The Impact of Supplementation in Winter-Run Chinook Salmon on Effective Population Size

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Supplementation of young raised at a protected site, such as a hatchery, may influence the effective population size of an endangered species. A supplementation program for the endangered winter-run chinook salmon from the Sacramento River, California, has been releasing fish since 1991. A breeding protocol, instituted in 1992, seeks to maximize the effective population size from the captive spawners by equaling their contributions to the released progeny. As a result, the releases in 1994 and 1995 appear not to have decreased the overall effective population size and may have increased it somewhat. However, mistaken use of non-winter-run chinook spawners resulted in artificial crosses between runs with a potential reduction in effective population size, and imprinting of the released fish on Battle Creek, the site of the hatchery, resulted in limiting the contribution of the released fish to the target mainstem population. Rapid genetic analysis of captured spawners and a new rearing facility on the Sacramento River should alleviate these problems and their negative effect on the effective population size in future years.

Factors involved in extinction include catastrophes, environmental and demographic stochasticity, and genetic deterioration (e.g., Hedrick et al. 1996; Shaffer 1981). These factors may be mitigated by supplementation of young raised at a protected site, such as a hatchery or zoo, which results in a higher early survival than naturally reared young (Griffith et al. 1989; Ryman and Utter 1987). In this way, some environmental and demographic problems may be avoided and genetic deterioration may be postponed by increasing the effective population size (Hedrick et al. 1995; Ryman and Laikre 1991), although the genetic effects are complicated (Waples and Do 1994).

As well as potential benefits of supplementation, there are several recognized possible problems (Waples 1991). For example, supplementation may have negative ecological effects, such as the introduction of diseases from captive-rearing facilities or competition with the native population. In addition, there may be detrimental genetic impacts, including the introduction of nonadaptive traits or reduction of the effective population size. Finally, reliance on programs like supplementation may divert attention and resources from rectifying basic environmental problems (Meffe 1992).

The annual number of spawners of the endangered winter-run chinook salmon (*Oncorhynchus tshawytscha*) from the Sacramento River, California, has declined from more than 100,000 in 1969 to low numbers in the late 1980s and to less than 200 in 1991. As a result, winter-run chinook salmon was listed as endangered by the State of California in 1989, federally listed as threatened in 1990, and federally listed as endangered in 1994. A number of factors appear to be responsible for this decline, but probably most significant have been the building of Shasta Dam on the Sacramento River, which blocked access to most of the traditional cool-water spawning habitat, and impediments to juvenile and adult migration, such as water diversions for agricultural and municipal uses.

A supplementation program at Coleman National Fish Hatchery (CNFH) on Battle Creek, a Sacramento River tributary, has been successfully releasing fish since 1991 to increase egg and juvenile survival and provide protection from possible catastrophes impacting juveniles. A breeding protocol, initiated in 1992, was designed as an attempt to equalize the contributions from the captured spawners (20 spawners or 15% of the estimated run size per year, whichever is larger, are permitted). In this

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protocol, eggs from each female are divided into two lots and fertilized with gametes from two different males. Also, the gametes of each male are used to fertilize at least two different females. Hedrick et al. (1995) determined the effective population size in the first 3 years of the program, 1991–1993, and found that the supplementation did not appear to greatly influence the effective population size of the run, neither significantly reducing nor increasing it.

Supplementation continued in 1994 and 1995 but was discontinued in 1996 and 1997 because it became apparent that some non-winter-run chinook had been mistakenly used as spawners and returning spawners were found primarily in Battle Creek, not on the spawning ground in the Sacramento River. To evaluate the overall impact of supplementation, we estimate the effective population size for 1994 and 1995. In addition, we evaluate the impact of the use of non-winter-run spawners and imprinting of released fish on Battle Creek, particularly the effects of these factors on the effective population size.

Methods

The effective population size for fish released from CNFH (symbolized by subscript c for captive) can be estimated using either the variance effective or the inbreeding effective population size. Here we will use the variance effective population size because this was recommended for endangered species by Crow and Denniston (1988) and our estimates of the variance and inbreeding effective population sizes are very close to each other. As in Hedrick et al. (1995), we will give results based on 10,000 simulations, an approach that both simulates the return of progeny as spawners and can be used to calculate 95% confidence intervals.

The variance effective size can be estimated as (Crow and Denniston 1988)

$$N_{ec(v)} = \frac{4N_f N_m}{xN_f + yN_m}$$

where

$$x = f + m\frac{\sigma^2_{km}}{\bar{k}_m}$$

and

$$y = m + f\frac{\sigma^2_{kf}}{\bar{k}_f}$$

and N_f and N_m are the actual numbers of breeding females and males in the captive program, and $\bar{k}_f$ and σ^2_{kf} and $\bar{k}_m$ and σ^2_{kf} are the mean and variance of the number of progeny produced by females and males, respectively. The proportion of female and male progeny at the same age (spawning) are f and m, where $f + m = 1$ (here $f = 0.4$; Hedrick et al. 1995).

The overall effective population size when considering both the wild run and the supplementation program can be estimated as (Ryman and Laikre 1991)

$$N_e = \frac{N_{ew}N_{ec}}{x^2_w N_{ec} + x^2_c N_{ew}} \qquad (2)$$

where N_{ec} and N_{ew} are the effective population sizes in the captive (hatchery) adults and the wild-run adults, respectively, and x_c and x_w are the proportions of progeny coming from the captive and wild adults, respectively. Ryman et al. (1995) showed that when the population is greatly changed in size by supplementation, the variance and inbreeding effective population sizes might have substantially different effects. However, in this case supplementation does not appear to significantly influence effective size so that the effect of the type of effective population size estimate will have little effect. Lower and upper bounds of the estimates of the effective size of the wild run can be obtained by subtracting the number of spawners taken captive from the estimated run size and then multiplying these values by 0.10 for the lower bound and by 0.333 for the upper bound (Hedrick et al. 1995).

The estimated captive proportion (x_c) was based on the number of female spawners, their egg production, and the survival of these progeny to smolt of the captive and wild groups (Hedrick et al. 1995). The number of captive presmolt surviving to release was multiplied by the estimated survival from presmolt (0.5) to give the estimated number of captive smolt surviving. The estimated number of wild female spawners was multiplied by the average egg production per female and then multiplied by the estimated survival of egg to smolt (0.147) to give the estimated number of wild smolt surviving (see Hedrick et al. 1995). x_c was then estimated as the proportion of captive smolt in the estimated total number of smolt from captive and wild spawners.

To identify non-winter-run spawners, first a baseline of winter-run allele frequencies for 11 microsatellite loci, a major histocompatibility complex (MHC) gene, and D-loop variation in mtDNA was constructed (Banks et al. 1996, submitted). From these data, the log likelihood (LOD score) of each individual spawner being winter run was determined (Hedgecock D, in preparation). The lowest LOD score for all confirmed winter-run chinook was 1.6 and most values were much higher.

In 1995, winter-run spawners were observed by video camera swimming upstream in Battle Creek through CNFH. Subsequently Battle Creek was monitored for winter-run spawners both by video and carcass surveys.

Table 1. The number (proportion in parentheses) of progeny released from the different females and males in the 1994 and 1995 brood years

Year	Female (age)	Number of progeny (proportion)	Male (age)	Number of progeny (proportion)
1994	3 (3)	3444 (0.080)	B (—)	4433 (0.102)
	4 (3)	3055 (0.070)	C (3)	3152 (0.073)
	5 (3)	2499 (0.058)	D (2)	4360 (0.107)
	6 (3)	2361 (0.054)	E (3)	6013 (0.139)
	7 (3)	2421 (0.056)	F (2)	5223 (0.120)
	8 (3)	2292 (0.053)	G (2)	5098 (0.128)
	9 (3)	2338 (0.054)	H (2)	4432 (0.102)
	11 (2/3)	2320 (0.054)	I (2)	6353 (0.147)
	12 (2/3)	2701 (0.062)	J (3)	3012 (0.070)
	13 (3)	3946 (0.091)	K (2)	1270 (0.029)
	14 (2/3)	1364 (0.032)		
	15 (2)	3426 (0.079)		
	16 (3)	2855 (0.066)		
	17 (3)	2766 (0.064)		
	18 (3)	3088 (0.071)		
	19 (3)	2470 (0.057)		
	Mean	2709 (0.062)	Mean	4335 (0.100)
1995	4 (2)	2219 (0.043)	D (3)	3253 (0.064)
	5 (3)	2086 (0.041)	E (3)	3341 (0.065)
	6 (3)	482 (0.009)	F (3)	1869 (0.036)
	7 (3)	2329 (0.045)	G (3)	3429 (0.067)
	8 (3)	3284 (0.064)	H (2)	1007 (0.020)
	9 (2)	1921 (0.038)	I (3)	5493 (0.107)
	10 (2/3)	687 (0.013)	J (3)	1691 (0.033)
	11 (2)	267 (0.005)	K (4)	5476 (0.107)
	12 (3)	1749 (0.034)	L (3)	3310 (0.065)
	13 (3)	3605 (0.070)	M (2)	2848 (0.056)
	14 (3)	2443 (0.048)	N (4)	5498 (0.107)
	15 (3)	3165 (0.062)	O (2/3)	4889 (0.095)
	16 (—)	3364 (0.066)	P (—)	1533 (0.030)
	17 (3)	102 (0.002)	Q (3)	5808 (0.113)
	18 (3)	3225 (0.063)	*S (3)	1822 (0.036)
	19 (3)	3987 (0.078)		
	20 (3)	3468 (0.068)		
	21 (3)	3732 (0.073)		
	22 (3)	3469 (0.068)		
	23 (3)	2930 (0.057)		
	24 (3)	1622 (0.032)		
	1C (4)	38 (0.001)		
	2C (3)	138 (0.003)		
	3C (4)	6 (0.000)		
	4C (4)	23 (0.000)		
	5C (4)	802 (0.016)		
	6C (4)	124 (0.002)		
	Mean	1899 (0.037)	Mean	3418 (0.067)

* Identified as probable non-winter run.

Results

Estimated Effective Population Size

Table 1 gives the number of progeny released from different females and males in

Table 2. Summaries from 1994 and 1995 of the estimates of the captive effective population size ($N_{ec(v)}$), the lower and upper bounds on the wild effective population size (N_{ew}), and the lower and upper bounds on the overall effective population size (N_e)

	1994	1995
Number of breeding parents ($N_f + N_m$)	26	42
$N_{ec(v)}$ (95% confidence interval)	23.2 (15.9, 30.8)	29.2 (21.3, 37.8)
Number of spawners	189	1361
Number taken captive	29	47
Difference	160	1314
N_{ew} (lower and upper bounds)	16.0–53.0	131.4–437.6
N_e (lower and upper bounds)	34.3–72.8	150.7–463.6

1994 and 1995. Of the 29 fish captured in 1994, 26 (16 females and 10 males) produced 43,335 released progeny. Overall the production was fairly equal over individuals, with the proportions of progeny produced for females ranging from 0.032 to 0.091 (mean of 0.062) and for males from 0.029 to 0.147 (mean of 0.1). All spawning females were successfully used in two matings each and the males, because there were lower numbers, were used in an average of more than three matings (male K, with the lowest male contribution, was used successfully in only one mating).

Of the 47 adults captured in 1995, 36 (21 females and 15 males) produced progeny (most of the adults not used appear to be non-winter run). In addition, six captive-reared females (1C–6C) from Bodega Marine Laboratory, five progeny from the 1991 broodstock and one from the 1992 broodstock, were also used. The release number per parent for two different family groups that were maintained together, group 1 from females 6, 10, 11, and 12 with 3185 progeny and group 2 from captive females with 1131 progeny, were estimated from distributing mortality within the hatchery randomly over the females. A total of 51,267 progeny were released. Again, the captured females were used on two males each and each male was used on two or more females except S. There was more variation in contribution over individuals in 1995 than 1994 with the range for wild-caught females from 0.002 to 0.070 (mean over all females of 0.037) and the range for males from 0.020 to 0.113 (mean of 0.067). The success of captive-reared females was quite limited, with only 1131 progeny produced over the 11 matings that produced progeny.

The estimated hatchery variance effective population size (95% confidence intervals in parentheses) for 1994 was 23.2 (15.9, 30.8) and for 1995 was 29.2 (21.3, 37.8) (summarized in Table 2). The estimates for inbreeding effective population size were slightly less at 22.3 and 28.6 for 1994 and 1995, respectively. The estimates were also fairly similar between years, with the estimate in 1995 somewhat larger than in 1994. Further, when considering the different number of wild-caught spawners used in the two years, 26 in 1994 and 36 in 1995 (excluding the six captive spawners), the ratio of the effective population size to the number of spawners is not much different in the two years, 23.2/26 = 0.89 in 1994 and 29.2/36 = 0.81 in 1995.

The estimates of returning spawners in 1994 (189) and 1995 (1361) were similar to those in 1991 (191) and 1992 (1180) (Hedrick et al. 1995). This is consistent with the observation that most winter-run chinook return at 3 years old to spawn. For the two different years, the impact of captured spawners is different, with approximately 29/189 = 0.153 of the wild run captured in 1994 and approximately 47/1361 = 0.035 captured in 1995. The estimate of the number of spawners left after the captured spawners are removed was 160 for 1994 and 1314 for 1995. Lower and upper bounds of the estimates of the effective size of the wild run for 1994 are 16.0 and 53.3 and for 1995 are 131.4 and 437.6 (Table 2). The estimated x_c values for 1994 and 1995 are 0.407 and 0.083. The large value for 1994 reflects the small number of spawners in the wild population and high survival in the captive progeny.

Figure 1 gives the overall effective population size as a function of the captive proportion for 1994 and 1995. There are two curves for each year, the upper one indicating the upper bound of the natural run and the lower one indicating the lower bound. The vertical lines indicate the estimated proportions of smolt that came from the supplementation program, x_c, and the two horizontal lines indicate the upper and lower bounds of the effective population size of the natural run if no fish were captured for the supplementation program. In 1994, given that x_c is 0.407, the supplementation program appears to have increased the effective population size for the lower bound from 18.9 to 34.3 (81% increase) and for the upper bound from 62.9 to 72.8 (16% increase). In 1995, given that x_c is 0.083, the supplementation program appears to have increased N_e for the lower bound from 136.1 to 150.7 (11% increase) and for the upper bound from 453.2 to 463.6 (2% increase).

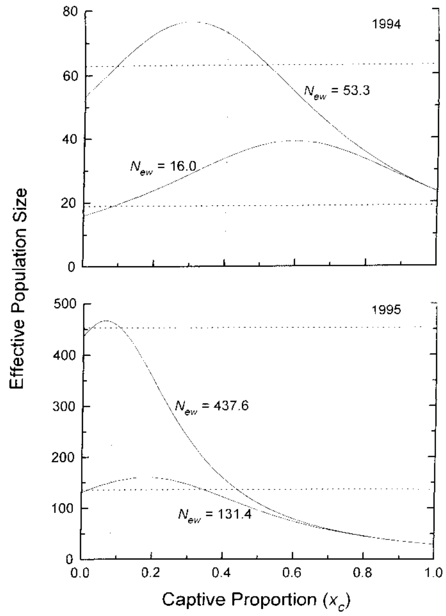

Figure 1. The estimated overall effective population size for the 1994 and 1995 runs using the estimated simulated variance N_e for the hatchery stock (23.2 in 1994 and 29.2 in 1995) and a high and low estimate of the natural run size.

Mistaken Use of Non-Winter-Run Chinook Salmon Spawners

The microsatellite markers identified five spawners, four females and one male, that produced progeny in the years 1991–1995 that had very low likelihoods of being winter run (Table 3). All of these spawners had very low negative LOD scores, ranging from −5.3 to −17.1. Two were the parents of a substantial number of progeny produced in a given year, female 8 was the parent of 41.1% of the fish produced in 1991 and female 10 was the parent of 25.4% of the fish produced in 1993. Except for female 24 and the captive female 6C, who were mated only to non-winter-run male S, the mates of these fish were mated to other individuals that appear to be winter run. For example, 1993 male C was mated to both non-winter-run 10 (4763 progeny) and three winter-run females 4, 6, and 7 (4762 progeny).

Using non-winter-run spawners has resulted in artificial matings between runs

Table 3. The five non-winter-run spawners used in the supplementation program

Year	Spawner (sex, age)	LOD	Number of progeny (prop.)	Mate	*Pr*
1991	8 (F, 4)	−5.6	4761 (0.411)	C	0.669
1993	2 (F, 4)	−14.3	836 (0.045)	I	0.207
	10 (F, 4)	−11.2	4763 (0.254)	C	0.500
	113 (F, 3)	−17.1	177 (0.009)	I	0.029
1995	S (M, 3)	−5.3	1622 (0.032)	24	1.000
			63 (0.001)	2C	0.457
			3 (0.000)	3C	0.500
			10 (0.000)	4C	0.435
			124 (0.002)	6C	1.000

F and M indicate female and male. Age is estimated in years. The LOD score is for 13 markers. The number of progeny are for the non-winter-run spawner and the mate. Proportion (prop.) is of the total number of progeny. *Pr* is the proportion of a mate's progeny with the non-winter-run fish.

(41.1%, 30.8%, and 3.6% in 1991, 1993, and 1995). Presumably the survival and reproductive success of the progeny from these matings between crosses is lower than that from the matings between two winter-run salmon, but if they do make some future contribution, then these progeny may result in a dilution of the winter-run gene pool. In addition, the effective population size of the winter-run population has been reduced. Assuming the progeny from the crosses with non-winter run do not contribute to the winter-run population, the supplementation contribution was reduced by the percentages given above. Finally, in two cases (females 24 and 6C in 1995), spawners were only mated to a non-winter run and their contributions have been diluted because they are present only in progeny with male S. In two other instances, more than 4700 progeny from a winter run were diluted because of matings with a non-winter run.

Imprinting of Winter-Run Chinook Salmon on Battle Creek

Estimates of the number of winter-run spawners returning primarily to Battle Creek for 1995, 1996, and 1997 were 88, 237, and 266, respectively. Coded-wire tags from carcasses indicated that a substantial proportion of these fish were descended from releases from CNFH. There were no recoveries of hatchery fish in the mainstem Sacramento River in 1995 and 1996, but in 1997, four spawners with coded-wire tags from brood year 1994 were recovered.

Overall it appears that the proportion of returning spawners from supplementation to the mainstem Sacramento population has been small and that many more fish have returned to Battle Creek, a location in which there is disagreement about the potential for successful spawning of winter run. If there were no returning salmon to the mainstem, x_c would be 0 and the estimated effective population size of the natural run would have been reduced by the taking of spawners for the supplementation program. In 1994, the lower bound would be reduced from 18.9 to 16.0 and the upper bound reduced from 62.9 to 53.3 (15.3% decrease for both, the reduction is equal to the proportion of estimated spawners taken for captive breeding). In 1995, the lower bound would be reduced from 136.1 to 131.4 and the upper bound from 453.2 to 437.6 (3.5% decrease for both). Because there is now some evidence of fish returning to the mainstem, x_c is probably somewhat larger than zero but still much lower than that used in Figure 1.

Discussion

In 1992, a breeding protocol was designed to equalize the contributions from captured winter-run spawners. This protocol has been successful in equalizing the contribution of spawners for 1992–1995, thereby increasing the effective population size. However, these effective size calculations make a number of assumptions (see Hedrick et al. 1995), in particular, the captive effective size estimates assume random survival and return of the released fish. Recently Geiger et al. (1997) reported that survival may not be random with respect to family in pink salmon. However, we now have genetic data from 1994 and 1995 returns that indicate the observed effective population size is about 87% that expected, supporting the assumption that survival is not greatly different from that expected at random (Hedrick et al., manuscript in preparation). Therefore it does not appear on these grounds that supplementation has had a detrimental effect on the overall effective population size.

Even though it appears that supplementation for winter-run chinook salmon has not greatly influenced the effective population size for the years 1991–1995, two other effects have decreased the possible benefits. First, a substantial proportion of fish used as spawners in 1991 and 1993 were not winter run, resulting in artificial crosses between runs and resulting in substantial reduction in the effective population size. The potential spawners were taken in a window of time appropriate for winter-run migration, but only genetic markers could distinguish the non-winter-run spawners. Now rapid genetic analysis using microsatellite markers is in place to determine whether captured spawners are winter run or not and to avoid this impact in the future.

Second, virtually all of the released winter-run salmon returned to a site where successful recruitment is questionable. Only because spawners were accidentally observed in Battle Creek did it become known that the returning spawners were imprinted on Battle Creek. As a result, the proportion of captive fish that could have potentially contributed to the mainstem effective population size was very limited. A new facility, just below Shasta Dam on the mainstem Sacramento River, has been constructed for rearing winter-run salmon to facilitate imprinting on the mainstem spawning grounds.

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