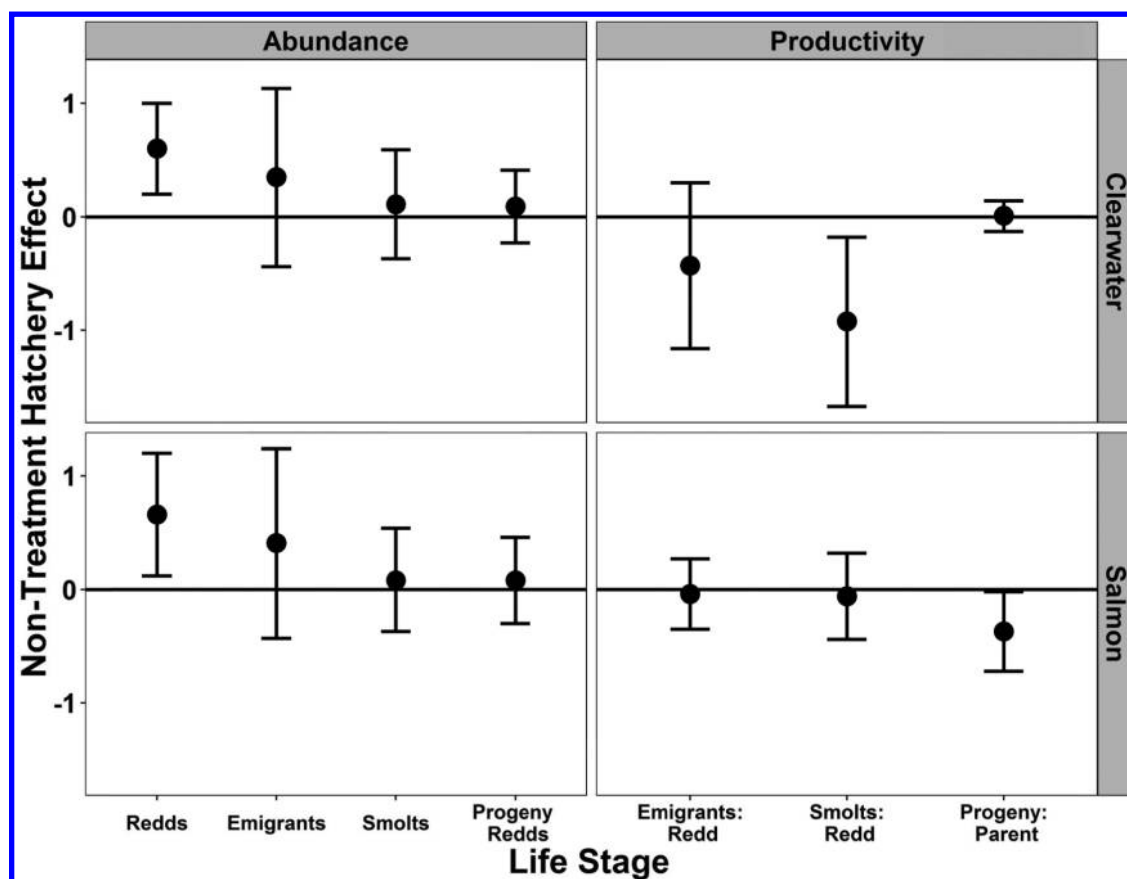

Table 4. Summary of model fit in the basin-level analyses.

Response	Clearwater basin		Salmon basin	
	Conditional R^2	Marginal R^2	Conditional R^2	Marginal R^2
Redd abundance	0.805	0.118	0.837	0.104
Emigrant abundance	0.662	0.044	0.645	0.119
Smolt abundance	0.671	0.035	0.531	0.127
Progeny redds	0.832	0.042	0.796	0.046
Emigrants per redd	0.169	0.169	0.550	0.020
Smolts per redd	0.327	0.327	0.659	0.018
Adult progeny per redd	0.570	0.093	0.611	0.098

Note: Conditional R^2 values represent the total variance explained, and marginal R^2 values represent the proportion of variance explained by fixed effects.

(*Oncorhynchus mykiss*) in the Hamma Hamma River (Washington, USA) increased redd abundance without reducing production of natural fish (Berejikian et al. 2008). In the Yakima River, supplementation increased spring Chinook salmon redd counts by 126% since supplementation began, compared with a 52% increase in an unsupplemented reference population (Fast et al. 2015).

In the Snake River basin, supplementation programs have had smaller effects on abundance. Scheuerell et al. (2015) did a large-scale analysis of 22 spring–summer Chinook salmon populations across the Salmon, Grande Ronde, and Imnaha river basins and found that spawner densities increased 0%–8% relative to un-supplemented years. We found similar effects of supplementation; boosting female abundance by 25% resulted in a change in progeny redds of –2.4% to +2.7%. Some evaluations concluded that supplementation sustained a population when returns were critically low but did not result in rebuilding populations (e.g., Cleary et al. 2014; Gallinat and Ross 2015).

All productivity effects were essentially the same in both basins, but only adult progeny per parent redd in the Salmon basin was precise enough for strong inference during Phase 2. The mean expected number of emigrants at RST per redd and smolts at LGR per redd were nearly identical between supplemented and reference populations. Confidence intervals were much wider for Phase 3 parameter estimates relative to Phase 2 because we estimated Phase 3 parameters based on fewer years with a concurrent reduction of the number of populations in the analyses due to non-study-related management actions.

NTH adults had a negative effect on population productivity across all phases. Effects in the Clearwater basin were greatest on smolts at LGR per redd. In the Salmon basin, the effect of nontreatment adults was greatest on adult progeny in the next generation. Five of the six life-stage-by-basin productivity parameters estimated were negative, and the effect on adult progeny per redd in the Clearwater basin was virtually zero. While the point esti-

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Fig. 9. Model-averaged coefficient estimates and 95% confidence intervals for the effect of natural females, supplementation ratio, and nontreatment hatchery adult ratio on abundance by life stage (β_1, β_2, and β_3 from eq. 2). Note that the coefficient values for natural origin females are on a different scale than the other two and cannot be directly compared.
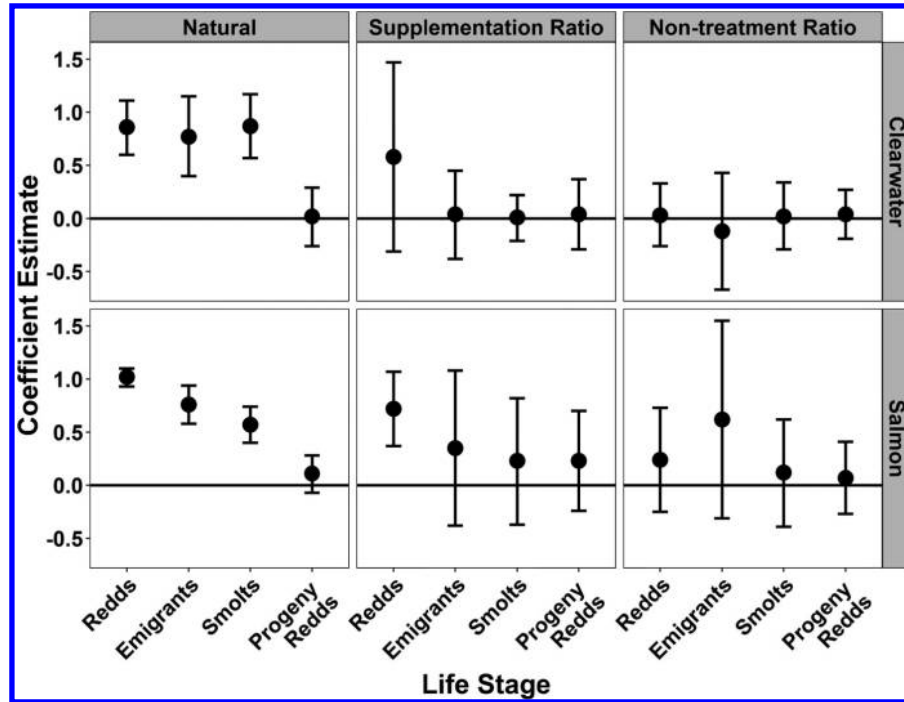
mates had wide CIs, there was an overall pattern of negative effects of nontreatment adults at all life stages. These findings are consistent with other studies that have shown that nonendemic stocks (Araki et al. 2007) or those with a history of hatchery rearing (Fleming et al. 2002; Huntingford 2004) typically underperform in the natural environment relative to those of natural origin.

In contrast with the trend in abundance, population productivity declined across phases in reference and supplemented populations. That is, per capita contribution to juvenile life stages and next-generation adults decreased even as total abundance increased in the study populations. Two nonexclusive potential mechanisms could explain these results. The first is that these populations may be operating at or near density dependence in the core habitats in which they are spawning (Walters et al. 2013; Boe and Crump 2015). The spatial distribution of spawning in the study area expands slowly with abundance (Isaak and Thurow 2006), which may lead to juveniles that emerge and forage together in a relatively small and unproductive space (see Walters and Juanes 1993). The second potential mechanism is that behavioral or genetic effects in hatchery fish may reduce their fitness in natural habitats relative to natural fish (McLean et al. 2003; Araki et al. 2008; Christie et al. 2014), thus reducing productivity.

Studies of productivity or individual reproductive success generally show negative effects of hatchery fish on the spawning grounds, and similar results are often found in supplementation evaluations. In general, reproductive performance of hatchery fish in natural environments is less than that of natural fish, although individual study results may be highly variable (Araki et al. 2008; Hess et al. 2012). Productivity of natural salmon and steelhead trout populations in the Pacific Northwest tended to be reduced in the presence of hatchery fish on the spawning grounds, and this effect was not related to type of brood stock (i.e., integrated or mitigation) or duration of exposure (Chilcote et al. 2011). Sharma et al. (2006) found an asymptotic relation of smolts to spawners such that natural productivity (smolts/spawner) declined as proportion of supplementation spawners increased.

The literature suggests a trade-off between the number of supplementation spawners and the demographic benefit that they provide to a natural population (Oosterhout et al. 2005; Fraser 2008), an observation consistent with our findings (Fig. 10). Our results show more adult progeny per redd in reference populations versus supplemented in Phase 2 and Phase 3, although differences are small and bounds overlap zero except during Phase 2 in the Salmon basin. Buhle et al. (2009) found that the density-dependent effects of hatchery Coho salmon were five times greater than that for natural fish and that population productivity decreased as juvenile releases and adult escapement of hatchery fish increased. When implementing a supplementation program, managers should expect productivity reductions as abundance is increased, and the trade-off of cost versus benefit should be built into the management plan.

Intensive analyses of supplemented populations with weirs

Some interesting patterns emerged when we addressed the effects of female origin on population abundance. Natural females were more effective than supplementation females (Fig. 10). Given the relationship between supplementation and NTH females (Fig. 9), natural females were also more effective than NTH females. These patterns were similar across life stages and basins, although effects attenuated through the life cycle. Additional supplementation and mitigation hatchery females had almost no effect on production in the Clearwater basin, except for the effect of supplementation females on redds. In the Salmon basin, the abundance of both supplementation and NTH females corresponded to changes in production across life stages. All positive effects disappeared or declined by the return of adult progeny in both basins, highlighting the influence of out-of-basin factors.

The primary difference between basins with respect to these findings is in brood stock origin. Supplementation in the Clearwater basin was done using localized, harvest mitigation brood stocks. Therefore, one should expect the supplementation effect should be the same as that of NTH females. Further, Clearwater basin populations continue to see high proportions of hatchery

Fig. 10. Mean expected change in abundance by life stage in the next generation relative to differing supplementation ratios, based on data from supplemented populations with weirs. Nontreatment hatchery females were assumed absent.
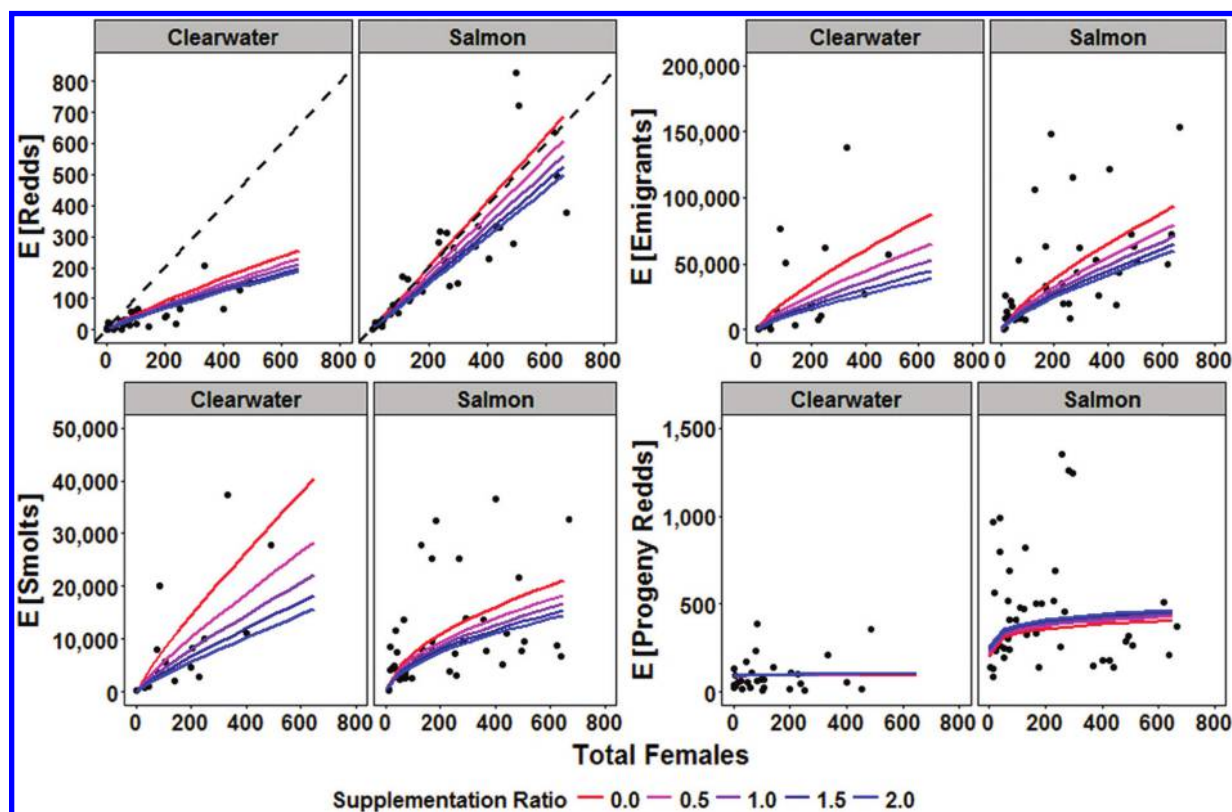

Table 5. Summary of model fit in the analysis of supplemented populations with weirs.

Response	Clearwater basin		Salmon basin	
	Conditional R^2	Marginal R^2	Conditional R^2	Marginal R^2
Redd abundance	0.820	0.676	0.944	0.904
Emigrant abundance	0.760	0.693	0.819	0.569
Smolt abundance	0.881	0.688	0.715	0.428
Progeny abundance	0.896	0.001	0.800	0.065

Note: Conditional R^2 values represent the total variance explained, and marginal R^2 values represent the proportion of variance explained by fixed effects.

fish on the spawning grounds. Even so, we found that natural spawners in the Clearwater basin had a greater effect on abundance than supplementation or NTH females. Salmon basin hatcheries in this study were founded with local stocks (Howell et al. 1985; Bowles and Leitzinger 1991). Thus, in the Salmon basin, both supplementation and NTH females should have a greater degree of local adaptation compared with stocks in the Clearwater basin, which may facilitate a more rapid population response to improved ocean and migratory conditions. Interestingly, across both basins the greatest effect in all life stages resulted from passage of natural females above the weir. The consistency in the results of the intensive studies across life stages corroborates observations made in the basin-level examinations.

Our modelling exercise showed that the stock–recruit relationship is maximized in an all-natural population and becomes progressively depressed as the population shifts toward increasing supplementation similar to Buhle et al. (2009), although this effect is undetectable over the full adult-to-adult life cycle (Fig. 10). That is, additional fish were produced but not as quickly as T_{jt}^{Ratio} increased (Fig. 10, redd, emigrant, and smolt panels). Although the number of NTH females was held at zero in the model, the slope of this relationship will decline faster in their presence. The number of natural adult progeny returns increased slightly in the Salmon

basin, but this increase was not observed in the Clearwater basin (Fig. 10, adult progeny panel).

Models used in the intensive analyses performed better than those used in the basin-level analyses. In the intensive analyses, the conditional R^2 averaged approximately 83% for both basins versus 58% in the Clearwater basin and 66% in the Salmon basin in the basin-level analyses. Here we were able to measure the population inputs directly (females of all origins upstream of weirs), and this reduced the amount of unexplained variance and provided better resolution on the actual supplementation effect. For redds, emigrants at RST, and smolts at LGR, marginal R^2 explained a large fraction of the total variance observed. However, fixed effects explained almost none of the total variance for adult progeny (0.1% in the Clearwater basin and 6.5% in the Salmon basin). Out-of-basin factors take over once fish pass LGR, because survival past this point is low and highly variable (Copeland et al. 2014; Schaller et al. 2014). This explains, in large part, why supplementation gains in this study were ephemeral.

The smaller-scale intensive studies corroborated the basin-level analyses. The general pattern of the intensive study results was consistent between basins and was also consistent with results from the basin-level analyses. The effect of the proportion of NTH adults on population abundance and productivity is consistent

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between analyses, and the results of the intensive analysis support our interpretation of the basin-level analysis. We also observed that out-of-basin effects had a dramatically larger effect than supplementation on the abundance of adult progeny, even though supplementation almost doubled the number of spawning females. This concordance of results provides a strong weight of evidence that demographic supplementation in natal habitats (as implemented here) as a stand-alone tool will contribute little to recovery, but can provide short-term demographic benefits. New individuals were created most effectively by additional natural fish, but passing supplementation fish did increase population abundance, at least within the spawning and rearing habitat.

For supplementation to be an effective conservation tool, managers must balance the trade-off of increased spawner abundance against genetic fitness costs (Fraser 2008). Theory suggests that the hatchery and natural populations are at different fitness optima, and gene flow between the two will reduce the fitness of the natural population (Ford 2002). Therefore, genetic risks to the natural population should be reduced if the genetic similarity between hatchery and natural fish is high. Further, with continued introgression of mitigation hatchery stocks into natural populations (as in the Clearwater basin), it is unlikely local adaptation will occur. A key uncertainty is how quickly populations recover from the influx of hatchery fish with a different fitness optimum (Venditti et al. 2013). Until we have a better understanding of this process, questions regarding the long-term genetic effects of supplementation will remain.

Guidance for supplementation programs

Environmental legislation has been enacted in various countries to prevent species from becoming threatened or endangered and to guide the management and recovery of listed species (e.g., the US Endangered Species Act, Canada's Species at Risk Act, the Berne Convention on the Conservation of European Wildlife, and Australia's Natural Habitats and the Environment Protection and Biodiversity Conservation Act of 1999). The first goal of a recovery program is a level of population viability warranting removal from legal protection. Higher-level goals might include sustainable harvest and ecological function. Supplementation is intended to be one of the tools by which managers might achieve those goals (e.g., Kline and Flagg 2014; Fast et al. 2015). As implemented by this study, supplementation failed to achieve even the lowest of the recovery goals. Supplementation alone cannot reverse population declines without concurrent efforts to rectify the factors ultimately responsible. However, we have shown positive results, indicating that supplementation can be useful for specific objectives and with sufficient guidance.

For supplementation to be a useful management tool, its proper uses must be defined and its implementation must be improved based on monitoring and research findings. We make four conclusions from this research: (1) population increases are more effectively generated by increasing the number of natural fish than by other means (e.g., habitat restoration); (2) supplementation ratios should be tied to risk of recruitment failure (e.g., by use of sliding scales); (3) when risk of recruitment failure is low, investigate alternative ways to minimize density effects and maximize the effectiveness of supplementation fish; (4) whenever possible, supplementation should be implemented using a brood stock integrated with the natural population to minimize fitness costs. Supplementation needs to be part of an integrated life-cycle strategy that addresses all limiting factors, especially to allow sustainable harvest. Given what we have learned, there are at least three goals appropriate for supplementation programs: (i) maintain smolt production during low escapements, (ii) seed unoccupied or restored habitats, and (iii) restore or maintain harvest opportunity concurrent with population recovery. Supplementation programs need to be customized to the intended target populations. Within the overall supplementation goal of maintaining

or increasing abundance without decreasing long-term productivity (RASP 1992), there is a continuum of strategies available based on degree of genetic and demographic risk. These range from population rescue (Kline and Flagg 2014) through captive rearing (Venditti et al. 2013; Stark et al. 2014) to augmentation with an integrated brood stock (HSRG 2009, 2014). The supplementation strategy employed should be guided by population status and management goals, and the strategy should include triggers for stopping supplementation when these are achieved.

Another important lesson was supplementation programs need to be adaptively managed. There are many sources of uncertainty regarding performance of salmon populations: a high degree of natural variability in important processes (e.g., life stage survival), logistical difficulties in making relevant measurements, and imperfect understanding of influential factors. Therefore, monitoring is vital and learning should be an explicit management goal.

In summary, supplementation can be useful as part of an integrated management approach to maintain population abundance in the face of poor survival conditions. Postsupplementation results show that temporary benefits can be achieved while keeping ecological costs low (i.e., the supplemented populations were still resilient after supplementation ceased). The decision to intervene is primarily a policy decision. As such, policy makers need to consider the substantial resources required for an effective supplementation program and the strategic collaboration necessary with other recovery programs. Supplementation alone is not a panacea because it does not correct fundamental limiting factors that must be addressed to achieve population levels capable of sustaining ecological function and fishery opportunities.

Acknowledgements

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