Evaluating surrogacy of hatchery releases for the performance of wild yearling Chinook salmon from the Snake River Basin

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Abstract.

The combined juvenile and adult detections of PIT-tagged Snake River yearling Chinook salmon (*Oncorhynchus tshawytscha*) migrating through the Federal Columbia River Power System were analyzed using the ROSTER statistical release-recapture model. This model was used to estimate the downriver survival of smolts, ocean survival, adult passage success, and smolt-to-adult ratios (SARs) for wild and hatchery-reared Chinook salmon released as yearlings in the Snake River Basin from 1996 through 2004. Estimates from wild and hatchery release groups were compared to assess the extent to which hatchery stocks may be used as surrogates for endangered wild stocks. Wild release groups included both spring and summer runs, while hatchery release groups were separated by run (spring vs. summer). Overall, there was a significant difference ($P<0.10$) between estimates from wild release groups and hatchery spring run release groups for all survival measures except ocean survival, but not between wild release groups and hatchery summer run release groups. Estimates of adult passage success ($P = 0.013$) and SAR ($P < 0.001$) were significantly higher for wild groups than for hatchery spring groups. There was high correlation ($r>0.8$) between estimates from wild fish and both spring and summer hatchery fish for all measures except adult passage success within a calendar year. It appears that hatchery summer Chinook salmon stocks from the Snake River basin may be used as surrogates for wild stocks for measuring survival on large temporal and spatial scales (e.g., annual basin-wide measures). Because of differences between survival estimates from wild fish and hatchery spring fish, hatchery spring Chinook salmon may be used as an index for trends in the survival of wild stocks but not as direct surrogates.

Key words: Endangered Species Act, integrated mortality, migration stage, PIT tag, smolt-to-adult ratio, survival

Introduction

An irony of listing a species under the Endangered Species Act (ESA) is that just when accurate and precise information is needed the most, the ability to handle and tag large numbers of individuals is severely curtailed. Models for animal dispersion suggest as mean abundance decreases, the spatial variance decreases but the coefficient of variation (i.e., CV = σ/μ) increases. It is the CV that determines the relative error in estimation. In the case of survival and abundance estimation studies, precision declines as release sizes and detection probabilities decrease. Consequently, the effects of natural variation and measurement error coincide to degrade the performance of monitoring and evaluation studies of threatened and endangered species.

For Pacific salmon species (*Oncorhynchus* spp.), hatchery fish have served as surrogates for status-and-trend monitoring of wild stocks when their numbers have been depressed (e.g., Muir et al. 1996; Smith et al. 2002, 2003). This role of hatchery fish as surrogates for wild fish is not without controversy, however. Upon release, hatchery fish may not behave or succeed the same as the wild fish they are meant to mimic. Differences in diel migration behavior between hatchery and wild Chinook salmon (*O. tshawytscha*) subyearlings have been observed by Roper and Scarnecchia (1996). Hoffnagle et al. (2008) observed differences in both run and spawn timing between hatchery and wild adult spring Chinook from the Imnaha River, while Knudsen et al. (2006) observed consistent differences in spawn timing, sex composition of adults, and age, length, and body weight at maturity between hatchery and wild spring Chinook salmon from the Yakima River. Nevertheless, the abundance and availability of hatchery stocks make them convenient subjects for tagging studies when wild stocks are depressed and regulated under the ESA.

The value of hatchery fish as surrogates will depend on how well they mimic the performance of wild fish. Ideally, they would perform similarly and have similar survival. Alternatively, performance measures for hatchery and wild fish might be offset but track one another with a predictable positive or negative bias. In the latter case, the hatchery fish would provide an index to wild stock performance, not an absolute measure of performance.

Using up to 12 years of PIT-tag data representing 9 annual cohorts, we compare the downriver survival of smolts, ocean survival, adult passage success, and smolt-to-adult ratios of hatchery and wild spring/summer Chinook salmon from the Snake River Basin. The purpose of the analysis is to assess the suitability of hatchery stocks as surrogates for wild yearling Chinook salmon performance and the relationships of these performance measures between fish sources.

Study Area

All fish used in the analysis were tagged with Passive Integrated Transponder (PIT) tags and released as smolts in the Snake River Basin upstream of Lower Granite Dam (rkm 695 from the mouth of the Columbia River; Fig. 1). See Muir et al. (2001) for an overview of the PIT-tagging program in the Columbia River Basin. The smolts had to pass through eight hydroelectric projects on the way to the ocean. Smolt transport programs in operation at Lower Granite, Little Goose, Lower Monumental, and McNary dams collected and barged a portion of smolts and released them below Bonneville Dam. Adult passage ladders existed at all eight hydroelectric projects. Average spring flows for 1996–2004 (15 April – 1 June) ranged from 1557 to 3483 $m^3 \cdot s^{-1}$ at Lower Granite Dam. The average of 3483 $m^3 \cdot s^{-1}$ flow in 1997 was the largest in the last 30 years, while the average of 1557 $m^3 \cdot s^{-1}$ in 2001 was the smallest during the same time period.

Methods

Data Used

We analyzed annual PIT-tagged release groups composed of wild or hatchery spring/summer Chinook salmon tagged and released in the Snake River Basin upstream of Lower Granite Dam, for the smolt migration years 1996 to 2004. The data requirements of the ROSTER release-recapture model (River-Ocean Survival and Transportation Effects Routine; Buchanan and Skalski 2007) demand large release groups because of low adult return rates following ocean residence. Therefore, it was necessary to pool fish from individual releases made at separate hatchery or trapping sites to form the annual release groups (Table 1). We pooled all release groups across the Snake River Basin by stock for each migration year. We omitted release groups that were tagged and released at Lower Granite Dam because of concerns regarding potential bias from tagging effects associated with intercepting, handling, and tagging fish during the smolting process.

For each release year, we analyzed three release groups: wild Chinook salmon, hatchery spring run Chinook, and hatchery summer run Chinook. The wild fish used in this study included both spring and summer run Snake River Chinook salmon, tagged and released at numerous traps and weirs throughout the Snake River Basin upstream of Lower Granite Dam. Most wild fish were tagged and released in the spring of their juvenile outmigration year, or in the previous fall. Because of low sample sizes, no effort was made to analyze spring and summer wild stocks separately. The hatchery spring Chinook salmon used in this study came from numerous hatcheries throughout the Snake River Basin, with the majority coming from Rapid River Fish Hatchery (Idaho), Lookingglass Fish Hatchery (Oregon), and Dworshak National Fish Hatchery (Washington). For each release year except 1997, over 93% of the hatchery summer Chinook salmon came from the McCall Fish Hatchery on the Payette River in Idaho. In 1997, 62% of the summer Chinook came from McCall and 37% came from Idaho's Pahsimeroi Fish Hatchery. Detailed description of the yearly contributions of the Snake River hatcheries, traps, and weirs to the release groups can be found in Buchanan et al. (2007; 2008). Hatchery spring and summer Chinook were tagged and released in late March or early April of their juvenile migration year.

Detection data for juvenile salmonids implanted with PIT tags were available from four sites in all years: Lower Granite, Little Goose, Lower Monumental, and McNary dams (Fig. 1). Detections were available at Bonneville Dam starting in 1997, and at John Day Dam starting in 1998. PIT-tag detection of returning adults became available at an increasing number of dams during the study period. Reliable adult detections were available at Lower Granite Dam throughout the study, while adult detections were available from Bonneville Dam starting in 2000, and from McNary and Ice Harbor dams starting in 2002.

Detections of all returning adults were used in estimating parameters of the release-recapture model, including age-1-ocean fish ("jacks") but not age-0-ocean fish. However, the performance measures presented here are reported only for age-2-ocean and older adults. This mirrors the approach taken elsewhere (e.g., Schaller et al. 2007), and is based on observations that age-1-ocean fish do not contribute largely to wild Chinook salmon returns (Healey 1991). Furthermore, fishery managers typically discount returns of age-1-ocean Chinook salmon (NMFS 2008a ch. 7-8, NMFS 2008b, ch. 7-8).

PIT-tag release and recapture data for release years 1996 – 2004 were downloaded from the PTAGIS database, maintained by the Pacific States Marine Fisheries Commission. We used the criteria outlined in Schaller et al. (2007: p. A-3) to define release groups for each migration year. For wild Chinook salmon, the release group for a given migration year consisted of wild spring and summer Chinook tagged from July 25 of the previous calendar year through May 20 of the migration year. For hatchery fish, sample sizes were large enough to analyze spring and summer stocks separately. Tags with unknown run (code 5 in the PTAGIS database) were omitted.

Statistical Methods

The statistical methods used for estimation of performance measures are described in Buchanan et al. (2007) and Buchanan and Skalski (2007). Briefly, the ROSTER release-recapture model (Buchanan and Skalski 2007) was used to generate maximum likelihood estimates (MLEs; Norden 1972) of downriver juvenile survival between dams, ocean survival (i.e., the age-specific probability of returning from Bonneville Dam as a smolt back to Bonneville as an adult), adult passage success ("perceived adult upriver survival," i.e., the age-specific conversion rates between dams), detection probabilities, and censoring (i.e., known removal) probabilities. The ROSTER model is an extension of the Cormack-Jolly-Seber (Cormack 1964; Jolly 1965; Seber 1965) model for estimating reach survival. The model allows for transportation of smolts and differential adult returns by downriver migration approach (i.e., inriver vs. transportation) and year of return.

Performance measures were defined in terms of the model parameters, and were estimated using the maximum likelihood estimates of the model parameters. Standard errors were estimated using the matrix of second derivatives of the likelihood function estimated during the numerical fitting process, in combination with the delta method (Seber 1982:7-9), and 95% confidence intervals were computed using normal theory. The performance measures estimated were juvenile inriver survival from Lower Granite Dam to Bonneville Dam (S_J), the ocean return probability from Bonneville back to Bonneville (S_O), adult passage success from Bonneville to Lower Granite (S_A), and the smolt-to-adult return ratio from Lower Granite back to Lower Granite (SAR). Although the ROSTER model incorporates effects of smolt transportation in performance measures, the results reported here represent only nontransported fish.

Sparse detection data meant that some parameters were not estimable for certain release groups. For example, estimation of S_J depends on detections of smolts at Bonneville Dam. In 1996, the smolt detection system at Bonneville Dam was inadequate for estimating S_J for any release group. Detection improved somewhat in 1997, but was nevertheless insufficient to yield estimates of S_J for the wild release group, which was smaller than the hatchery release groups. Additionally, low flows in 2001 meant that most hatchery summer Chinook salmon smolts that arrived at the estuary had been transported around most of the hydrosystem, and thus were not detected at Bonneville Dam. This meant that S_J was not estimable for hatchery summer Chinook in 2001.

The ocean return probability ("ocean survival"; S_O) is the probability that a fish returns from passing Bonneville Dam as a smolt back to Bonneville as an adult (i.e., age-2-ocean or older). Estimating S_O requires detection of both smolts and adults at Bonneville Dam, and so is not available for release years before 1999 when there was no adult PIT-tag detection at Bonneville Dam. Furthermore, it was not possible to estimate the ocean return probability if too few smolts were detected at Bonneville, as happened for the 2001 release group of hatchery summer Chinook salmon.

Average adult passage success (or "perceived adult upriver survival" as in Buchanan and

Skalski 2007) from Bonneville to Lower Granite was estimated both on a release group basis ($S_{A_{\text{Release}}}$, abbreviated $S_{A_{\text{Rel}}}$), and also for all tagged adults present at Bonneville Dam in a given calendar year ($S_{A_{\text{Return}}}$, abbreviated $S_{A_{\text{Ret}}}$). The two measures provide estimates of adult passage success through the hydrosystem from two complementary viewpoints, with $S_{A_{\text{Rel}}}$ useful for relating adult survival back to a brood year, and with $S_{A_{\text{Ret}}}$ useful for assessing effects of annual operations and river environment directly on migrating adults. Both measures represent "perceived" survival because their complements include both straying and harvest, in addition to natural mortality and non-detection of tagged adults at Lower Granite Dam. Estimates of adult passage success were available for release years 1999 – 2004, and return years 2001 – 2007.

In addition to the performance measures listed above, we estimated measures of the contribution of each migratory stage to the SAR. The SAR is the product of survival through the juvenile (smolt), ocean, and adult migratory life stages. The contribution of each of these stages to the overall migration mortality (from passing Lower Granite as a juvenile to return there as an adult) can be represented in two ways. First, the proportion of the total mortalities that occurred in each migratory stage can be calculated. This approach may be misleading because the migratory stages occur in succession instead of concurrently, with the result that the amount of mortality within a stage is confounded with stage order. For example, an early stage may have more mortalities because more fish survive to reach that stage. The confounding effect of stage order can be removed by measuring the relative survival probabilities on the log scale as demonstrated below.

The SAR can be expressed as the product of the conditional survival probabilities for each stage: SAR = $S_J S_O S_A$. Each of the stage-specific survival probabilities may be rewritten as a function of the instantaneous mortality rate (r) for the stage and the time (t) spent in the stage, i.e., $S = e^{-rt}$. This gives

$$\text{SAR} = e^{-r_J t_J - r_O t_O - r_A t_A}$$

or equivalently,

$$-\ln \text{SAR} = r_J t_J + r_O t_O + r_A t_A \,.$$

The measure $-\ln \text{SAR}$ integrates the stage-specific instantaneous mortality rates over the time spent in each life stage. The contribution of a life stage to the total integrated mortality is found by comparing $-\ln \text{SAR}$ to $-\ln S$ for the stage. For example, the fraction

$$\mu_J = \frac{-\ln S_J}{-\ln \text{SAR}} = \frac{r_J t_J}{r_J t_J + r_O t_O + r_A t_A}$$

is the proportion of the total integrated mortality accounted for by the juvenile inriver stage. Analogous expressions are available for the ocean (μ_O) and adult upriver (μ_A) life stages. Examining the components of the total integrated mortality in this way focuses attention on the relative risks of mortality in different life stages without confounding with the stage order. Estimates of μ_J, μ_O, and μ_A depend on estimates of S_J, S_O, and $S_{A_{Rel}}$, and thus are available for release years 1999 through 2004 for wild and hatchery Chinook salmon, excluding 2001 for hatchery summer Chinook.

Comparisons were made between wild and hatchery results by release year. Because hatchery spring and summer Chinook salmon were analyzed separately, results from wild Chinook were compared to hatchery spring and summer results separately. We made no attempt to make inference to untagged fish by accounting for migration differences between tagged and untagged smolts. Comparisons were made for all measures of survival, including SAR, and for the proportions of integrated mortality.

Wild and hatchery results were compared in several ways. For each performance measure, the correlation between wild and hatchery estimates was estimated for the release years in common. Because the estimated correlation values are based on estimates of performance measures, rather than on their true values, the correlations reported here include measurement error. This means that the correlation between actual (unknown) values of the performance measures will generally be higher than the values reported here. The small sample sizes available for wild fish prevented removal of measurement error from the correlation estimates.

In addition to simple correlation, we tested for the effect of rearing type (i.e., wild or hatchery) on estimated values for each performance measure using weighted analysis of variance (WANOVA). The weights were selected to stabilize the variance across release years and depended on the variance structure of the performance measure estimate. For all measures except ocean survival, we used weights inversely proportional to the square of the coefficient of variation. For ocean survival, we used weights inversely proportional to the variance. The WANOVA used a two-way classification of year by rearing type. In each case, we removed the effect of release year before testing for rearing type using *F*-tests. Because our goal was to determine if wild and hatchery fish have common survival through various migratory life stages, it was more important to maintain a small Type II error probability (β) than a small Type I error probability ($\alpha < 1 - \beta$) for the null hypothesis of common survival. Thus, we used a high significance level for testing for differences ($\alpha = 0.10$), corresponding to a low β.

Those performance measures found to have a significant effect of rearing type were further examined for a consistent linear relationship between estimates from hatchery and wild fish. Estimates from hatchery fish were regressed onto estimates from wild fish using orthogonal regression (Fuller 1987: 30-48), which accounts for measurement error in both dependent and independent variables.

Results

Model estimates for all survival parameters varied among years and populations, and the underlying annual trends differed markedly for each life stage. Key trends are described for each performance measure below. Point estimates are followed by 95% confidence intervals (in parentheses).

Juvenile Inriver Survival (S_J)

For both wild and hatchery Chinook salmon, estimates of S_J were highest in 1998 and lowest in 2001 (Fig. 2A), with an average of 0.532 (95% confidence interval: 0.458-0.606) for wild stocks (omitting 1997), 0.587 (0.499-0.675) for hatchery spring stocks, and 0.613 (0.521-0.705) for hatchery summer stocks (omitting 2001). The 2001 estimate of S_J was missing for hatchery summer Chinook because too few fish were detected at Bonneville. It is likely that juvenile inriver survival was low in 2001 for hatchery summer fish, and that the true average S_J from 1997 to 2004 was less than 0.613. There was high correlation between estimates of juvenile inriver survival from wild and hatchery Chinook salmon ($r > 0.80$; Fig. 2A). Analysis of variance found a significant difference in juvenile survival estimates between wild Chinook and hatchery spring Chinook ($P = 0.003$), with lower estimated survival for wild stocks than for hatchery spring stocks on average. For hatchery spring stocks, the estimated relationship was

$$\hat{S}_{J-\text{Hatchery}} = 1.156\hat{S}_{J-\text{Wild}}$$

with a standard error of $\hat{\text{SE}}(\hat{\beta}) = 0.152$ for the proportionality constant (β). There was no significant difference in estimated juvenile inriver survival between wild stocks and hatchery summer stocks ($P = 0.383$).

Ocean Return Probability (S_O)

Estimates of the ocean return probability (i.e., survival from Bonneville Dam back to Bonneville, S_O) varied considerably from year to year, but were consistently low (<6%) for all stocks (Fig. 2B). The highest estimates were for the 1999 and 2000 release years, followed by the lowest estimate in 2001. As mentioned above, no estimate of S_O was available for hatchery summer Chinook salmon in 2001. However, the 2001 estimate of SAR for this stock (0.005) suggests that ocean survival was low.

Estimates of S_O for the wild release groups and the hatchery spring release groups were highly correlated (*r* = 0.990), with lower correlation between estimates for wild release groups and the hatchery summer release groups (*r* = 0.903; Fig. 2B). Wild Chinook often had higher point estimates of the ocean return probability than either spring or summer hatchery Chinook, but there was no significant difference between the wild and hatchery estimates overall (*P* = 0.145 for hatchery spring Chinook, and *P* = 0.883 for hatchery summer Chinook).

Adult Passage Success $\left(S_{A_{\mathrm{Rel}}}\ \textit{and}\ S_{A_{\mathrm{Ret}}}\right)$

Estimates of adult passage success by release year ($S_{A_{\mathrm{Rel}}}$) averaged 0.849 (0.802-0.896) for wild Chinook salmon, 0.787 (0.728-0.846) for hatchery spring Chinook, and 0.827 (0.776-0.878) for hatchery summer Chinook over the years 1999 to 2004 (Fig. 2C). Wild and hatchery estimates were highly correlated for both spring and summer Chinook salmon (*r* >0.8; Fig. 2C). This high correlation was determined largely by the estimate for the 2004 release year, which was considerably lower than previous estimates for both wild and hatchery stocks. Analysis of variance found a significant difference between estimates of adult passage success from wild release groups and those from hatchery spring run groups (*P*=0.037). The estimated relationship between wild groups and hatchery spring groups was

$$\hat{S}_{\mathrm{A}_{\text{Rel-Hatchery}}} = 0.930\hat{S}_{\mathrm{A}_{\text{Rel-Wild}}}$$

with a standard error of $\hat{\mathrm{S}}\mathrm{E}(\hat{\beta}) = 0.022$ for the proportionality constant. Hatchery spring stocks exhibited significantly lower adult passage success than wild stocks (*t*-test, *P*=0.013). No significant difference was found in adult passage success estimates between wild groups and hatchery summer run groups (*P*=0.703).

Estimates of adult passage success by return year ($S_{A_{\text{Ret}}}$) averaged 0.822 (0.761-0.883) for wild Chinook salmon, 0.778 (0.719-0.837) for hatchery spring Chinook, and 0.821 (0.784-0.858) for hatchery summer Chinook over the years 2001 to 2007 (Fig. 2D). The 2007 estimate was based solely on age-3-ocean adults from the 2004 release group. The 2006 estimate also depended primarily on the performance of the 2004 release group because most adults returned after 2 years in the ocean. The relatively poor performance of the 2004 release group resulted in low estimates of adult passage success by return year for the hatchery release groups in 2006, and for the hatchery spring and wild release groups in 2007 (Fig. 2D). The hatchery summer release group had relatively high estimated adult passage success in 2007, but the estimate was based on only 20 fish and had high uncertainty.

There was moderate correlation between the estimates of adult survival by return year for wild Chinook and hatchery spring Chinook salmon ($r = 0.781$) over the 7 years of available data (Fig. 2D), and low correlation between estimates for wild stocks and hatchery summer stocks ($r = 0.229$). The low correlation between wild stocks and hatchery summer stocks was driven mostly by the 2007 estimate. A significant difference was observed between estimates for wild stocks and hatchery spring stocks ($P = 0.069$), with estimates from hatchery spring stocks significantly lower than those from wild stocks (*t*-test, $P = 0.045$):

$$\hat{S}_{\mathrm{A}_{\text{Ret-Hatchery}}} = 0.948\hat{S}_{\mathrm{A}_{\text{Ret-Wild}}},$$

with $\hat{\mathrm{S}}\mathrm{E}(\hat{\beta}) = 0.026$. There was no significant difference between estimates from wild stocks and hatchery summer stocks ($P = 0.260$).

Smolt-to-Adult Return Ratio (SAR)

Estimates of the smolt-to-adult return ratio (SAR) varied widely for each stock from 1996 to 2004 (Fig. 3). Temporal patterns for hatchery Chinook salmon closely followed those of wild fish ($r > 0.95$), with peaks for all stocks occurring in 1999 and 2000, and low estimates in 1996, 2001, 2003, and 2004 (Fig. 3). From 1996 to 2004, the mean estimated SAR was 0.009 (0.003-0.015) for wild Chinook salmon, 0.005 (0.003-0.007) for hatchery spring Chinook, and 0.008 (0.002-0.014) for hatchery summer Chinook (Fig. 3). These estimates were not adjusted for harvest and straying.

There was a significant difference between SAR estimates from wild Chinook and hatchery spring Chinook ($P<0.001$), with SAR estimates significantly lower for hatchery spring stocks (*t*-test, $P<0.001$):

$$S\hat{A}R_{\text{Hatchery}} = 0.596 S\hat{A}R_{\text{Wild}},$$

with $\hat{\mathrm{S}}\mathrm{E}(\hat{\beta})=0.029$. Although the point estimates of SAR were generally higher for wild Chinook than for summer hatchery Chinook, the difference was not significant ($P=0.504$). In general, confidence intervals were wider for the wild fish because of lower tagging numbers.

Proportion of Total Integrated Mortality

The largest contribution to total integrated mortality between passing Lower Granite Dam as a smolt and returning there as an adult came from the ocean life stage for both wild and hatchery Chinook salmon (Fig. 4). On average, the ocean life stage accounted for between 80%

and 90% of the total integrated mortality for both wild and hatchery Chinook salmon, with little variation in estimates across years (Fig. 4).

The juvenile migration from Lower Granite to Bonneville Dam accounted for an average of 0.135 (0.117-0.153) of the total integrated mortality for wild Chinook salmon, 0.094 (0.072-0.116) for hatchery spring Chinook, and 0.122 (0.087-0.157) for hatchery summer Chinook (excluding the 2001 release group; Fig. 4). The smallest proportion of total integrated mortality came from the adult upriver migration from Bonneville Dam to Lower Granite Dam, which consistently contributed less than 5% of the total integrated mortality for both wild and hatchery stocks (Fig. 4).

Analysis of variance found significant differences in the proportions of total integrated mortality between wild Chinook salmon and hatchery spring stocks for both the juvenile (P=0.001) and ocean (P=0.009) life stages. Compared to hatchery spring Chinook, wild Chinook experienced higher relative mortality during their juvenile migration and lower relative mortality during the ocean stage (Fig. 4). There was no significant difference between wild Chinook salmon and hatchery spring Chinook for the adult stage (P=0.173). Comparisons between wild Chinook and hatchery summer Chinook followed a different pattern, with analysis of variance showing no significant difference between rearing types (P=0.874 for the juvenile life stage, P=0.691 for the ocean stage, and P=0.989 for the adult stage).

Discussion

Salmon hatcheries were initially constructed to supplement populations of wild salmon for fisheries, under the assumption that hatchery-produced fish would have higher egg-to-smolt survival but would otherwise be identical to naturally-produced fish (Lichatowich 1999). However, differences between hatchery- and naturally-produced salmon have been documented relating to genetics, morphology, disease-resistance, predator avoidance, survival, and age structure, among others (e.g., see Raymond 1988; Mullan et al. 1992; Reisenbichler and Rubin 1999). For example, hatchery smolts are generally larger than wild smolts (Zabel and Williams 2002), with the potential consequence of faster maturation, so that hatchery adults tend to be younger and smaller than their wild counterparts (Mullan et al. 1992). How to incorporate hatchery-produced fish when assessing population status under the Endangered Species Act has also been controversial (Long 2007).

The Snake River Basin has more than 15 hatcheries considered to be part of the Snake River spring and summer Chinook salmon Evolutionarily Significant Unit. Hundreds of thousands of smolts from these hatcheries are PIT-tagged and released annually. Naturally-produced (i.e., wild) Chinook salmon smolts are PIT-tagged and released, as well. However, most PIT-tagging studies focus on hatchery fish because of the relative ease of tagging captive fish that are available in large numbers. For example, in 2004, 88% of the Snake River spring/summer Chinook salmon PIT-tagged were reared in hatcheries, while only 12% were produced naturally. Furthermore, although management guidelines for the Federal Columbia River Power System (FCRPS) pertain to naturally-produced fish, survival standards and monitoring often use hatchery or run-of-river salmon because of their easy availability (NMFS 2008a, 2008b). Thus, wild and hatchery fish are not always distinguished when assessing for survival through the hydrosystem.

With most tagged salmon coming from hatcheries, managers are using hatchery-reared salmon as *de facto* surrogates for naturally-produced salmon for the purpose of measuring migratory survival. Our analysis supports this approach to some extent, suggesting that hatchery summer Chinook salmon and, to a lesser degree, hatchery spring Chinook have the same inriver and ocean survival trends as wild spring/summer Chinook from the Snake River. However, we found significant differences between survival estimates for wild Chinook and hatchery spring Chinook, indicating that hatchery spring Chinook salmon should not be used as direct surrogates for wild stocks for certain survival measures. In particular, we found that hatchery spring Chinook tended to have higher juvenile survival estimates through the hydrosystem than wild stocks, a finding that agrees with some previous work (e.g., Zabel and Williams 2002) but not others (e.g., Smith et al. 2002). We also found that despite their higher estimated juvenile survival, hatchery spring Chinook salmon had lower estimates of overall survival (i.e., SAR) than wild Chinook. This agrees with older results from Raymond (1988) and recent results from Williams et al. (2005) and Schaller et al. (2007: p. 78), but contradicts Zabel and Williams (2002), who found that hatchery Chinook salmon released at Lower Granite Dam in 1995 and 1996 had higher SAR than wild fish. The disagreement between their results and ours may reflect different methods of incorporating jack returns. Zabel and Williams (2002) included jacks in their analyses, whereas we did not. Because hatchery fish tend to produce more jacks than wild fish (Mullan et al. 1992), including jacks would tend to result in higher SAR estimates for hatchery fish but not for wild fish. Repeating this analysis in another 5 to 10 years would help clarify the uncertainty in our results.

Analysis of most PIT-tag studies focuses on either juvenile inriver survival or SAR (e.g., Muir et al. 2001; Smith et al. 2002; Schaller et al. 2007), while the adult conversion rates used by managers do not typically differentiate between wild and hatchery fish (e.g., NMFS 2008b, Appendix). Nevertheless, current management guidelines call for monitoring the upstream passage survival of returning adults (NMFS 2008a, RPA 52). Adult passage success may depend on multiple factors, including energy stores, water temperature and flow, straying, and harvest and predation pressures. Our analysis found that estimates of adult passage success for wild fish varied more by release year (SD = 0.065) than by return year (SD = 0.037), suggesting that passage success of wild fish may depend on inherent fish traits that dictate energy stores and straying rates. Hatchery fish, on the other hand, had similar variability in adult passage success whether measured by release year or by return year. However, estimates of adult passage success for wild and summer hatchery stocks diverged markedly for the 2007 return year, suggesting that hatchery fish may be more influenced by river conditions or harvest and predation pressure than are wild fish.

Our analysis detected more differences in survival between wild fish and hatchery spring Chinook than between wild fish and hatchery summer Chinook, although the statistical power to detect differences was comparable for the two runs of hatchery fish. The distinction between spring and summer runs is based on the time of year when the adults return to freshwater for their spawning migrations, with spring runs generally returning earlier than summer runs (Fig. 5). Spring runs also tend to spawn both earlier and farther upriver than summer runs (Burner 1951; Lichatowich 1999). Differences in run timing mean that spring and summer run adults encounter different environmental conditions and possibly different harvest pressures, although since 2005, Snake River spring and summer Chinook have been managed as a single stock for harvest purposes (NMFS 2008b, p. 5-43).

The wild release groups analyzed here included both spring and summer run Chinook salmon that were tagged and released in the same regions as the hatchery release groups. The consistent pattern of high correlation between hatchery summer stocks and wild stocks suggests the wild release groups may have been primarily summer run salmon. However, on average, only approximately 45% (range = 38% - 66%) of the fish in the annual wild release groups were classified as summer run at the time of tagging. On the other hand, the median adult passage date for wild adults at Bonneville Dam was closer to the median passage date for hatchery summer adults than for hatchery spring adults (Fig. 5). However, adult passage date provides information only on the run composition of the successful migrants. Thus, it is not obvious that our wild release groups were predominantly summer run fish.

Abundant populations are often used as surrogates for populations that are too sparse for direct study or else present insurmountable logistical challenges in tagging studies. For example, in the Columbia River Basin, Snake River spring and summer Chinook salmon and steelhead (*O. mykiss*) are used as surrogates for Snake River sockeye salmon (*O. nerka*), Snake River fall Chinook salmon are used as surrogates for Lower Columbia River coho (*O. kisutch*), and Snake River steelhead are used as surrogates for Mid-Columbia River steelhead (NMFS 2008a, RPA 52). Although Snake River hatchery spring and summer Chinook salmon are not currently used as direct surrogates for wild spring and summer Chinook, the abundance of hatchery fish make them the *de facto* surrogates for the wild fish. In the Snake River Basin, we had the luxury of having sufficient wild Chinook migrants to perform surrogacy trials with hatchery fish. This may not be true for other threatened or endangered stocks or populations. For such populations, the use of non-calibrated surrogates might be better than no information at all.

Even if surrogacy is deemed appropriate for some monitoring purposes, it may not be appropriate for all objectives. For example, for trend analysis, response from the surrogate stock need only track the performance of the target stock. Our analysis suggests that Snake River hatchery spring Chinook salmon may be adequate surrogates for monitoring survival trends but not absolute survival of wild spring and summer Chinook. This recommendation agrees with results reported elsewhere (e.g., Berggren et al. 2005), which found that estimates from wild and hatchery fish tracked each other consistently despite a difference in magnitude. When monitoring for compliance or population recovery, on the other hand, surrogates must have similar survival values. Our analysis suggests that Snake River hatchery summer Chinook salmon may be used for estimating smolt-to-adult return ratios and survival through the different migratory life stages for wild Chinook. For yet more demanding needs such as calculating the finite rate of population change (λ), age structure and response levels for the surrogate and target stocks need to be the same. The analyses performed here address only the migratory life stages of wild and hatchery stocks, and so cannot be used to support using hatchery stocks as surrogates for wild stocks in measuring either abundance or λ. Thus, managers must carefully evaluate the circumstances and performance metrics for which hatchery or other surrogate information may be adequate for management of wild populations.

Effective management of endangered or threatened populations requires accurate and precise demographic studies just when large-scale tagging studies are impractical or impossible. Ideally, such studies are performed on the listed populations. Practically, we must study the populations that are available. Quantitative comparisons of target and surrogate populations, such as the analysis presented here, should be performed whenever possible to support the surrogacy policy. Continued tagging studies of both wild and hatchery Snake River spring and summer Chinook salmon will provide useful data for assessing the surrogacy question, as well as tracking effects of hatchery and habitat management decisions and comparing the populations' responses to environmental change. Based on the tagging data currently available, we conclude that for Snake River spring and summer Chinook salmon, hatchery fish may be used to make inference to wild populations, at least over the broad regional and temporal (i.e., annual) scales used to define release groups in this analysis. In particular, with no significant differences in estimates of either juvenile inriver survival, SAR, ocean return probability, or adult passage success between wild Chinook and hatchery summer Chinook salmon, the hatchery summer stocks may serve as surrogates for wild Chinook salmon until such time that the abundance of wild stocks recovers.

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Tables

Table 1. Release numbers of PIT-tagged wild and hatchery yearling Chinook salmon smolts used in the ROSTER (River-Ocean Survival and Transportation Effects Routine; http://www.cbr.washington.edu/paramest/roster/) analyses.

	Release numbers		
Year	Wild Chinook salmon	Hatchery spring Chinook salmon	Hatchery summer Chinook salmon
1996	18,908	67,496	28,062
1997	9,601	115,057	85,020
1998	30,615	161,693	50,261
1999	73,319	180,085	51,172
2000	62,780	131,832	58,479
2001	44,372	162,255	59,588
2002	59,025	303,302	68,484
2003	92,304	304,850	87,654
2004	89,077	171,050	85,167

List of Figures

Figure 1. Columbia and Snake river basins, with hydroelectric dams passed by Chinook salmon from the Snake River Basin. Regions outside these two basins are shaded. Abbreviations of dam names are: LGR = Lower Granite, LGO = Little Goose, LMO = Lower Monumental, IH = Ice Harbor, MCN = McNary, JD = John Day, TDA = The Dalles, and BON = Bonneville. All dams except The Dalles have PIT-tag monitoring capability.

Figure 2. Estimates of (A) juvenile inriver survival $\left(\hat{S}_J\right)$, (B) ocean return probability from Bonneville back to Bonneville $\left(\hat{S}_O\right)$, (C) perceived adult passage success by release year $\left(\hat{S}_{A_{\text{Rel}}}\right)$, and (D) perceived adult passage success by return year $\left(\hat{S}_{A_{\text{Ret}}}\right)$ for nontransported wild and hatchery spring and summer Chinook salmon from the Snake River Basin, with 95% confidence intervals and estimated coefficient of correlation with wild estimates (r). Estimates in (D) incorporate adult detections from multiple release years.

Figure 3. Estimated smolt-to-adult return ratio $\left(S\hat{A}R\right)$ for nontransported wild and hatchery yearling Chinook salmon from the Snake River Basin, with 95% confidence intervals and estimated coefficient of correlation with wild estimates (r).

Figure 4. The average estimated components of total integrated mortality with 95% confidence intervals for wild and hatchery Chinook salmon. Wild Chinook results (A) represent release years 1999 – 2004, hatchery spring Chinook results (B) represent years 1999 – 2004, and hatchery summer Chinook results (C) represent years 1999, 2000, and 2002 – 2004.

Figure 5. Bonneville passage dates (10th, 50th, and 90th percentiles) of PIT-tagged Chinook salmon adults in wild, hatchery spring, and hatchery summer release groups. Passage dates refer to the second and third calendar years after the release year.

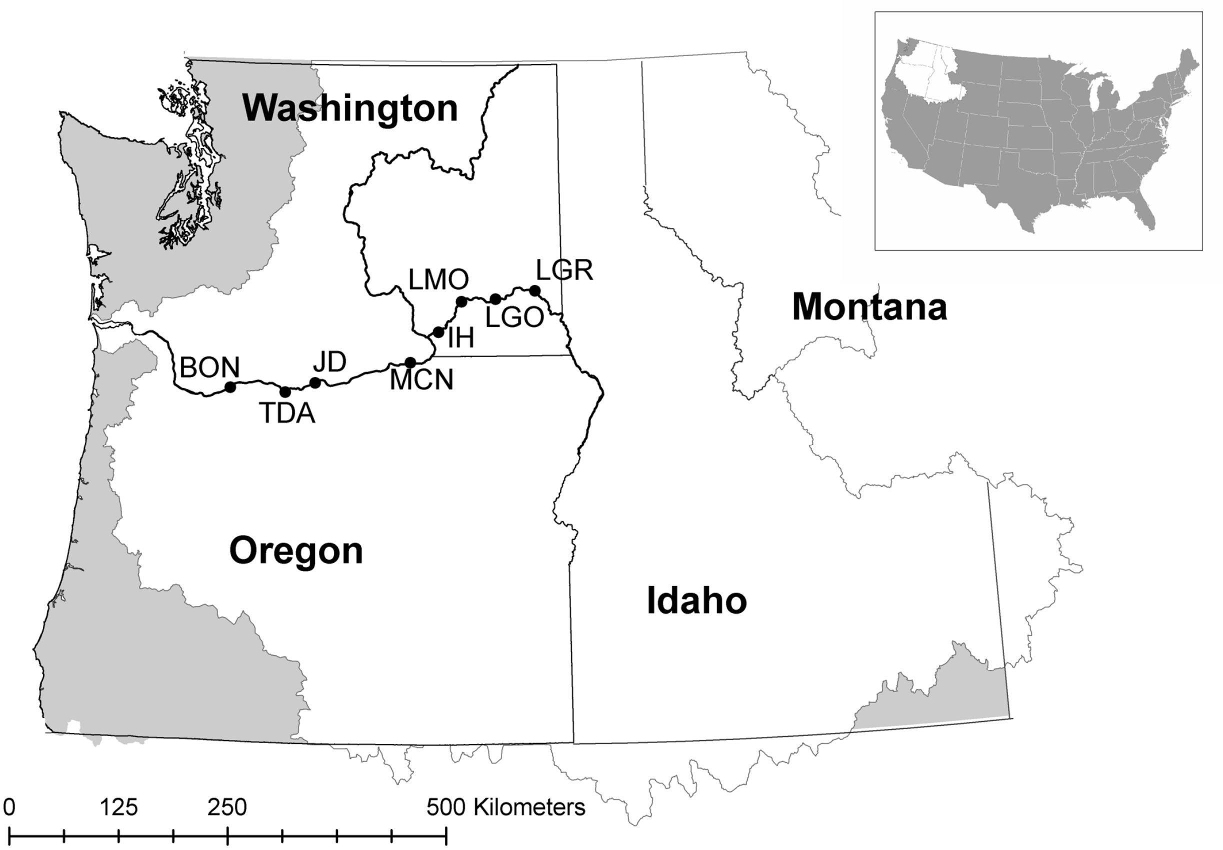

Washington
Montana
Oregon
Idaho
LMO
LGR
LGO
IH
BON
JD
MCN
TDA
0
125
250
500 Kilometers

Figure 1.

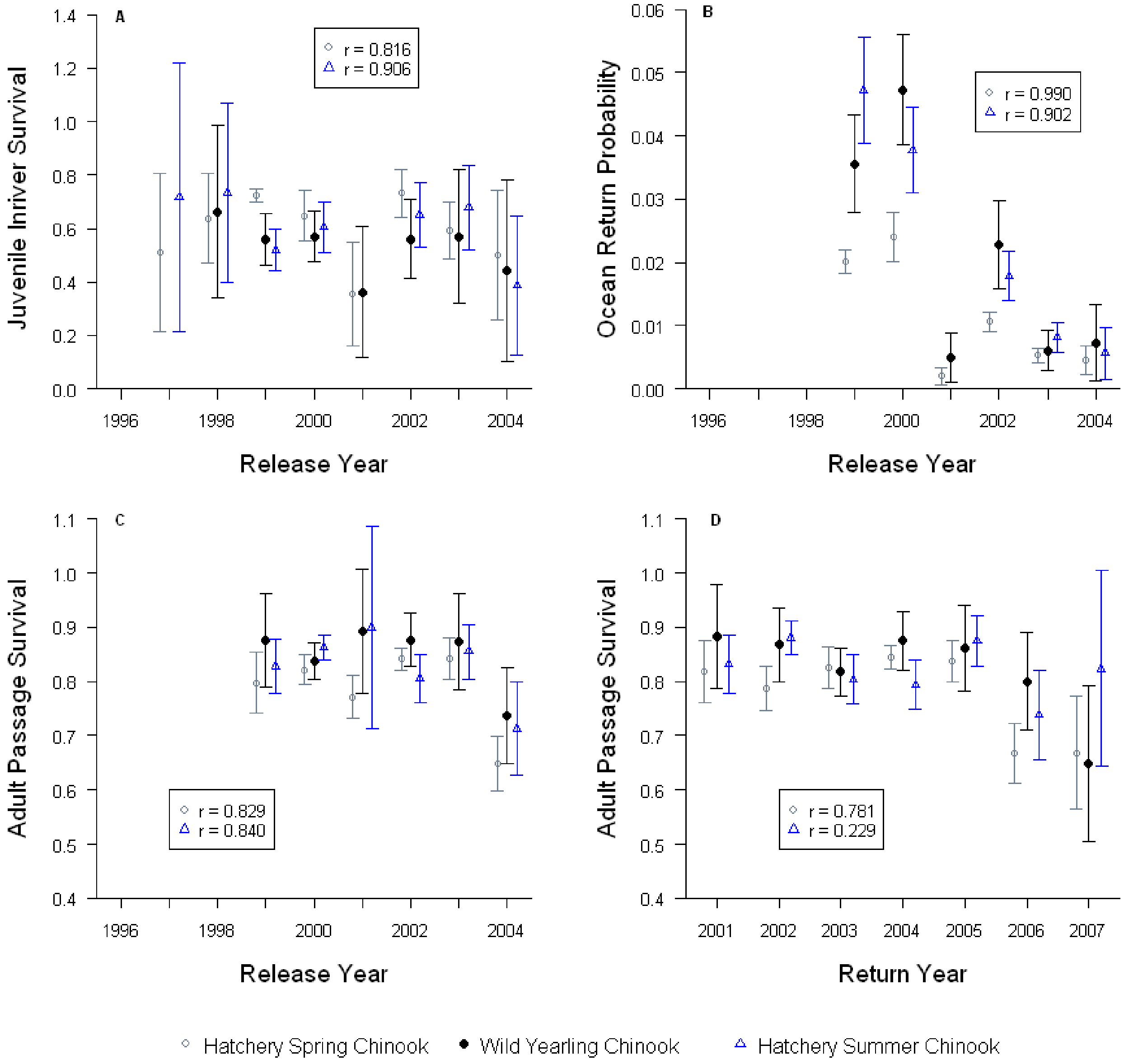
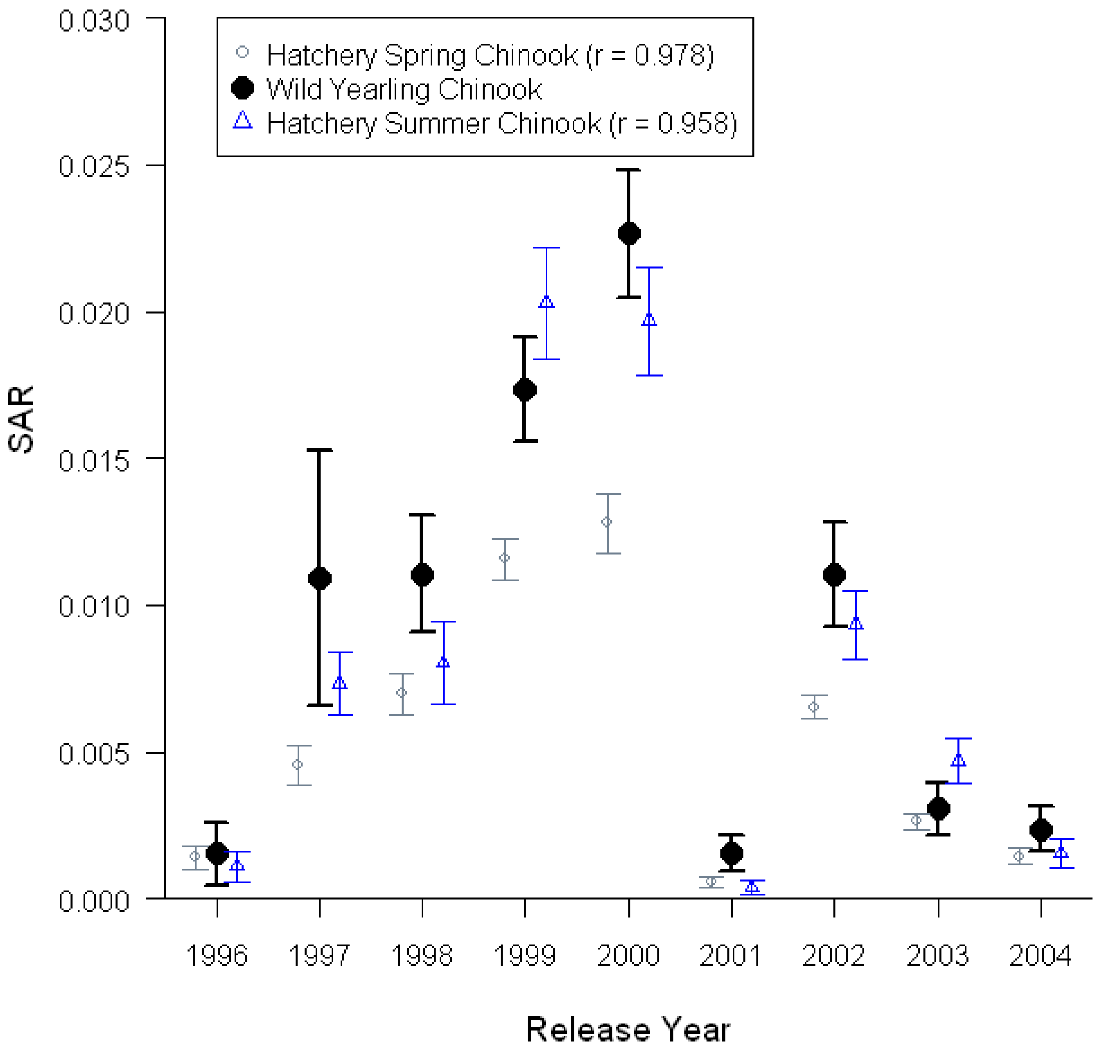

A
Juvenile Inriver Survival
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
◇ r = 0.816
△ r = 0.906
1996
1998
2000
2002
2004
Release Year
B
Ocean Return Probability
0.06
0.05
0.04
0.03
0.02
0.01
0.00
◇ r = 0.990
△ r = 0.902
Release Year
C
Adult Passage Survival
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
◇ r = 0.829
△ r = 0.840
Release Year
D
Adult Passage Survival
◇ r = 0.781
△ r = 0.229
2001
2002
2003
2004
2005
2006
2007
Return Year
◇ Hatchery Spring Chinook
● Wild Yearling Chinook
△ Hatchery Summer Chinook

Figure 2.



0.030
0.025
0.020
0.015
0.010
0.005
0.000
SAR
○ Hatchery Spring Chinook (r = 0.978)
● Wild Yearling Chinook
△ Hatchery Summer Chinook (r = 0.958)
1996
1997
1998
1999
2000
2001
2002
2003
2004
Release Year

Figure 3.

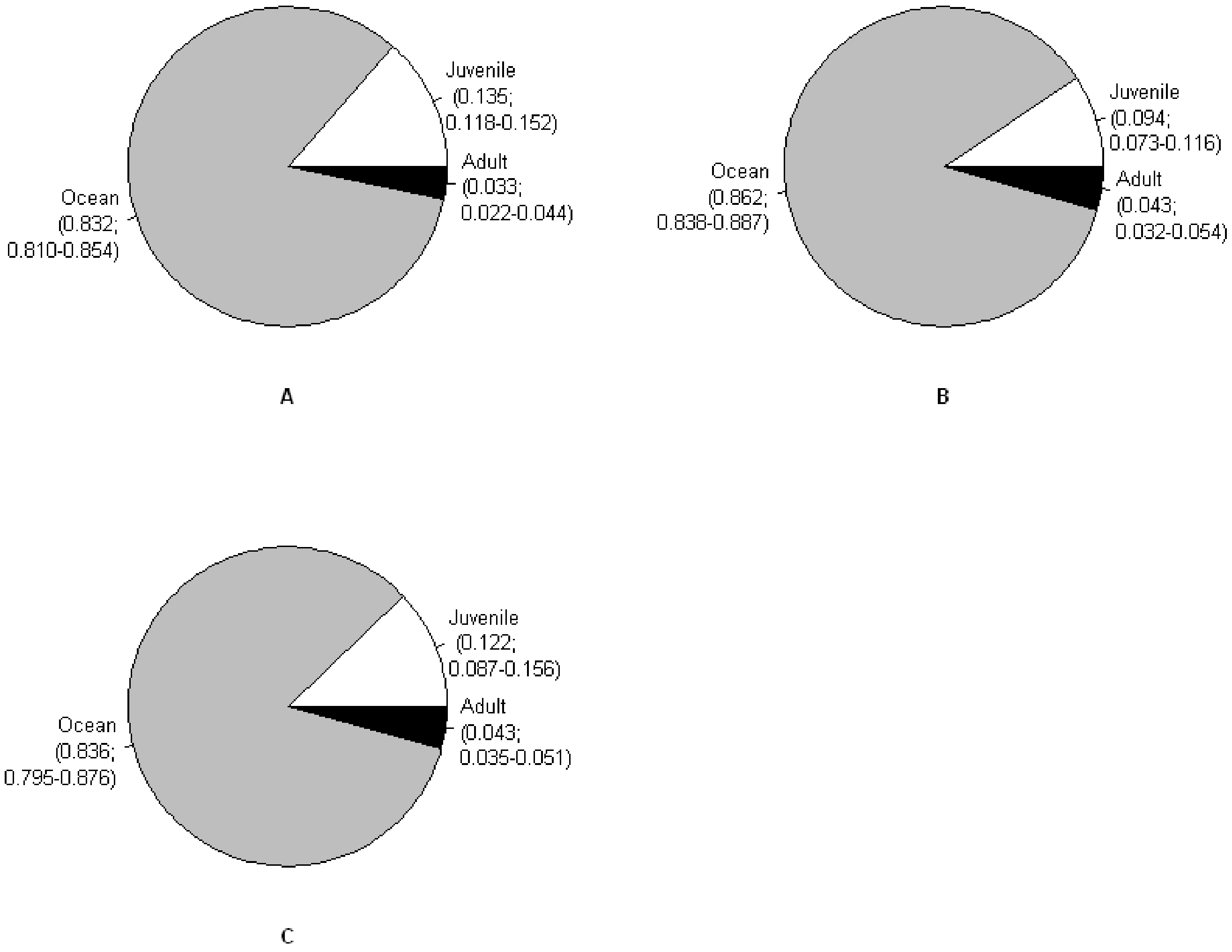

Juvenile (0.135; 0.118-0.152)
Adult (0.033; 0.022-0.044)
Ocean (0.832; 0.810-0.854)
A
Juvenile (0.094; 0.073-0.116)
Adult (0.043; 0.032-0.054)
Ocean (0.862; 0.838-0.887)
B
Juvenile (0.122; 0.087-0.156)
Adult (0.043; 0.035-0.051)
Ocean (0.836; 0.795-0.876)
C

Figure 4.

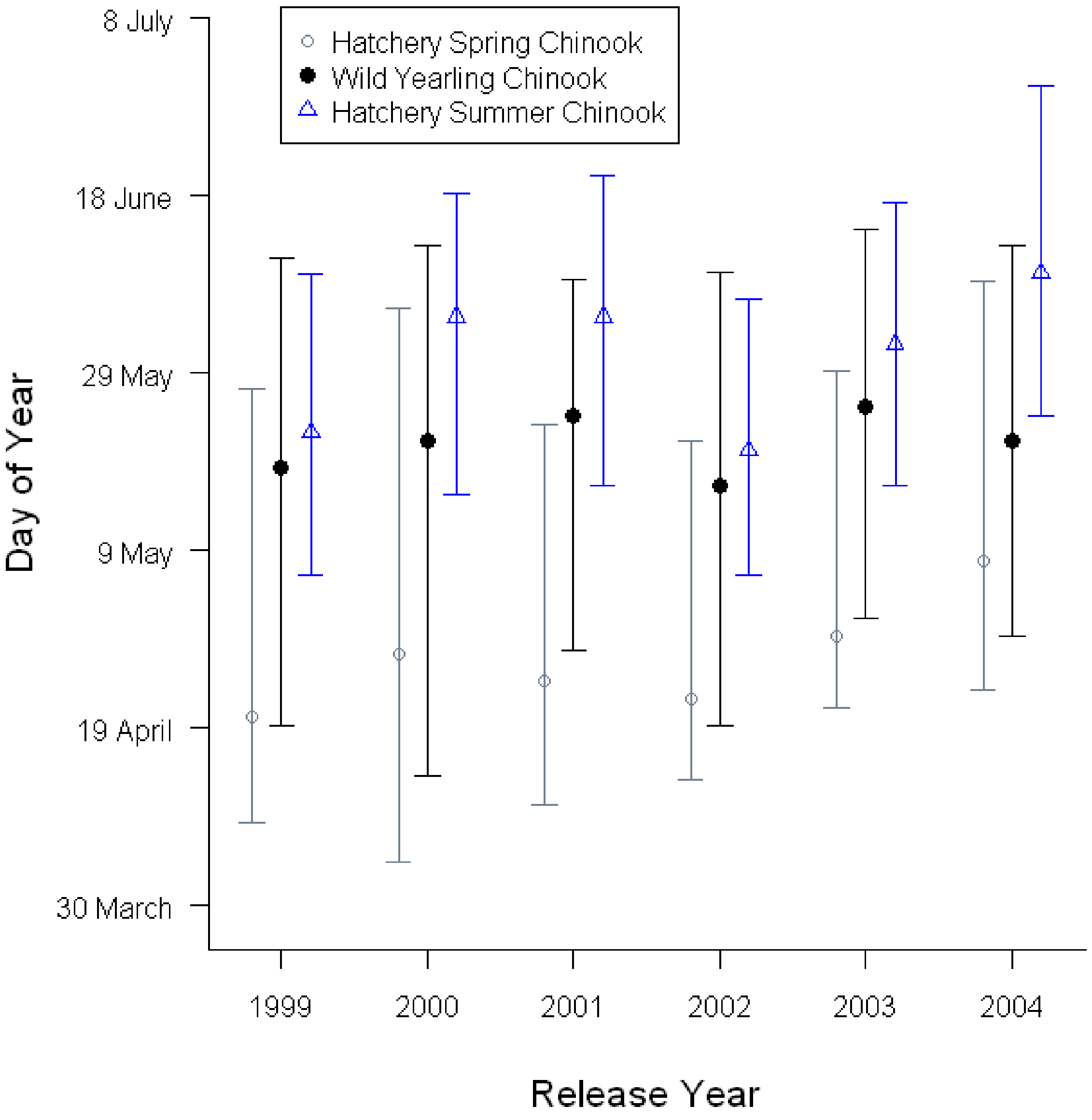

Hatchery Spring Chinook
Wild Yearling Chinook
Hatchery Summer Chinook
8 July
18 June
29 May
9 May
19 April
30 March
Day of Year
1999
2000
2001
2002
2003
2004
Release Year

Figure 5.