Increases in steelhead (*Oncorhynchus mykiss*) redd abundance resulting from two conservation hatchery strategies in the Hamma Hamma River, Washington

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Abstract: Conservation hatcheries for anadromous salmonids that aim to increase production and minimizing genetic, ecological, and demographic risks have not been experimentally tested for their ability to increase number of adults spawning in the natural environment. The conservation hatchery program for steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) evaluated in this study caused an increase in the number of redds in the supplemented Hamma Hamma River compared with the presupplementation period. Three control populations (nonsupplemented) either remained stable or declined over the same period. The increase in redds from hatchery-produced spawners did not reduce the redd production from natural-origin spawners. The strategy of rearing and releasing adult steelhead accounted for the greatest proportion of redd abundance increases. Environmentally induced differences in spawn timing between the adult release group and anadromous adults of hatchery and natural origin may explain why the adult release group and anadromous adults assortatively formed pairing combinations on the spawning grounds. Although captively reared adults produced the majority of redds in years they were released in substantial numbers, uncertainty regarding the relative reproductive success of this strategy suggests caution in recommending one strategy over the other. A demographic boost to the naturally spawning population was effected while managing to minimize negative ecological consequences.

Résumé : Les piscicultures de conservation de saumons anadromes cherchent à augmenter la production, tout en minimisant les risques génétiques, écologiques et démographiques; cependant, leur capacité à accroître le nombre d'adultes reproducteurs dans le milieu naturel n'a jamais été vérifiée expérimentalement. Le programme de pisciculture de conservation de la truite arc-en-ciel (*Oncorhynchus mykiss*) anadrome que nous évaluons a eu comme résultat d'augmenter le nombre de frayères dans la rivière Hamma Hamma après l'empoissonnement par rapport à la période antérieure. Trois populations témoins (sans empoissonnement) sont ou bien demeurées stables ou ont décliné pendant la même période. L'augmentation du nombre des frayères produites par les reproducteurs provenant de la pisciculture n'a pas réduit la production de frayères pour les poissons d'origine naturelle. La stratégie d'élevage et de libération de truites arc-en-ciel anadromes explique la plus grande partie de l'augmentation de l'abondance des frayères. Les différences dans le calendrier de la fraye induites par l'environnement entre le groupe d'adultes empoissonnés et les adultes anadromes d'origine naturelle ou de pisciculture peuvent expliquer pourquoi les adultes empoissonnés et les adultes anadromes s'assortissent en combinaisons de couples de même nature sur les milieux de fraye. Bien que les adultes élevés en captivité construisent la majorité des frayères les années où l'empoissonnement est important, l'incertitude entourant le succès reproductif relatif de cette stratégie incite à être prudent dans la recommandation d'une stratégie plutôt que de l'autre. Il s'est produit un accroissement de la population naturelle des reproducteurs, alors que les conséquences écologiques ont pu être minimisées.

[Traduit par la Rédaction]

Introduction

Artificial propagation of Pacific salmon (*Oncorhynchus* spp.) and steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) for conservation purposes is considered an experimental approach for maintaining or rebuilding depleted populations in the northwestern United States and Canada (ISAB 2003). The management objectives of conservation hatcheries vary, but most aim to prevent imminent biological extinction by amplifying the abundance of adult fish while at the same

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time maintaining the genetic integrity of the target population (Berejikian et al. 2004). Conservation hatchery programs collect embryos, juveniles, or adult broodstock from the wild and rear and release these same fish or their offspring into their natal or ancestral watersheds. Hatchery programs designed to supplement natural populations typically produce more spawners per artificially spawned parent than spawners produced per naturally spawning parent because of increased egg-to-smolt survival in the hatchery (ISAB 2003; Berejikian et al. 2004; Sharma et al. 2006). Conservation hatchery programs have yet to demonstrate that increases in adult returns lead to an increase in natural spawning in the composite (hatchery + natural) population.

Most published studies evaluating the effects of releasing hatchery-reared salmon or steelhead have concluded that the hatchery programs may reduce the survival or productivity of the natural populations (Levin et al. 2001; Nickelson 2003; but see Sharma et al. 2006). Studies published thus far have assessed the effects of large-scale hatchery programs operated to augment harvest or those utilizing non-native or highly domesticated hatchery broodstock. Analyses have relied on post hoc correlations (e.g., Levin et al. 2001; Chilcote 2003; Nickelson 2003) or modeling exercises (Oosterhout et al. 2005) rather than planned experiments. A true experimental approach requires reference populations that do not receive hatchery fish (Goodman 2004) and, ideally, a priori hypotheses tested with data from the presupplementation phase. Recent studies have compared the productivity of hatchery and natural coho salmon (*Oncorhynchus kisutch*) populations in a single watershed before and during supplementation (Sharma et al. 2006) and the relative reproductive success of hatchery and wild steelhead (Araki et al. 2006). However, neither study had the opportunity to include reference populations to account for factors such as spatial variability among watersheds or temporal variability in ocean productivity that may confound the evaluations of spawner abundance in supplemented streams (e.g., Hilborn and Winton 1993). The present study compares the number of steelhead redds before and during the implementation of a supplementation program and compares the response to three reference populations that were not supplemented to account for natural variability among populations.

Steelhead hatcheries throughout the Pacific Northwest almost invariably involve artificial spawning of adult broodstock and releasing age-1 smolts (natural-origin steelhead in Washington State typically undergo smoltification and migrate to sea at age-2; Busby et al. 1996). Artificial spawning, rearing, and release practices have been shown to advance spawn timing in conventional hatchery operations (steelhead: Ayerst 1977; McLean et al. 2005; coho salmon: Ford et al. 2006), reduce steelhead reproductive success (Leider et al. 1990; McLean et al. 2004), and alter juvenile steelhead behavior and predator-avoidance ability (Berejikian 1995; Berejikian et al. 1996). Hatchery programs operated for conservation purposes generally attempt to minimize genetic selection caused by artificial spawning and hatchery rearing, mimic the characteristics of natural fish, and scale the number of released smolts to the carrying capacity of the natural system (Flagg et al. 2004).

Conservation of several other anadromous salmonid populations listed as threatened or endangered under the US Endangered Species Act have recently been including nonconventional approaches to removing fish from the wild for culture and re-introducing them or their offspring. One such conservation hatchery program, the Hamma Hamma River Steelhead Supplementation Project, was initiated in 1998 with the goal of increasing the abundance of naturally spawning steelhead. This project included several nonconventional approaches aimed at minimizing potential negative impacts artificial propagation on the target natural population (no artificial spawning, natural age-at-smoltification, low numbers of released fish, and release of captively reared adults; see Materials and methods).

The goals of this evaluation were (*i*) compare changes in the abundance of redds produced in the Hamma Hamma River before and during the implementation of the hatchery program, (*ii*) estimate the contribution of captively reared adults to redd construction, and (*iii*) quantify spawn timing and breeding interactions between captively reared and anadromous spawners.

Materials and methods

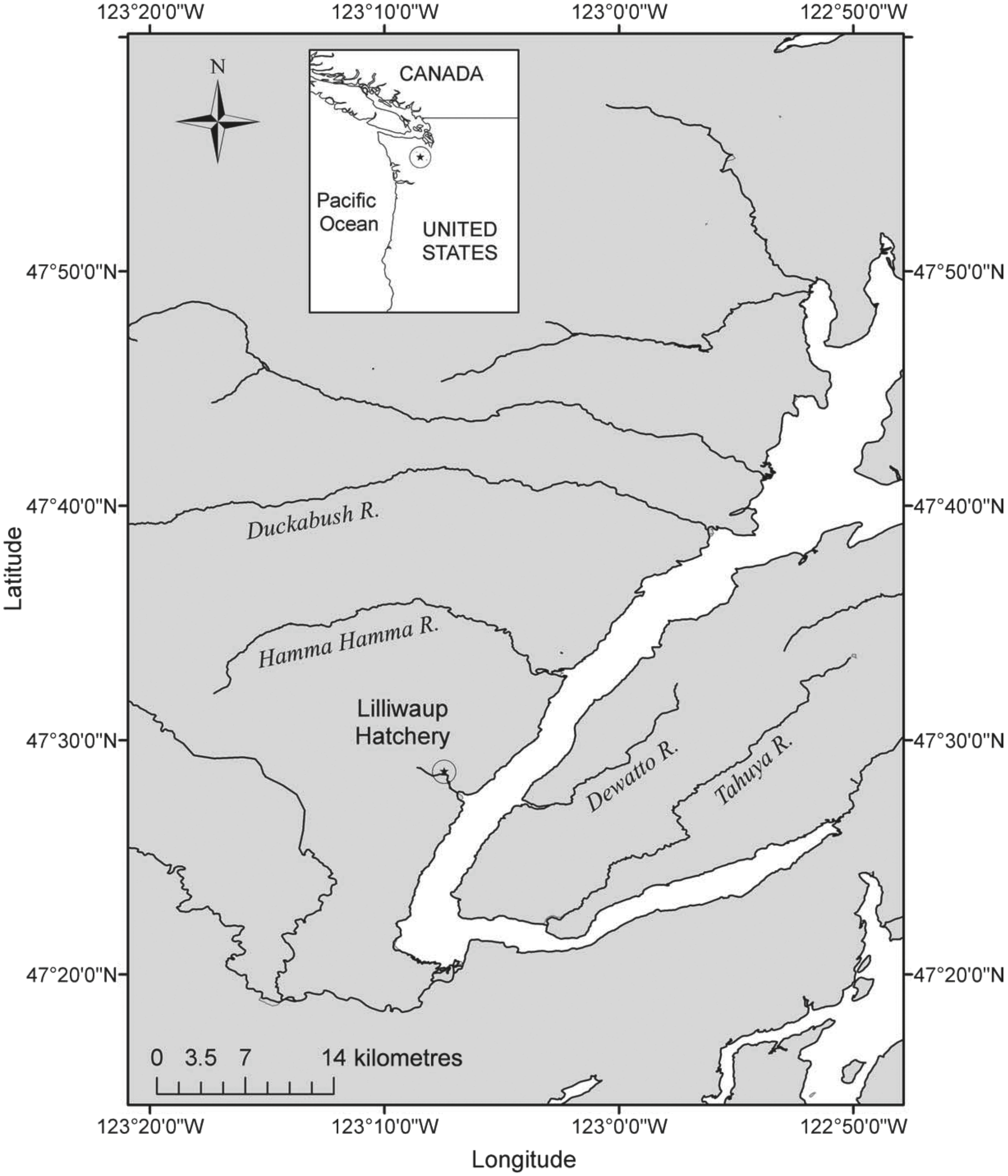
Study populations

The Hamma Hamma River drains the eastern slopes of the Olympic Mountains and flows into Hood Canal near the town of Eldon, Washington (Fig. 1). The Hamma Hamma watershed is about 137 km^2 in area, contains 29 km of mainstem and 150 km of tributary habitat, and has an average annual discharge of 16.1 m^3·s^{-1}. However, anadromous fish passage is limited to the lower 3.8 km, where a natural fall blocks upstream migration of adults. Habitat in the anadromous habitat below river km 3.8 contains a mix of forest land including old growth and second growth timber, pasture, and residential property, all of which is owned by the Hamma Hamma Timber Company.

The Hamma Hamma River wild steelhead sport angler harvest averaged 89 adults between 1950 and 1987. In the subsequent 3 years, reported sport angler harvest dropped to 11, 8, and 4 adults, respectively, and harvest of wild adults has been prohibited since 1990. Prior to supplementation effort initiated in 1998, the Hamma Hamma River received only a single outplanting of 5930 hatchery smolts in 1953. An unknown proportion of adult *O. mykiss* in the Hamma Hamma River exhibit a resident life history, do not migrate to sea, and mature in fresh water (see Kuligowski et al. 2005).

Three rivers in the Hood Canal Watershed contained nonsupplemented “control” populations, located on the west and east sides of Hood Canal and north and south of the Hamma Hamma River (Fig. 1). The Dewatto River watershed (48 km^2) contains 14 km of mainstem and has an average annual discharge of 2.16 m^3·s^{-1}. The Tahuya River contains 33.9 km of mainstem and has an annual average discharge of 4.3 m^3·s^{-1}. The Duckabush watershed (194 km^2) contains 40 km of mainstem and has an average annual discharge of 13.6 m^3·s^{-1}. Anadromous steelhead have access to the lower 10 km of the Duckabush River watershed, the lower 19 km of the Tahuya River watershed, and 10 km of the Dewatto River watershed, although a large wetland complex may limit adult steelhead migrations to the lower 5 km of the Dewatto River.

Fig. 1. Map of the Hood Canal watershed showing the supplemented river (Hamma Hamma), the three control rivers (Duckabush, Dewatto, and Tahuya), and the Lilliwaup hatchery in Washington, USA.



No smolts were released into the Dewatto or Tahuya rivers during the course of this study. Releases of hatchery-reared steelhead smolts into the Duckabush River from 1995 to 2002 (1997 to 2004 return years) have averaged (± standard deviation, SD) 8442 (±3598). The smolts released into the Duckabush River were derived from a Puget Sound population (Chambers Creek) that had been selected for substantially advanced spawn timing, with peak spawning occurring in December and January (Ayerst 1977). Thus, redds produced by hatchery females escaping to the spawning grounds would not have been counted in the redd surveys occurring when wild fish spawn (from late February through early June of each year). Similarly, McMillan et al. (2007) found no evidence over 5 years of spawning interactions between steelhead derived from the same hatchery stock and natural-origin steelhead in two western Washington streams.

The Hamma Hamma River hatchery population was established by hydraulic removal of eyed steelhead eggs (em-

Table 1. The number of eyed embryos collected, number of juveniles released at age-1 and age-2, and number of maturing adults released at age-4 and age-5.

			John Creek Pond		Lilliwaup Hatchery	Adult release group	
Brood year	Redds represented	Eggs collected	Age-1[b]	Age-2	Age-2	Age-4	Age-5
1998[a]	8	4683	1711	0	1524	81 F, 116 M	2 F, 2 M
1999	6	2588	466	435	901		
2000	7	1622	601	8	481	35 F, 41 M	10 F, 15 M
2001	4	2000	577	150	727		

Note: Adults from brood year 1998 were released in 2002 (age-4) and 2003 (age-5); adults from brood year 2000 were released in 2004 (age-4) and 2005 (age-5). F, female; M, male.

[a] The majority of smolts released from the 1998 brood year would be expected to spawn for the first time in 2002 at age-4.

[b] Age-1 fish "released" from the John Creek Pond represent escapees resulting from various temporary pond failures during the winter prior to their intended release. Escapes occurred in every year when the fish were approximately 16–18 months of age. Escaped fish entered John Creek and still may have contributed to adult returns (all were marked prior to escape).

bryos) in spring–summer of 1998–2001 using methodology similar to that described by Collins et al. (2000). Each year, the resulting fry were reared at two locations: (*i*) an earthen spring-fed pond located near John Creek, the main tributary of the Hamma Hamma River below the anadromous barrier, and (*ii*) circular rearing vessels at the Long Live the Kings Hatchery near Lilliwaup, Washington, approximately 10 km south of the Hamma Hamma River. Hereafter, fish reared and released at the smolt stage are referred to as the smolt release group (SRG), and fish reared and released at the adult stage are known as the adult release group (ARG). The ARG fish were reared only at the Lilliwaup Hatchery.

Age-2 smolts were released on 1 May each year beginning in 2000, and adults were released between 12 February and 6 March (depending on the year) to coincide with the onset of ovulation in females from the ARG population (Table 1). The fork length of ARG fish at the time of release averaged 525 mm in 2002, 633 mm in 2003, 502 mm in 2004, and 683 mm in 2005. The fork length of SRG fish at the time of release averaged 185 mm in 2000, 182 mm in 2001, 206 mm in 2002, and 178 mm in 2003. The SRG fish reared at the Lilliwaup Hatchery were marked by removal of the adipose fin and insertion of a coded-wire tag approximately 1 month prior to release. The SRG fish reared at the John Creek Pond had their adipose fin removed, but were not coded-wire-tagged. A uniquely numbered 3 cm long Floy anchor tag was inserted into the dorsal musculature of every released ARG fish (a different color was used each year).

Redd surveys

Redd surveys were conducted in the Hamma Hamma River and the three control rivers during each year of the study. The presupplementation period was represented by surveys conducted annually from 1997 through 2001, and the supplementation period included the years 2002–2006. Surveys were conducted by walking along the stream banks and in the streams. We used data from annual Washington Department of Fish and Wildlife (WDFW) redd surveys in all study streams. Redd survey frequency in the Hamma Hamma River increased beginning in 2002 to facilitate other data collection (e.g., reproductive behavior, marking redd locations for embryo collections, and capturing adult steelhead for genetic and age data). Survey frequencies were intentionally increased in the Duckabush River from 2003 through 2006 and in the Dewatto River from 2004 through 2006 to more closely match the increased survey frequency in the Hamma Hamma River during the supplementation period and to provide a basis for estimating the effect of survey frequency on redd abundance.

Redd surveys are a frequently used and widely accepted method for estimating adult salmon and steelhead abundance (Nickelson 2003; Gallagher and Gallagher 2005; Sharma et al. 2006). Crews of two walked the index reaches of each stream searching for redds. All redds were uniquely marked with labeled flagging, tied to vegetation on the stream bank. Redds were identified as described in previous studies (Gallagher and Gallagher 2005) by a clear "tail-spill" (usually crescent-shaped), resulting from material excavated to construct a nest pocket. Redds containing a minimum of 1 m of unexcavated gravel between them were considered separate. In cases where redds had remained the same size for at least 4 days and were later enlarged (or altered to account for superimposition), the enlarged area was counted as an additional redd. Berejikian et al. (2005) found that female steelhead spawned, on average, over a 4.0-day period, with females observed to be enlarging the redd each day from the onset to termination of spawning. In this study, we used the numbers of redds as the response variable for statistical tests to eliminate potential random error associated with redds-per-female and sex ratio estimates.

Spawning behavior and timing

The reproductive behavior of maturing steelhead in the Hamma Hamma River was monitored several days each week from the stream bank during the spawning season from 2002 to 2004 for three purposes: (*i*) test the null hypothesis that ARG and anadromous (SRG or wild) steelhead did not exhibit assortative mating as inferred from pairing combinations; (*ii*) test the null hypothesis that ARG and anadromous females did not differ in spawn timing; and (*iii*) obtain point estimates for the proportion of redds that were constructed by ARG and anadromous females in years where substantial numbers of each group were present (i.e., 2002 and 2004). Behavioral observation methods and data on just the pairing combinations in 2002 are presented in Berejikian et al. (2005). In both years, observers walked along both stream banks to locate nest-digging females and attempted to determine their rearing history based on the adipose fin marks and the presence or absence of an anchor tag. Unfortunately, observers could not reliably determine adipose fin presence and absence, so SRG and wild fish could not be distinguished from one another and were combined into an "anadromous" category. Observers determined the dominant or courting male within the hierarchy of males surrounding each nest-digging female. Courting males were those holding the position closest to a nest-digging female and exhibiting courtship behavior (quivers and crossovers). Courting males would also frequently chase off other peripheral males that held positions downstream and would frequently dart into the nest. Courting frequency has been shown to be a strong indicator of actual breeding success in this population of steelhead (Berejikian et al. 2005), which is generally confirmed by other studies of salmonids (e.g., Quinn and Foote 1994; Mjölnerod et al. 1998; Blanchfield et al. 2003). The number of different nesting females from each group and the frequency of each pairing combination (i.e., a nest-digging female and courting male) were tabulated for each year in which observations were made.

Spawner abundance

Counts of live adult steelhead were made by snorkel surveys to calculate the proportions of observed ARG, SRG, and wild adult steelhead present in the Hamma Hamma River during the supplementation period (2002–2006). Snorkel surveys were conducted approximately weekly from river km 3.0 downstream to the area of tidal influence (approximately river km 1.2) to count fish. Surveyors walked upstream along the entire study section before snorkeling to look for fish and count redds. Surveyors kept track of the number of redds visible while on foot (redds observed during snorkeling that were not observed in the preceding foot survey were recorded separately). Once at the upstream end the study section, surveyors floated downstream to look for fish. When a steelhead was spotted, surveyors attempted to identify the presence or absence of an adipose fin, anchor tag presence or absence and color, and body length. Surveyors categorized *O. mykiss* as either greater or less than 42 cm in length (surveyors previously practiced identifying the size of objects underwater by comparing them to objects of known length). The robust body condition and often silvery appearance of *O. mykiss* greater than 42 cm suggested that these fish were anadromous (i.e., steelhead). Analyses of scales from 12 *O. mykiss* collected from the Hamma Hamma River between 42 and 50 cm have shown that six were anadromous, two were nonanadromous, and the life history of the other four could not be determined because of scale regeneration (J. Sneva, WDFW, 600 Capitol Way North, Olympia, WA 98501, USA, personal communication, 2005). We calculated the average number of fish from each group per survey within each year to estimate the proportion of adult steelhead from the ARG, SRG, and wild groups. Ten surveys were conducted in 2002, 11 in 2003, 16 in 2004, 14 in 2005, and 13 in 2006.

Redd construction by ARG, SRG, and wild steelhead

We calculated point estimates for the relative contribution of the ARG, SRG, and wild steelhead to redd construction in the Hamma Hamma River using a behavior-based estimate (in 2002 and 2004) and an abundance-based estimate (all years from 2002 through 2006). For the behavior-based estimate, we calculated the proportion of ARG and anadromous females that were observed to be constructing redds in 2002 ($N = 24$) and 2004 ($N = 20$). Females observed digging a nest were considered to have constructed the redd at that location.

The abundance-based estimate assumed that per capita redd production would be the same for adults from each of the three groups present on spawning grounds, which is supported by the following. First, a portion (24 females and 24 males) of the ARG were released into an experimental spawning channel in 2002. The females deposited an average of 98% of their estimated fecundity, no females spawned fewer than two times, and 100% of the 24 females produced fry (as determined by DNA pedigree analysis, Berejikian et al. 2005). Second, the average number of redds constructed by ARG females (1.42 redds per female) in the spawning channel was similar to other estimates of redds per female for wild steelhead (1.6 redds per female by wild steelhead in the Hamma Hamma River, Kuligowski et al. 2005; 1.5 redds per female in the Nestucca River, Oregon, Susac and Jacobs 2001; and 1.2 redds per female in Snow Creek, Washington, Johnson and Cooper 1992). Third, 10 of 14 ARG females that were recaptured by hook and line in 2002 had deposited all of their eggs; the other four had eggs that could be easily expressed, but appeared viable (i.e., not overripe or water-hardened), indicating they still had the potential to deposit the eggs. In 2004, 10 of 14 females had deposited all of their eggs, two had not yet ovulated, and two were ovulated with apparently viable eggs (B.A. Berejikian, unpublished data).

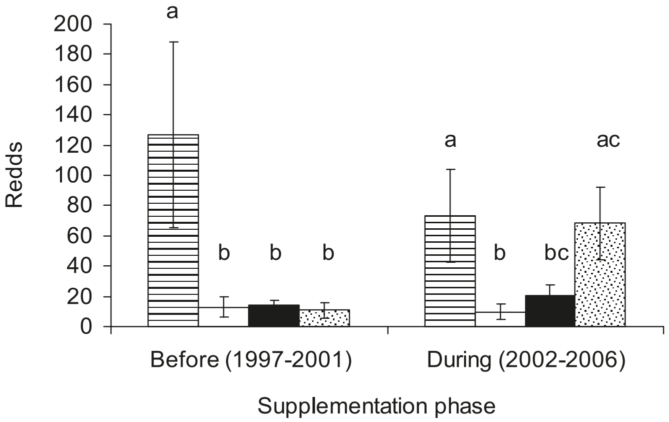
For the abundance-based estimate, we calculated the number of redds constructed by each group by multiplying the proportionate abundance of adults from each group observed during the snorkel surveys by the total number of redds observed in the same year. To evaluate concordance between the abundance- and behavior-based estimates, we compared the anadromous versus ARG behavior-based estimates in 2002 and 2004 with the anadromous versus ARG abundance-based estimates in those same years.

Statistical analyses

To assess whether the number of redds observed may have been influenced by survey frequency, redd survey frequency in a given year was regressed against the number of redds observed. Regressions for the Tahuya, Dewatto, and Duckabush rivers include all years (presupplementation and during supplementation). The Hamma Hamma River regressions were run separately for presupplementation and during supplementation periods because the substantial numbers of hatchery-reared fish observed constructing redds during the supplementation period would have confounded an analysis across the two periods.

In the absence of significant correlations between survey frequency and number of redds observed for any of the populations (see Results), redd abundance data were subjected to an analysis of variance (ANOVA), in which the main effects were period (before and during supplementation) and population (Dewatto, Duckabush, Tahuya, and Hamma Hamma). We tested the hypothesis that supplementation would have a different effect on redd abundance in the Hamma Hamma population than that in the other three populations. This effect

Fig. 2. The annual average number redds (±95% confidence intervals) in the supplemented river (Hamma Hamma, stippled bars) and the three control rivers (Tahuya, striped bars; Duckabush, open bars; and Dewatto, solid bars) before (1995–2001) and during (2002–2006) supplementation in the Hamma Hamma River. Different letters indicated significant differences as determined by Tukey's honestly significant difference tests ($\alpha = 0.05$).



would be reflected in a significant interaction between population and period. We conducted pairwise Tukey's honestly significant difference comparisons of cell means (e.g., Hamma Hamma River presupplementation versus Hamma Hamma River during supplementation) to identify changes in the relative abundance of redds in the Hamma Hamma River and the three control rivers.

We used the behavioral data to test the hypothesis that ARG and anadromous steelhead formed pairs without regard to whether their mates were ARG or anadromous; data were analyzed by χ^2 tests of independence (Sokal and Rolf 1995). The same nesting and courting data were used as surrogate measures of spawn timing. We tested for differences in spawn timing between ARG and anadromous males and females in 2002 and 2004 with a two-factor ANOVA (main effects: year and group; separate test for each gender). Significance level was $\alpha = 0.05$ for all statistical tests.

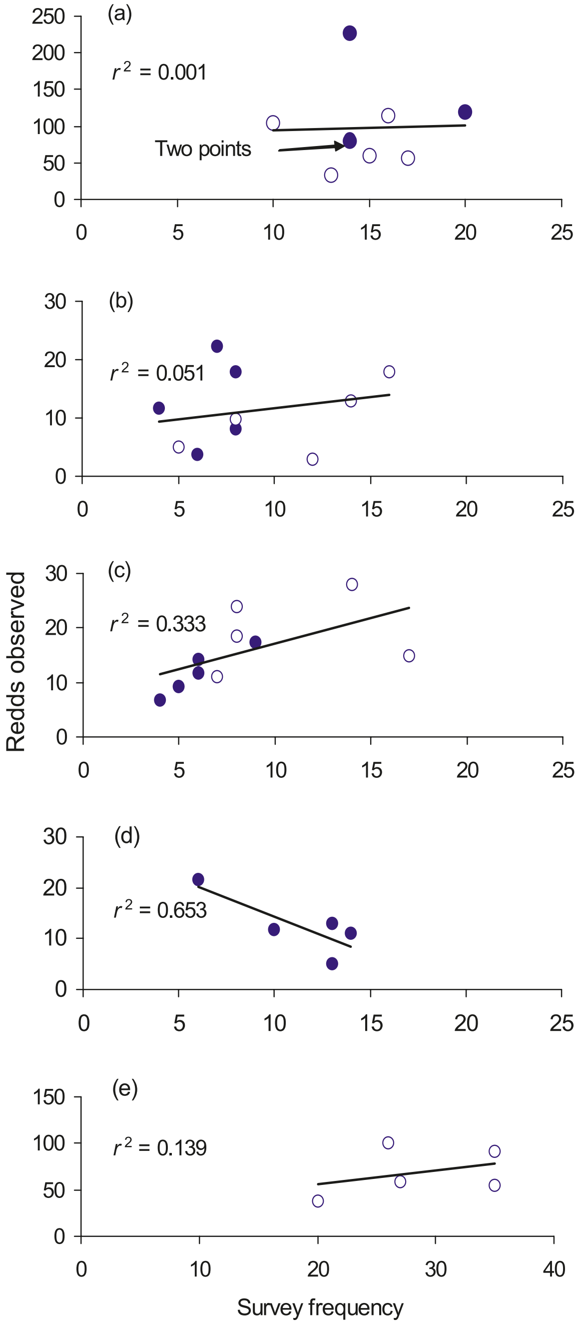
Results

Redd and spawner abundance

There was a significant interaction between the two main factors (supplementation phase and population) for the number of redds observed ($F_{[3,31]}$, $P = 0.001$; Fig. 2). The number of redds in the Hamma Hamma River during supplementation was significantly greater than that in the presupplementation period. In contrast, average redd abundance in the Dewatto and Duckabush populations was quite similar in the presupplementation and during supplementation periods, and the Tahuya population showed a decline (Fig. 2). No significant changes were detected between the before and after supplementation periods within the nonsupplemented rivers (e.g., Tahuya River before supplementation versus Tahuya River after supplementation; $P > 0.05$ for all comparisons, Fig. 2).

Redd survey frequencies in both the Hamma Hamma River and control rivers were greater during the supplementation period than during the presupplementation period; however, the increase was greatest in the Hamma Hamma River (Fig. 3).

Fig. 3. Simple linear regression analyses testing the correlations between the annual redd survey frequency and the number of redds observed in the three control rivers: Tahuya (*a*), Duckabush (*b*), and Dewatto (*c*). The presupplementation (solid circles) and during supplementation (open circles) years in Hamma Hamma River data (panels *d* and *e*) were analyzed separately to minimize confounding effects of adding hatchery fish, which were observed spawning. None of the correlations were significant ($\alpha = 0.05$).



Survey frequency did not explain a significant portion of the variability in redd abundance in any of the three control populations or the Hamma Hamma population (Fig. 3). The presupplementation period in the Hamma Hamma population showed the strongest correlation ($r^2 = 0.653$, $n = 5$, $P = 0.098$) between survey frequency and redd abundance; however, the slope was negative. The slopes of the linear regression rela-

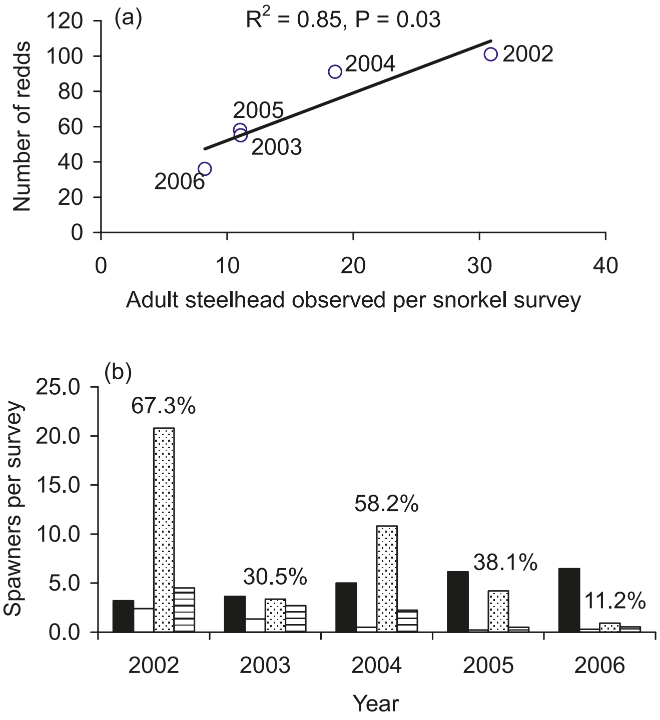


Fig. 4. (*a*) The relationship between the annual number of redds observed and the annual average number of adult steelhead (*Oncorhynchus mykiss*) observed during the snorkel surveys from 2002 through 2006. (*b*) The average annual number of adult steelhead identified by group (wild, solid bars; smolt release group (SRG), open bars; adult release group (ARG), stippled bars; unknown origin, striped bars). The percentage of adults belonging to the ARG group is shown above each ARG bar.

Table 2. The number of adult release group (ARG) and anadromous (combination of wild and returning hatchery-reared) male and female steelhead (*Oncorhynchus mykiss*) participating in courtships in the Hamma Hamma River in 2002 and 2004.

	ARG male	Anadromous male
2002		
ARG female	14	3
Anadromous female	3	4
2004		
ARG female	10	1
Anadromous female	3	6
Combined		
ARG female	24	4
Anadromous female	6	10

tionships tended to be weakly positive in the Tahuya population (r^2 = 0.001, *n* = 9, *P* > 0.50) and Duckabush population (r^2 = 0.051, *n* = 10, *P* > 0.50); the slope was stronger in the Dewatto population, but still nonsignificant (r^2 = 0.333, *n* = 10, *P* > 0.05). These data suggest redd survey frequency differences among streams or between periods did not bias the analysis comparing redd abundance before and during supplementation in the four populations.

In the Hamma Hamma River, the number of redds observed was significantly and highly correlated with the average number of adult steelhead observed during snorkel surveys during the supplementation period (Fig. 4*a*). The proportion of adult steelhead from the three groups varied substantially among years and appeared to be largely a result of the numbers of ARG fish that were released in a given year (Table 1, Fig. 4*b*).

Spawning behavior and timing

We observed 24 courting pairs of steelhead in 2002 and 20 pairs in 2004. In 2002, 70% (17 of 24) of females observed constructing nests were from the ARG, and 30% were anadromous (SRG and wild combined). In 2004, 55% (11 of 20) of the nesting females were from the ARG, and 45% were anadromous. The χ^2 analysis indicated that the two groups paired assortatively when data from both years were combined (χ^2 = 10.91, *P* < 0.01; Table 2). The results were similar when analyzing data from 2004 (*P* < 0.01) and 2002 (*P* = 0.05).

The assortative pairing was consistent with differences between the ARG and anadromous groups in the observed timing of spawning activity. Females from the ARG were observed nesting earlier than anadromous females in both years (group effect: $F_{[1,41]}$ = 14.96, *P* < 0.001; year effect: $F_{[1,41]}$ = 2.22, *P* = 0.144; group × year interaction: $F_{[1,41]}$ = 0.18, *P* = 0.673; Fig. 5). Males from the ARG group were observed courting earlier than anadromous males (group effect: $F_{[1,41]}$ = 8.66, *P* = 0.005; year effect: $F_{[1,41]}$ = 1.54, *P* = 0.222; group × year interaction: $F_{[1,41]}$ = 0.811, *P* = 0.373; Fig. 5).

Redd construction by ARG, SRG, and wild steelhead

The behavior-based estimates of redd construction indicate that the ARG steelhead constructed 70% of the redds in 2002 and 55% of the redds in 2004. The abundance-based estimate of redd construction indicate that ARG steelhead constructed 67% and 58% of the redds in those two years, respectively (Fig. 4*b*, Fig. 6). Thus, there was strong concordance in the results using these two approaches. The abundance-based estimates for all supplementation years indicate that ARG females constructed the greatest number of redds in years when more were released and fewer in years when fewer were released; the fewest number of redds was constructed by the SRG group in all years (Table 1; Fig. 6). The lowest number of redds during the supplementation period was in 2006. The majority of adults observed were wild and may have represented age-5 offspring of wild steelhead spawning in 2001, age-4 offspring of hatchery or wild parents spawning in 2002 (age-4 offspring), or age-3 offspring of hatchery or wild parents spawning in 2003. Hatchery-produced spawners were expected to be at low abundance, because only age-5 and older SRG or age-6 repeat spawning ARG adults were present. Nevertheless, the number of redds in 2006 (*n* = 39) was approximately 3.5 times greater than the 5-year presupplementation average (*n* = 11; Fig. 6).

Discussion

The salient findings of this study are as follows: (*i*) the conservation hatchery program has caused an increase in the

Fig. 5. The cumulative frequency of adult release group (ARG) females (■), anadromous females (□), ARG males (●), and anadromous males (○) observed participating in courtships in the Hamma Hamma River in 2002 (*a*) and 2004 (*b*).

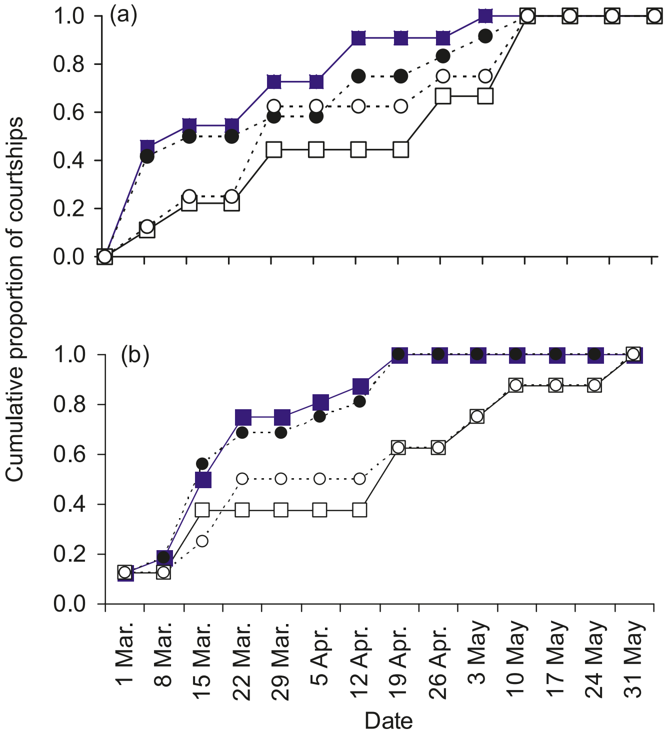
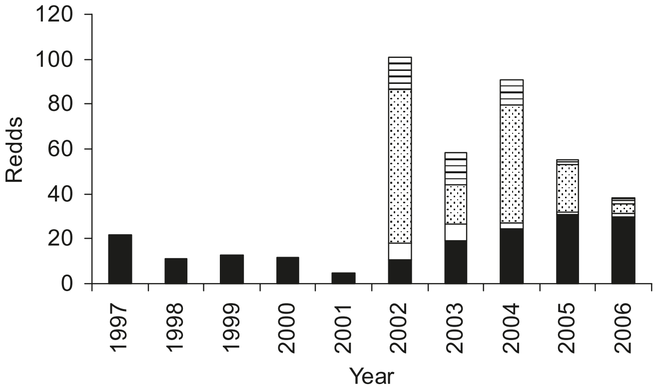


Fig. 6. Point estimates of the number of redds constructed by wild (solid bars), smolt release group (SRG, open bars), adult release group (ARG, stippled bars), and unknown origin (striped bars) steelhead in the Hamma Hamma River from 2002 through 2006. Estimates were made by multiplying the annual proportion of adults in each category observed during snorkel surveys by the total number of redds observed by foot surveys.



number of redds in the Hamma Hamma River without reducing the redd production from natural-origin spawners, (*ii*) the adult release strategy contributed the greatest proportion of the increase in years when substantial numbers of ARG steelhead were released, and (*iii*) differences in spawn timing probably explain the assortative pairing in the ARG and anadromous groups.

The findings of the present study add to other recent indications that supplementation programs may contribute to short-term increases in salmon and steelhead populations. A coho salmon supplementation project that brought wild spawners into the hatchery, spawned them, and released their offspring as smolts appears to have increased smolt production capacity, while the natural population productivity remained fairly stable (Sharma et al. 2006). Araki et al. (2006) extrapolated results of the relative reproductive success of hatchery-born and wild-born steelhead to conclude that each wild female adult brought into the hatchery would produce 4–10 times as many granddaughters (i.e., F_1 offspring of naturally spawning, hatchery-produced females) as wild females not brought into the hatchery had they been allowed to spawn naturally. In both of these studies, however, the response of the natural population in the absence of the hatchery program remains in question. The significant increase in redd abundance in the Hamma Hamma River in the face of stable or declining (nonsignificant) abundance in the three control streams makes this the first study to demonstrate an increase in natural spawning while accounting for spatial and temporal variability that can lead to changes in natural spawner abundance.

The approach of collecting embryos from wild steelhead redds appears to have represented a larger portion of the gene pool with a lesser demographic risk to the natural population than would have been possible with a more conventional approach. To explain, the project removed a total of 10 829 embryos (equivalent to the fecundity of roughly three females) from natural redds from 1998 through 2001. Kuligowski et al. (2005) showed that a subsample of the 4683 embryos collected in 1998 from eight redds descended from five different females and 16 different males. The embryos not removed may still have contributed to natural production. The more conventional approach of collecting adult broodstock and spawning them in the hatchery would have required the removal of approximately 15 females (45 000 to 60 000 eggs) and approximately 45 males to obtain a similar number of parental contributors, based on the number of redds sampled ($N = 25$) between 1998 and 2001. The smolts produced would either have to be released into the Hamma Hamma River, which would far exceed carrying capacity, or be removed from the population altogether. The embryo collection approach has been used in other conservation hatchery programs, but it is recognized that it may not be practical to collect the much larger number of eggs required for large-scale hatchery programs that rear and release tens of thousands of fish or more.

The adult reintroduction strategy produced a greater number of spawners, the majority of the redd production, and did so with fewer natural embryos removed from the wild than the smolt release strategy. The escape of some of the SRG from the John Creek facility and unknown smolt-to-adult survival rates make it difficult to calculate the number of embryos needed to produce a redd from the SRG strategy. A reasonable smolt-to-adult survival rate might be 2%–4% (cf. Ward 2000), compared with >90% smolt-to-adult survival rate in the hatchery for fish allocated to the ARG. The estimates of redd construction from the two groups clearly reflected the greater short-term demographic boost to the population from the adult release strategy. The far fewer number of embryos required to produce an equal number of spawning adults certainly lessens the demographic impact on the natural population.

The greater survey frequency in the Hamma Hamma River during the supplementation phase did not bias the analysis of redd abundance towards counting more redds in the Hamma Hamma River during the supplementation period. The strongest correlation between survey frequency and redd abundance was a nonsignificant negative one in the Hamma Hamma River during the presupplementation phase. All of the correlations for the other populations were slightly positive, but none were significant. Where evaluated, steelhead redds have been found to be visible for at least 1 week, and the great majority of redds are still visible after 2 weeks (Freymond and Foley 1985; Gallagher and Gallagher 2005; T. Johnson, unpublished data). Redd survey frequency in the Hamma Hamma River during the presupplementation period was approximately weekly and therefore sufficient to quantify redd abundance. Furthermore, the Dewatto and Duckabush rivers had greater survey frequencies during the supplementation period, so any potential bias associated with increased survey frequency would have tended to obscure rather than amplify the significant interaction between population and supplementation phase that we detected.

Although the adult release strategy provided the greater demographic boost, other trade-offs make it difficult to recommend one strategy over another. First, the reproductive success of hatchery-reared steelhead from natural-origin broodstock (similar to our SRG) can exhibit lifetime reproductive success that is similar to wild fish (Araki et al. 2006). Comparable reproductive success from the ARG is far less certain. For example, naturally spawning farmed Atlantic salmon (*Salmo salar*) have very poor reproductive success, perhaps caused by many generations of intense artificial selection (not a factor in our study) and full-term hatchery rearing experience (Fleming et al. 2001). Siblings of the steelhead observed in this study were closely examined for breeding behavior in a spawning channel and were found to be very successful at constructing nests and depositing eggs, and DNA pedigree analyses revealed that all females and 23 of 24 males contributed to fry production (Berejikian et al. 2005). However, the overall egg-to-fry survival rate was approximately 25% in the absence of any predators. It remains unclear how spawning density, spawning channel conditions, and gamete quality may have contributed to this result.

Second, the observed assortative pairing and its underlying causes raise interesting questions with respect to the potential contributions of the adult release strategy. The advanced spawn timing was an environmentally induced artifact of full-term rearing in the hatchery and exemplifies the phenotypic plasticity in this trait. One goal of a conservation hatchery program is to have hatchery-origin and wild fish interbreeding and for both groups to exhibit a natural level of fitness. If the current modal spawn timing of the wild population represents a naturally selected optimum trait distribution, then early-spawning females may have lower fitness owing to greater embryo mortality. Alternatively, to the extent that past harvest pressures have eliminated or reduced the early spawning portion of the population, early-spawning ARG females may function to recover historic diversity in spawn timing, and offspring of early-spawning females may fill a vacant niche and contribute to population productivity and life history diversity. Early-emerging fry could have an early growth and competitive advantages over later-emerging fry (Chandler and Bjornn 1988; Einum and Fleming 2000). However, embryonic developmental rate is positively correlated with temperature (Billard and Jensen 1996), which increases as the spawning season progresses. Therefore, the approximately 3-week difference in median spawn timing would actually result in less than a 3-week difference in median emergence timing and would tend to temper the effects of spawn timing differences. The absence of information on the reproductive success of the ARG fish in the natural environment and genetic concerns (e.g., domestication selection) associated with full-term captive rearing suggests that further use of this approach continue to proceed with caution.

As demonstrated in this and the aforementioned studies, conservation hatcheries might reasonably be expected to maintain or increase population abundance and maintain existing levels of genetic variability in the short term (which we will address in a future publication) to buy time until the factors causing population declines can be identified and addressed. A more ambitious and far less certain expectation for conservation hatcheries is to contribute to increasing the productivity of natural populations experiencing a positive relationship between population growth rate and density (e.g., depensatory mortality). Depensatory mechanisms may function to inhibit recovery of animal populations or increase the likelihood of extinction (Courchamp et al. 1999) and may include skewed sex ratios, nonlinear response of predation, nutrient limitation related to scarcity of spawner carcasses, and reproductive inefficiencies. Evidence for depensation has been detected for Pacific salmon (Myers et al. 1995). Thus far, no study, including this one, has empirically identified such a mechanism or the potential to increase natural population productivity through artificial propagation. To determine the impact of the hatchery program on natural population productivity, the release of hatchery fish will need to be terminated and the supplemented and control populations monitored for through the F_2 generation; this is the plan for the program evaluated in the present study.

To meet their goals, conservation hatcheries must strike a balance between increasing production and minimizing genetic, ecological, and demographic risks. Goodman (2004) noted that the idea of supplementation (as opposed to production hatcheries) did not arise from an inability to produce or dissatisfaction with the ability of hatchery programs to produce fish. It came out of conservation concerns for the wild stock. Moving towards a situation that is less risky for wild stocks almost invariably means reducing the potential of the hatchery stock to increase abundance in the short term. For example, release of smaller fish may reduce the potential for predation on wild fish, but smaller fish may not survive as well to adulthood. Releasing fewer hatchery fish will undoubtedly reduce the potential for competition that has been documented in natural streams (Nielsen 1994; McMichael et al. 1999), once again at the expense of adult production. These types of operational changes will reduce the impacts of hatchery fish on natural stocks; after all, the extreme example is the complete absence of hatchery fish. A major question has been whether hatcheries operated in a conservative fashion can substantially boost the number of naturally spawning adults (e.g., Oosterhout et al. 2005). The results of this study suggest they can.

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