# Reproductive behavior and relative reproductive success of natural- and hatchery-origin Hood Canal summer chum salmon (*Oncorhynchus keta*)

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**Abstract:** Estimates of the relative fitness of hatchery- and natural-origin salmon can help determine the value of hatchery stocks in contributing to recovery efforts. This study compared the adult to fry reproductive success of natural-origin summer chum salmon (*Oncorhynchus keta*) with that of first- to third-generation hatchery-origin salmon in an experiment that included four replicate breeding groups. Hatchery- and natural-origin chum salmon exhibited similar reproductive success. Hatchery- and natural-origin males obtained similar access to nesting females, and females of both types exhibited similar breeding behaviors and durations. Male body size was positively correlated with access to nesting females and reproductive success. The estimates of relative reproductive success (hatchery/natural = 0.83) in this study were similar to those in other studies of other anadromous salmonids in which the hatchery population was founded from the local natural population and much higher than those in studies that evaluated the lifetime relative reproductive success of nonlocal hatchery populations.

**Résumé :** Des estimations de la fitness relative des saumons d'origine naturelle et de pisciculture peuvent aider à déterminer la valeur que représentent les stocks de pisciculture dans les efforts de récupération. Notre étude compare le succès reproductif de l'adulte à l'alevin chez des saumons kéta (*Oncorhynchus keta*) d'été d'origine naturelle à celui de saumons de pisciculture de première à troisième génération dans une expérience qui comporte deux séries de quatre groupes reproducteurs. Les saumons kéta d'origine naturelle et de pisciculture ont des succès reproductifs semblables. Les mâles de pisciculture et les mâles d'origine naturelle ont des accès semblables aux femelles au nid et les femelles des deux types ont des comportements reproducteurs et des durées de fraie semblables. Il y a une corrélation positive entre la taille corporelle du mâle et son accès aux femelles en nidification et son succès reproductif. Les estimations du succès reproductif relatif (pisciculture/origine naturelle = 0,83) dans notre étude sont semblables à celles d'autres études d'autres saumons anadromes dans lesquelles la population de pisciculture a été fondée à partir de la population naturelle locale et elles sont beaucoup plus élevées que celles d'études qui ont évalué le succès reproductif au cours de la vie de populations de pisciculture d'origine non locale.

[Traduit par la Rédaction]

## Introduction

Breeding populations of Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) typically include fish of hatchery and natural origin. Natural population productivity, which is a critical parameter for determining status under the United States Endangered Species Act (McElhany et al. 2000), can be difficult to estimate in populations that include hatchery-produced salmon because the relative fitness of hatchery fish is highly variable, usually unknown, and typically less than that of co-mingling natural populations (Berejikian and Ford 2004; Araki et al. 2008). Estimates of the relative fitness of hatchery- and natural-origin salmon can provide data to parameterize productivity models, improve the assessments of natural population productivity (e.g., McClure et al. 2003), and assist in determining the value of hatchery stocks in contributing to recovery efforts (Fraser 2008).

Current information on relative fitness of hatchery- and natural-origin salmon (i.e., ratio of hatchery recruits per spawner to natural recruits per spawner) is biased towards one iteroparous species (steelhead) and towards nonlocally adapted hatchery populations that have been highly domesticated (sometimes intentionally; reviewed by Berejikian and Ford (2004) and Araki et al. (2008)). However, Araki et al. (2007*a*) measured relative lifetime fitness of hatchery- and

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natural-origin steelhead and concluded rapid fitness loss (one to two generations) that had a genetic basis. In contrast, McGinnity et al. (2004) indicated no difference in relative genetic fitness (embryo to adult) in a locally derived, multigenerational hatchery-reared Atlantic salmon (*Salmo salar*) population. Hatchery-reared steelhead and other species (Atlantic salmon, brown trout (*Salmo trutta*), and coho salmon (*Oncorhynchus kisutch*)) for which relative fitness studies have been published (reviewed by Berejikian and Ford (2004) and Araki et al. (2008)) typically spend between one-third to one-half of their lifetime in the hatchery prior to release, so environmental influences of hatchery rearing on the reproductive success of those species may be substantial (Fleming et al. 1997).

Summer chum salmon (*Oncorhynchus keta*) are semelparous, typically live to 3 or 4 years of age, and tend to spawn in the lower reaches of streams in late summer and their offspring migrate to sea upon emergence from late winter to early spring (Quinn 2005). Summer chum salmon populations in Hood Canal, Washington, USA, underwent severe declines during the 1970s and 1980s and were extirpated from some streams (Washington Department of Fish and Wildlife and Point No Point Treaty Tribes (WDFW–PNPTC) 2000). A supplementation program involving the collection and artificial spawning of locally derived, natural-origin adults was initiated in the Quilcene River in 1992 and ended with the last fish being released in 2002. The Hood Canal summer chum salmon evolutionarily significant unit was listed as threatened under the US Endangered Species Act in 1999. Hatchery-produced summer chum salmon continue to be released into some Hood Canal streams. Information on the relative reproductive success (RRS) of hatchery- and natural-origin salmon provides an important measure of the efficacy of this strategy in contributing to overall recovery efforts for this species.

We tested the null hypothesis that the relative adult-to-fry reproductive success of hatchery-origin summer chum salmon does not differ from that of natural-origin fish by quantifying the ability to produce offspring in a spawning channel near Big Beef Creek (Kitsap County, Washington). This study did not directly test genetic fitness because hatchery- and natural-origin fish resided in different environments during their first month of life. However, it compares hatchery and natural fish that experienced the same environment (seawater) for a much longer portion of the life cycle (over 90%) than previous studies on other species (reviewed by Araki et al. (2008)). We compared reproductive behavior between hatchery- and natural-origin chum salmon to understand whether any behavioral differences would be associated with potential differences in reproductive success. Chinook salmon hatchery programs can influence age- and size-at-maturity (Hankin et al. 1993; Knudsen et al. 2006), and the same may occur for other species. Therefore, we also investigated relationships between body size, behavior, and reproductive success and discuss implications for salmon hatchery programs designed to supplement natural populations. By evaluating reproductive success to the juvenile offspring life stage, this study isolates differences between hatchery and natural fish that may occur during the freshwater phase of the life cycle (breeding, incubation, and outmigration) and does not address relative fitness after seawater entry.

## Materials and methods

### Study populations and experimental design

The US Fish and Wildlife Service's Quilcene National Fish Hatchery has collected summer chum salmon adults in the Quilcene River estuary for supplementation programs since 1992. Prior to that, no summer chum salmon hatchery programs were present in the Quilcene River or anywhere else in Hood Canal. The adult chum salmon were spawned artificially and their offspring were reared to approximately 1 g (1.5 months) and released into the Quilcene River. All released hatchery fish had their adipose fins removed. Those fish returning in 2004 and 2005 that did not have an adipose fin came from the hatchery program and those with an adipose fin were naturally produced either from natural-origin fish or from hatchery-reared fish spawning naturally (as early as 1995). Thus, we do not know the ancestry of the hatchery- and natural-origin fish used in this study prior to their parental generation. However, the hatchery fish used in the experiments had had at least one more generation of hatchery ancestry (i.e., their parents were spawned in the hatchery) than the natural-origin fish used in the study, the parents of which spawned naturally.

Adult chum salmon were collected by beach seining in Quilcene Bay on 7 and 20 September 2004 and 7 and 21 September 2005. On each date, seining continued until the required number of males and females from each population was obtained. Immediately after each collection, the fish were transported by tank truck to the University of Washington's Big Beef Creek Research Hatchery in oxygenated transport containers. Upon arrival at Big Beef Creek, the fish were weighed, measured, and marked with individually numbered Peterson disc tags (Floy Tag Co., Seattle, Washington). Tissue samples for DNA genotyping were collected and preserved in 100% nondenatured alcohol. In each year, fish collected on the first date were released together into one side of a quasinatural spawning channel (described below), and fish collected on the second date were stocked into the other side of the channel. The stocking date, origin (hatchery or natural), body size, and age of the fish used in both years of the experiment are provided (Table 1).

The study was conducted in an experimental stream channel at the Big Beef Creek facility. The portion of the stream channel used in this study measured 35 m long × 4 m wide and was supplied with water (approximately 0.05 $m^3 \cdot s^{-1}$) from a combination of Big Beef Creek and a local groundwater well. The channel was divided lengthwise into two similar sections (east channel and west channel) prohibiting movement of adults between them. The stream channel had substrate that ranged from silt and sand to gravel 20 cm in diameter. A mix of natural early succession vegetation and mature cedar trees comprised the riparian vegetation, which is typical of spawning habitat for Hood Canal summer chum salmon. Observation blinds were placed alongside both sides of the channel to minimize disturbance of the fish during observations.

### Behavioral observations

In 2004, behavioral observations were conducted three times each day at approximately 0700, 1300, and 1900 h. In 2005, observations were conducted twice daily, once in the

**Table 1.** The number (*n*), mean length (± standard deviation, SD), mean weight (±SD), and mean age (±SD) of adult hatchery- and natural-origin (natural) chum salmon (*Oncorhynchus keta*) stocked into east and west sides of the spawning channel at Big Beef Creek in 2004 and 2005.

| | | 2004 | | | | 2005 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *n* | Length (mm) | Weight (g) | Age (years) | *n* | Length (mm) | Weight (g) | Age (years) |
| **Females** | | | | | | | | | |
| East | Hatchery | 12 | 680 (27) | 3708 (522) | 3.9 (0.3) | 10 | 643 (44) | 3060 (748) | 3.2 (0.4) |
| | Natural | 12 | 682 (23) | 3729 (415) | 4.0 (0.0) | 14 | 647 (29) | 3188 (470) | 3.5 (0.6) |
| West | Hatchery | 12 | 683 (23) | 3770 (425) | 3.5 (0.5) | 10 | 638 (27) | 3030 (441) | 3.4 (0.7) |
| | Natural | 12 | 681 (28) | 3697 (490) | 3.9 (0.3) | 12 | 638 (43) | 2971 (660) | 3.3 (0.6) |
| **Males** | | | | | | | | | |
| East | Hatchery | 12 | 681 (27) | 3708 (522) | 3.9 (0.3) | 10 | 643 (44) | 3060 (748) | 3.2 (0.4) |
| | Natural | 12 | 682 (23) | 3729 (415) | 4.0 (0.0) | 14 | 647 (29) | 3188 (470) | 3.3 (0.7) |
| West | Hatchery | 12 | 684 (24) | 3770 (425) | 3.5 (0.5) | 10 | 637 (27) | 3030 (441) | 3.7 (0.5) |
| | Natural | 12 | 681 (28) | 3697 (490) | 3.9 (0.3) | 12 | 638 (43) | 2971 (660) | 3.8 (1.0) |

**Note:** The sex ratios are similar to those used in the majority of other reproductive success studies (reviewed by Araki et al. 2008).

morning and once in the evening. Observers began at a randomly selected location of the stream channel and recorded several behaviors for each female (Table 2). Typically, each female was observed for up to 10 min; females that were inactive, stationary, and not near other females were observed for a shorter period of time (5 min) before the next female was sampled. All behaviors observed during that time were recorded.

Selection on female spawning ground entry timing has been demonstrated in studies of other Pacific salmon (Dickerson et al. 2002; Ford et al. 2006). Early spawners may have access to high-quality nest sites but risk nest superimposition by later-spawning females (van den Berghe and Gross (1989). Because hatchery- and natural-origin salmon can differ in spawn timing, we calculated the following durations from the observed behaviors: (*i*) latency to onset of sexual activity (time from introduction to the first signs of nest digging), (*ii*) duration of sexual activity (time from first to last episodes of nest digging), and (*iii*) duration of nest guarding (time from first to last observation of nest guarding). We compared these traits between the hatchery- and natural-origin females.

In both years, we quantified how often individual males dominated access to a sexually active female (dominant male) and how often they held a "satellite" position downstream of a courting pair. We identified all males associated with a nest-building female. The male that maintained closest proximity to a nesting female, delivered a greater number of attacks towards other males than it received, and exhibited courtship behaviors was considered dominant (Berejikian et al. 2001). When aggressive contests appeared to be equal and proximity to the female was similar, we used coloration patterns to identify the dominant fish based on our own observations and the descriptions provided by Schroder (1981). In male chum salmon, the "bar" color pattern consists of black and red streaks that run perpendicular to the length of the fish, overlying a mottled green–yellow background that becomes tan on the dorsal surface of the peduncle. The "stripe" pattern, which mimics female coloration, consists of a single black–purple band that runs parallel to the length of the fish. Bar patterns were present in clearly dominant fish and striped patterns were present in clearly subdominant fish.

The time of death for all fish was recorded. The numbers of eggs retained in the body cavities of females were counted.

## Fry collection

The downstream end of the experimental spawning channel was fitted with wood-framed, wire mesh traps in attempts to collect all fry that emerged from the gravel and emigrated. The traps were checked each morning during the emergence and outmigration period, and all fry were counted. We subsampled the fry populations such that emigrants proportionately represented each day's collection over the entire outmigration period (Fig. 1). With these methods, we assumed that outmigrating fry were sampled in an unbiased manner and results of the pedigree analyses reflect adult-to-outmigrant reproductive success. In a previous study, sampling 5.5% of emergent fry was sufficient to represent offspring of 98% of naturally spawning steelhead trout (Berejikian et al. 2005). In the present study, collections were sampled at an average (± standard deviation, SD) daily rate of 7.3% (±1.2%) in 2005 and 8.8% (±4.2%) in 2006 for days in which more than 10 fry were captured. However, on days when fewer than 10 fry were captured, which were typically at the very beginning and end of the outmigration season, one fry was preserved. It was important to sample fry at the same rate each year to produce comparable data sets. However, the total number of outmigrant juveniles in 2006 was substantially less than in 2005, which resulted in unequal numbers of offspring available for genotyping (see Results).

## Genotyping and pedigree analysis

All of the adult summer chum salmon stocked into the experimental stream channels in 2004 and 2005 were uniquely identified by analyzing genomic DNA isolated from fin tissue samples. Genomic DNA was subjected to polymerase chain reactions (PCR) to amplify eight loci: *One18* (Scribner et al. 1996), *One102*, *One106*, *One111* (Olsen et al. 2000), *Ots3* (Banks et al. 1999), *Ots103* (Small et al. 1998),

**Table 2.** Definitions of behaviors to determine the status of individual female chum salmon (*Oncorhynchus keta*) over the course of the experiments in 2004 and 2005 (cf. Fleming et al. 1997; Schroder et al. 2008).

| Behavior | Definition |
|---|---|
| Inactive | Not yet showing signs of sexual activity; not attended by male(s) |
| Courted | Female is paired with 1 or more males, but no spawning behaviors are being displayed; record all males associated with female |
| Test digging | Scattered digging not concentrated in one area |
| Nest digging | Digging that results in deepening and shaping of a nest depression |
| Spawning | Female deposits eggs while accompanied by an ejaculating male |
| Egg covering | Female quickly covers eggs with very frequent, 2–3 body flexure digging motions immediately after releasing eggs |
| Redd covering | Prolonged digging around perimeter of redd (8–12 body flexures) with body almost parallel to substrate that results in gravel being mounded on top of the redd |
| Nest guarding | Holding over redd and exhibiting aggression toward other fish |
| Senescent | Female has spawned, looks thin, exhibits no sexual activity, and is usually away from her redd |

*OtsG311*, and *OtsG422* (Williamson et al. 2002). A fragment analysis was conducted on the PCR products using a genetic analyzer (model 3100; Applied Biosystems, Foster City, California). Results of the electrophoretic runs were analyzed using Genescan and Genotyper software (Applied Biosystems) to determine the genotypes of every individual for each locus.

A pedigree analysis was conducted to determine the adult-to-fry reproductive success of individual adult summer chum released into the spawning channel. The subsampled outmigrant juveniles were genotyped for the same loci as the adults. Parentage assignments were made using the computer program CERVUS (Marshall et al. 1998) by initially using an exclusionary approach. If exclusion alone was insufficient to identify a single parental pair for a particular juvenile, a likelihood method was used to assign parentage.

### Statistical analyses

We tested the hypothesis that reproductive behavior and adult-to-fry reproductive success of hatchery and natural chum salmon did not differ over the course of this 2-year study. For females, we tested for differences in prespawning, spawning, and nest-guarding durations, egg retention, number of matings, and reproductive success. Males were tested for differences in dominance and satellite frequencies and reproductive success. Data were analyzed by a two-way mixed-model analysis of variance (ANOVA). Origin (hatchery or natural) was the fixed main effect of interest and breeding group, representing all spawners in one channel in one year (i.e., 2004 east (E), 2004 west (W), 2005E, and 2005W) was the random factor. The following variables were square-root-transformed to improve normality: number of fry produced (males and females), number of mates (males and females), and spawning duration (females only). The relative number of fry produced by each adult chum salmon was the primary variable of interest. Therefore, we also calculated the RRS of hatchery fish by dividing the mean number of fry produced per hatchery fish by the mean number produced per natural fish for each breeding group. A value of 1.0 would reflect equal reproductive success. One RRS value was produced for each breeding group, and we presented the mean ± 95% confidence interval for the estimates of RRS ($N$ = 4). This provided a basis for comparison with studies on other species (Berejikian and Ford 2004; Araki et al. 2008). Using the same paired-sample approach, we conducted a post-hoc power analysis to determine the number of independent breeding groups that would be required to detect the calculated mean differences in reproductive success at $\alpha = 0.05$ and $\beta = 0.80$.

We tested for assortative mating using separate 2 × 2 contingency table analyses, with a Yates correction, for each breeding group. Male parent (hatchery or natural origin) and female parent (hatchery or natural origin) were the column and row categories, respectively. Matings were evident by the production of at least one offspring as determined by the pedigree analysis. Assortative mating could lead to reproductive isolation and divergence between hatchery and natural populations and may reflect mate choice related to unobserved differences in phenotypic characters between hatchery- and natural-origin spawners. Nonassortative mating would suggest similar mate choice and intrasexual selection patterns. We tested for correlations between male and female body weight and the various behavioral and reproductive success response variables by simple linear regression analyses. Separate analyses were conducted within each breeding group.

## Results

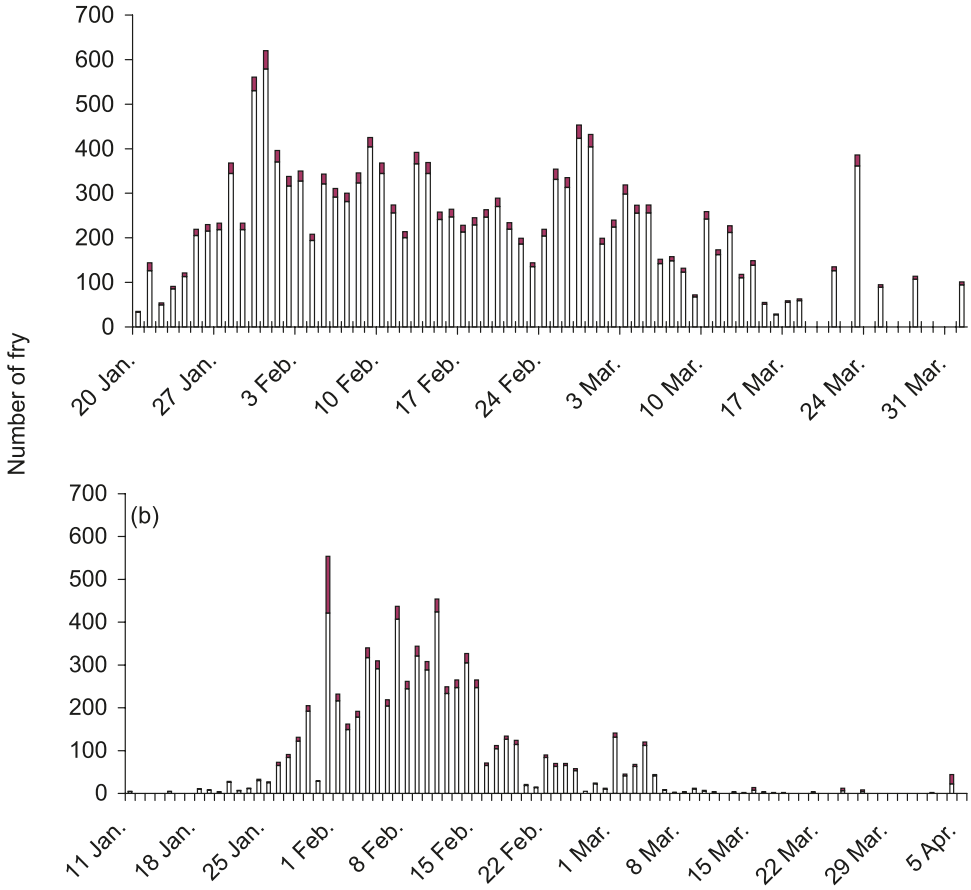
### Pedigree analyses

A total of 1208 of the 1230 fry sampled in 2005 (2004 spawning season) were assigned to a single pair mating. Of those, 97% were assigned by exclusion and 3% by likelihood analysis ($P > 0.95$). A total of 457 of 487 fry sampled in 2006 (2005 spawning season) were assigned to a single pair mating. Of those, 83% were assigned by exclusion and 17% by likelihood analysis ($P > 0.95$). Twenty-two fry were dropped from the 2005 data set and 30 fry were dropped from the 2006 data set because they could not be assigned to two parents with a high level of confidence.

### Female behavior and reproductive success

None of the statistical interactions between stock origin (natural and hatchery) and breeding group (2004E, 2004W, 2005E, and 2005W) was significant for any of the female behaviors, matings, or reproductive success measures ($P >$ 0.18 in all cases), with the exception of spawning duration ($P = 0.05$). In 2005W, hatchery females took longer on aver-

**Fig. 1.** Outmigrating summer chum (*Oncorhynchus keta*) fry captured in (*a*) 2005 and (*b*) 2006. Shaded portions of the bars represent the number of fry subsampled for the DNA pedigree analyses. Fry were caught in traps at the downstream end of the spawning areas. The channel was electrofished on 23 and 25 March and 1 April 2005 (all data shown) and on 4 April 2006 (22 fry caught; data not shown). In each year, all fry migrating from the two sides of the channel were able to mix and were captured in a single trap. Emigrating fry averaged less than 40 mm and 0.4 g in each year, suggesting that they outmigrated shortly after emergence.




age to complete spawning than the natural-origin females, whereas spawning durations in the other three groups were similar. The overall adult-to-fry reproductive success of hatchery females was not significantly different from that of natural-origin females ($P$ = 0.27; Fig. 2). The RRS point estimates were less than 1.0 in three of the breeding groups (0.62 in 2004E, 0.77 in 2004W, and 0.15 in 2005E) and greater than 1.0 in the other (1.34 in 2005W). The results of a post-hoc power analysis ($\alpha$ = 0.05, $\beta$ = 0.80) suggests that 10 replicate breeding groups with the same number of females per breeding group used in this study would have been required to detect the estimated 28% reduction in reproductive success (Fig. 2).

The mean number of mates per female (hatchery origin = 1.7; natural origin = 1.9) was similar ($P$ = 0.47). Hatchery- and natural-origin females did not differ significantly in time to onset of spawning or spawning duration (Fig. 3). Natural-origin females were observed nest guarding on average 40 h longer than hatchery females, but this difference was also not significant ($P$ = 0.18; Fig. 3). Finally, female hatchery- and natural-origin fish retained similar numbers of eggs at death ($P$ = 0.58). Reproductive success, egg retention, and each of the behavioral response variables differed significantly among breeding groups ($P$ < 0.05).

### Male behavior and reproductive success

None of the statistical interactions between stock origin and spawner group was significant for any of the male behaviors or reproductive success measures ($P$ > 0.17 in all cases). The overall adult-to-fry reproductive success of hatchery-origin males was very similar to that of natural-origin males ($P$ = 0.53; Fig. 2). As with the females, the RRS estimates were less than 1.0 in 2004E (0.81), 2004W (0.64), and 2005E (0.95) and greater than 1.0 in 2005W (1.70). The results of a post-hoc power analysis ($\alpha$ = 0.05, $\beta$ = 0.80) suggest that 24 replicate breeding groups with the same number of males per breeding group used in this study would have been required to detect the 3% estimated increase in reproductive success exhibited by hatchery-origin fish (Fig. 2).

The mean number of mates per hatchery-origin male (1.4) equaled that for natural-origin males ($P$ = 0.98). Hatchery- and natural-origin males were observed with similar frequency in the dominant ($P$ = 0.99), satellite 1 ($P$ = 0.61), and satellite 2 ($P$ = 0.21) positions in male hierarchies and thus appeared equally capable of obtaining access to nesting females. Reproductive success and the frequency of attending females as either a dominant or satellite male differed significantly among the four breeding groups ($P$ < 0.05).

**Fig. 2.** The relative reproductive success of hatchery-produced and natural-origin summer chum salmon (*Oncorhynchus keta*). A value of 1 would represent equal reproductive success of hatchery- and natural-origin fish. The bars represent mean values (±95% confidence intervals around the mean value; $N = 4$ breeding groups).

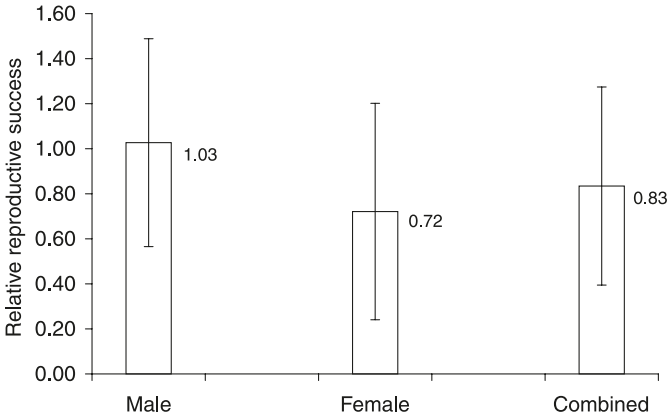
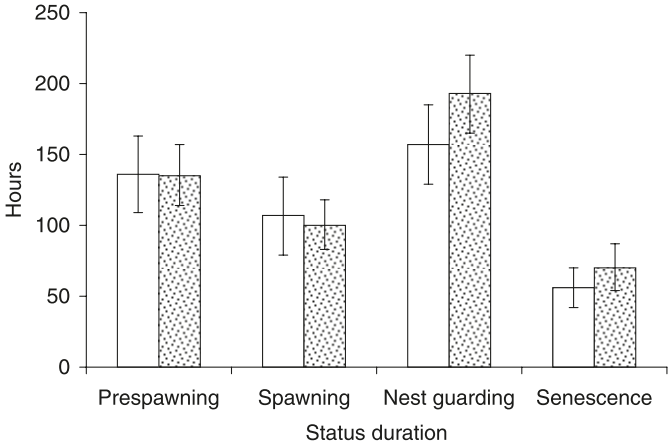



**Fig. 3.** Graph of mean spawning durations (±95% confidence interval) for each behavioral status quantified for hatchery-origin (open bars) and natural-origin (stippled bars) female chum salmon (*Oncorhynchus keta*).




### Body size and dominance

We assumed that dominance and reproductive success may each depend on body size, but not the reverse; therefore, we first tested for a positive correlation between body size (independent variable) and dominance frequency (dependent variable). Male body weight was positively correlated with dominance frequency in 2004W, 2005E, and 2005W but not in 2004E (Fig. 4). Male body weight was significantly and positively correlated with reproductive success in 2004E, 2004W, and 2005E but not in 2005W (Fig. 4). The standardized residuals of the weight vs. dominance frequency regression relationship were positively and significantly correlated with reproductive success in 2004E ($r^2 = 0.185$, $P = 0.010$) and 2005W ($r^2 = 0.121$, $P = 0.036$) but not in 2004W ($r^2 = 0.001$, $P = 0.921$) or 2005E ($r^2 = 0.071$, $P = 0.092$). Thus, the potential effect of dominance on reproductive success is not entirely an advantage conferred by large body size. Female body size was not significantly correlated with any of the female reproductive behaviors, egg retention, number of mates, or reproductive success in any of the four breeding groups ($P > 0.05$ for all tests).

### Mating combinations

The summer chum salmon in this study did not appear to mate assortatively with respect to origin (hatchery or natural) in any of the four breeding groups (2004W and 2004E, $\chi^2 = 0.00$, $P = 1.00$; 2005W, $\chi^2 = 0.483$, $P = 0.487$; 2005E, $\chi^2 = 0.671$, $P = 0.413$; overall, $\chi^2 = 0.540$, $P = 0.463$). Of the 161 matings detected in the pedigree analysis for all four breeding groups combined, 33 were hatchery × hatchery, 42 were natural origin × natural origin, 46 were hatchery female × natural-origin male, and 42 were natural-origin female × hatchery-origin male.

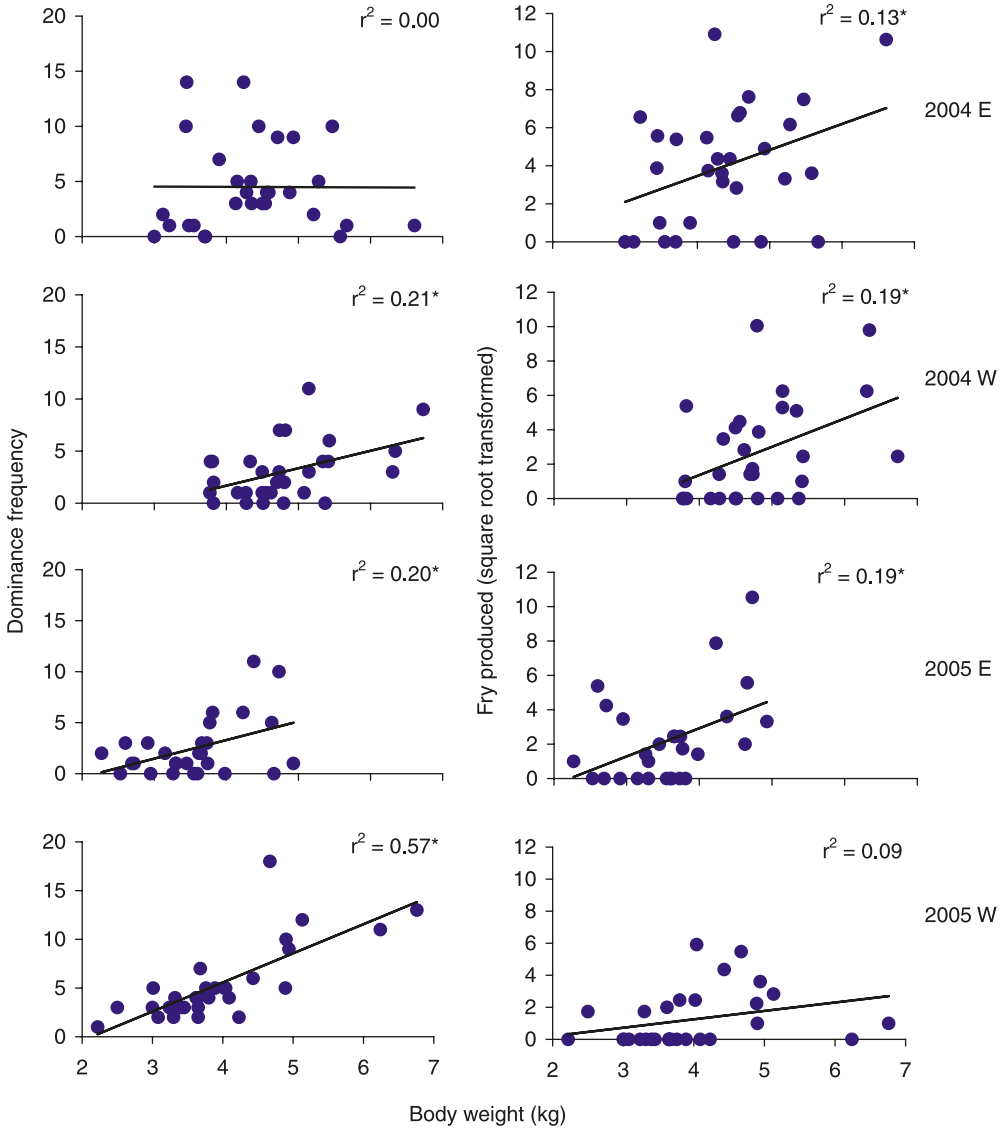
## Discussion

We found no significant differences in reproductive success of hatchery- and natural-origin summer chum salmon. Mean RRS estimates for both males and females have fairly large 95% confidence intervals, which indicate low statistical power to detect differences between populations. Although variation in individual reproductive success was high, the overall mean reproductive success of hatchery- and natural-origin males was nearly identical. Therefore, our results suggest no real between-population differences in male reproductive success. The RRS of hatchery females averaged 0.72 and may indicate reduced fitness that we were unable to detect. However, hatchery- and natural-origin males and females exhibited similar reproductive behavior, spawned synchronously, and did not mate assortatively with respect to origin, providing no indication of reduced breeding performance of hatchery fish that might compromise offspring production.

With one exception, the few studies that have evaluated the RRS of hatchery fish derived from the local wild broodstock have indicated low to moderate reductions in relative fitness. Ford et al. (2006) estimates of the relative lifetime fitness of hatchery coho salmon in Minter Creek, Washington (0.74 for females and 1.01 for males), approximated the adult-to-fry estimates in our study, although their estimates of adult-to-fry fitness were somewhat higher (females = 1.16, males = 1.26). Araki et al. (2007*b*) found nearly equal relative fitness in hatchery- and natural-origin winter steelhead; however, their updated analysis in 2007, including a total of six run years, indicated mean RRS of 0.88 and 0.70 for females and males, respectively. Schroder et al. (2008) did not calculate relative fitness in the same way in which we and others have; they estimated equal egg deposition and a 5.6% reduction in the egg-to-fry survival of female spring Chinook salmon (*Oncorhynchus tshawytscha*) spawning with the natural founder population in an experimental stream channel. In stark contrast, several studies of steelhead have demonstrated dramatically reduced reproductive success of nonlocal hatchery fish (e.g., Leider et al. 1990; Kostow 2004; Araki et al. 2007*b*). Similar studies of nonlocal farmed Atlantic salmon (Fleming et al. 2000) and nonlocal wild Atlantic salmon (McGinnity et al. 2004) have also indicated comparably poor relative fitness.

One interpretation of the apparent performance disparity between locally derived versus nonlocal hatchery populations is that utilizing local-origin adults for broodstock

**Fig. 4.** Relationships between male body weight (kg) and courting frequency (left column) and fry production (right column, square-root-transformed). An asterisk next to the squared correlation coefficient indicates a significant linear relationship ($P < 0.05$).




might ameliorate reductions in hatchery fish fitness; however, one recent study would predict a different outcome. Araki et al. (2007*a*) estimated that hatchery-origin fish with two hatchery-origin parents had only 55% of the relative lifetime RRS of hatchery-origin fish with one hatchery-origin and one natural-origin parent, suggesting a genetic basis for the fitness loss. A follow-up modeling exercise suggested that either simultaneous selection on multiple traits or intense selection coupled with very high heritability could generate fitness loss of this magnitude (Araki et al. 2008). Our study suggests reproductive similarities between natural-origin summer chum salmon and hatchery-produced salmon. Our study primarily tested potential domestication selection following one to three generations of artificial spawning, hatchery incubation, and brief juvenile rearing in addition to the environmental effects of early experience in the hatchery. The results of ongoing studies on Chinook salmon and steelhead throughout the Pacific Northwest US will soon provide a further context and help in assessing whether the findings of Araki et al. (2008) reflect (*i*) a species-specific vulnerability to rapid fitness loss, (*ii*) some artifact of the particular river system, population, or hatchery practices, or (*iii*) a more widespread phenomenon in hatchery-produced salmonids.

Domestication selection (adaptation to the hatchery environment) may result from prespawning captivity in the hatchery collection facility, broodstock selection, and artificial spawning (Campton 2005; McLean et al. 2005), adaptation to incubation and early rearing environments (reviewed by Fraser 2008), and selection on hatchery-induced phenotypic variation in the postrelease environment (Reisenbichler et al. 2004). The present study is the first to examine a species with a very brief juvenile freshwater life-history phase. Juvenile chum salmon begin migration to sea within days or weeks after emergence, so the opportunity for domestication selection on juvenile traits combined with juvenile hatchery rearing experience that might affect reproductive success is more limited than for other salmon. Therefore, our results

probably pertain more to genetic effects of artificial spawning and incubation, because the hatchery- and natural-origin chum salmon experienced similar environments through nearly their entire postemergence lifetime. All previous studies of hatchery salmon RRS have involved species that spend a year (coho salmon and stream-type Chinook salmon) or more (steelhead and Atlantic salmon) in fresh water and therefore are subject to selection pressures in the hatchery-rearing environment for an extended period, are probably more prone to unnatural selection on hatchery-modified phenotypes (Kostow 2004) after release, and are more strongly affected by early experience (Fleming et al. 1997).

All RRS studies of hatchery- and natural-origin salmon using DNA pedigree analyses include some degree of competition, because the hatchery- and natural-origin fish were spawning in the same river or spawning channel (Berejikian and Ford 2004). We chose high spawner densities (approximately one female and one male per 3 $m^2$ of available habitat) to provide a competitive environment and to determine whether competitive asymmetries might exist and manifest in differences in breeding success between hatchery- and natural-origin chum salmon. Fleming and Gross (1993) experimentally manipulated spawner densities and found that hatchery coho salmon suffered increasingly lower relative breeding success as spawner densities were increased from 5.0 $m^2$ to 2.5 $m^2$ to 1.25 $m^2$ of habitat per male or female spawner, and the effects were greater on hatchery males than females. The breeding success of farmed Atlantic salmon males decreased as spawner density increased from 3.9 $m^2$ to 3.6 $m^2$ to 2.6 $m^2$ of habitat per male (Fleming et al. 1997) in a similar study. Although the comparisons are across species (coho salmon) and across genera (Atlantic salmon), the densities that we created should have been sufficient to detect competitive asymmetries had they existed.

Hatchery rearing can reduce body size either by advancing age-at-sexual maturity through broodstock selection (Hankin et al. 1993) or through environmentally mediated effects on growth (Larsen et al. 2004; Knudsen et al. 2006). Hatchery fish may also be substantially smaller than natural-origin fish during the first year of returns in new supplementation programs when the hatchery fish are younger, or they may be larger during the last year of a supplementation program when only the oldest hatchery fish return to spawn. Therefore, it is reasonable to predict that hatchery-origin males will exhibit differential breeding success based, in part, on size-mediated access to nesting females. The positive correlations between male body size and breeding success in this study appear to be fairly widespread among anadromous salmonids (Atlantic salmon, Fleming et al. 1997; steelhead, Seamons et al. 2004; coho salmon, Fleming and Gross 1992; pink salmon (*Oncorhynchus gorbuscha*), Dickerson et al. 2002; chum salmon, Schroder 1981; sockeye salmon (*Oncorhynchus nerka*), Quinn and Foote 1994). However, in natural streams, predation, arrival timing, or other factors may present additional or opposing selection factors (Dickerson et al. 2005; Seamons et al. 2007).

The Hood Canal summer chum salmon conservation program (WDFW–PNPTC 2000) should reasonably expect that the reproductive success of hatchery-origin fish is sufficient to contribute to rebuilding of depleted stocks along with other management actions, including harvest reductions and habitat improvement projects. To guide artificial propagation of salmon more broadly, it will be important to have several measures of relative fitness for each anadromous salmonid species that is bred in captivity and released with the explicit goal of contributing to natural reproduction.

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