An evaluation of the Clearwater River supplementation program in western Washington

Rishi Sharma, Gary Morishima, Shizhen Wang, André Talbot, and Larry Gilbertson

Abstract: This paper presents preliminary results of a study to evaluate the potential utility of supplementation of natural origin coho salmon (*Oncorhynchus kisutch*) on the Clearwater River, a tributary of the Queets River in western Washington. The study, initiated in 1984, involves the collection of natural origin brood stock, rearing in a combination of hatchery and natural environments, and volitional releases, combined with marking and sampling of natural origin fish. Primary findings relative to five essential research questions of this study concluded that (*i*) smolts from supplementation returned at a lower rate than natural smolts; (*ii*) the reproductive efficiency (spawner to spawner) of fish taken for supplementation was higher than that for fish allowed to spawn naturally; (*iii*) supplemental fish successfully reproduced and the combined supplemental–natural spawning population had a high productivity; (*iv*) supplementation did not appear to have affected the overall reproductive performance of the population for the duration of the project; and (*v*) supplementation increased the overall spawner return on the Clearwater River and is required to maximize adult production, unless conditions in both freshwater and ocean environments are optimal.

Résumé : Nous présentons les résultats préliminaires d'une évaluation de l'utilité potentielle des empoissonnements d'appoint de saumons coho (*Oncorhynchus kisutch*) d'origine naturelle dans la rivière Clearwater, un tributaire de la Queets dans l'ouest du Washington. Cette étude, initiée en 1984, implique la récolte d'un stock reproducteur d'origine naturelle, l'élevage dans une combinaison de conditions de pisciculture et de conditions naturelles et des remises à l'eau volontaires, avec en plus le marquage et l'échantillonnage des poissons d'origine naturelle. Les principaux résultats de l'étude concernant cinq questions fondamentales de recherche sont les suivants: (*i*) les saumoneaux issus des empoissonnements d'appoint ont un taux de retour inférieur à celui des saumoneaux naturels; (*ii*) l'efficacité reproductive (de reproducteur à reproducteur) des poissons récoltés pour l'empoissonnement est plus grande que celle des poissons qui ont pu se reproduire naturellement; (*iii*) les poissons ajoutés lors des empoissonnements se reproduisent avec succès et la population combinée des reproducteurs naturels et ajoutés a une forte productivité; (*iv*) l'empoissonnement d'appoint ne semble pas affecter la performance reproductive globale de la population dans le cadre de ce projet et (*v*) l'empoisonnement d'appoint accroît le retour global de reproducteurs dans la Clearwater et il est nécessaire pour maximiser la production des adultes, à moins que les conditions à la fois dans les milieux d'eau douce et de mer ne soient optimales.

[Traduit par la Rédaction]

Introduction

The potential value of artificial propagation techniques as a means to reduce extinction risks and rebuild depressed spawning populations of Pacific salmon (*Oncorhynchus* spp.) has not been extensively studied or reported in the literature (Waples 1999; Waples et al. 2006). Several concerns over potential deleterious effects of artificial propagation on naturally spawning populations have been reported in the literature. For example, the productivity of hatchery-reared fish has been reported to be lower than that of wild fish (Reisenbichler and McIntyre 1977; Nickelson et al. 1986; Waples 1999). Other studies have described the potential for artificial selection and domestication in the hatchery environment (Vincent 1960; Hindar et al. 1991). However, limited studies have evaluated the benefits of a supplementation program in terms of increased abundance or increased harvest opportunities (Waples et al. 2006).

Recent studies on salmonids emphasize the adverse effects of hatchery fish on the natural environment. Nickelson (2003) suggests that productivity of wild salmonids can be reduced by the presence of large numbers of hatchery smolts

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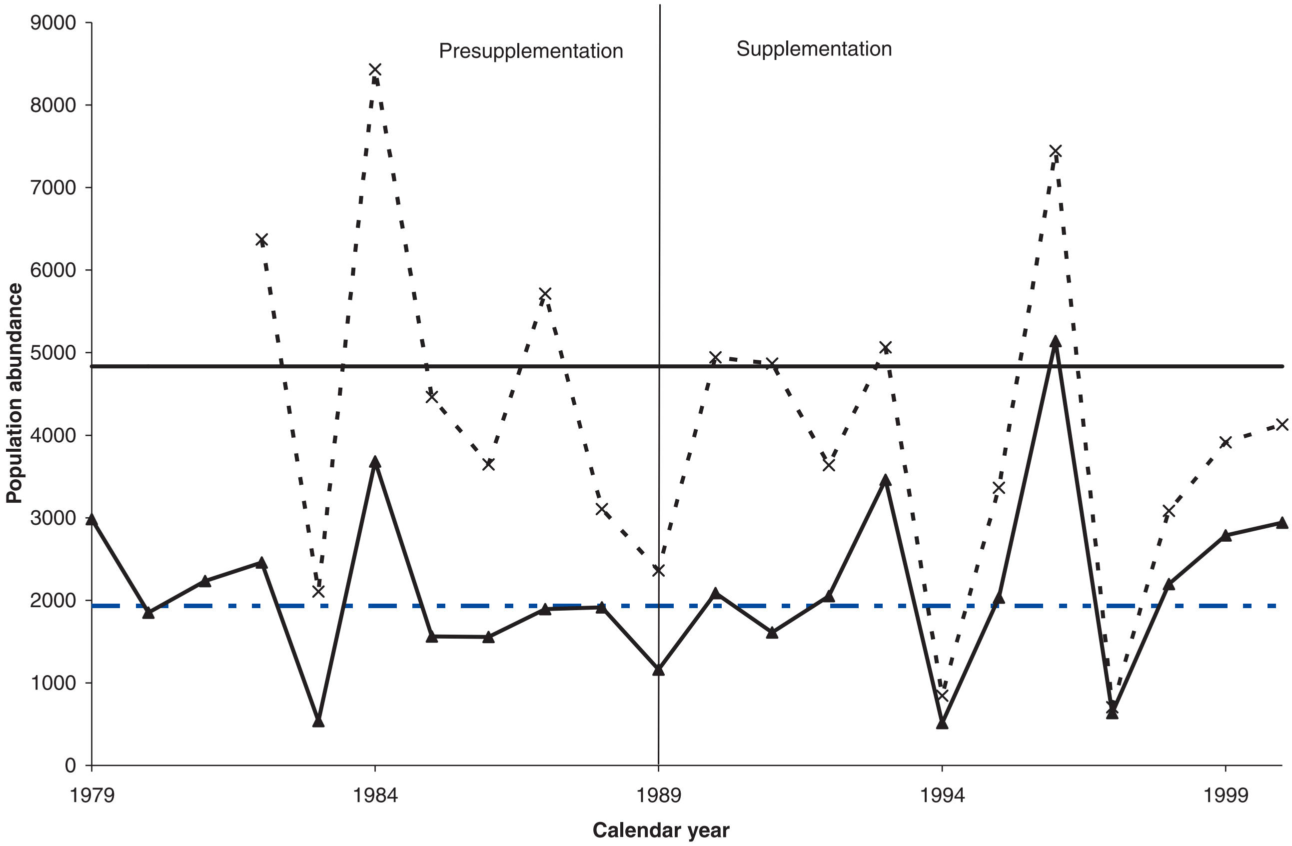
Fig. 1. Escapement and pre-terminal ocean abundance estimates for the Clearwater River (a component of the Queets River coho, *Oncorhynchus kisutch*, population). The broken line represents pre-terminal ocean abundance (×), and the solid line represents escapement (▲). The lower horizontal broken line is the estimated lower escapement goal, and the upper horizontal line is the estimated higher escapement goal for the Clearwater River.



in lower rivers and estuaries that attract predators. Chilcote (2003) states that populations that comprised equal numbers of wild and hatchery fish would produce 63% fewer recruits per spawner than a population comprising entirely wild fish. Kostow (2004) found that phenotypic differences from the same parental gene pool can lead to eventual genetic divergence in new hatchery stocks and in source wild populations, thus limiting the usefulness of stocks for conservation purposes to only the first few generations. However, no study has empirically demonstrated a loss in productivity of the overall population when the goal was to enhance the natural spawning population using indigenous brood stock.

Generally, most of the studies mentioned above involved long-term hatchery cultivation. There are many ways that hatchery practices can produce fish that are less fit than wild fish to propagate viable offspring in the natural environment. For example, artificial rearing conditions and brood stock selection protocols can foster phenotypic (e.g., Verspoor 1988; Nielsen et al. 1994; Danielsdottir et al. 1997) and genotypic (Woodward and Strange 1987; Swain et al. 1991; Fleming and Gross 1993) divergence of hatchery and wild fish. Even with a common ancestral heritage, hatchery and natural population characteristics can diverge within only a few generations of domestic rearing (Reisenbichler and McIntyre 1977; Chandler and Bjornn 1988; Reisenbichler and Rubin 1999). In addition, initial (and continuous) utilization of inadequate number of spawners in hatchery programs can decrease genetic variation in subsequent generations that potentially results in lower effective population size, possibly leading to inbreeding depression (Wang et al. 2002).

Queets River coho (*Oncorhynchus kisutch*; the Clearwater River coho is a subset of this population) are managed for natural production with the objective of constraining fishery impacts so as to maintain spawning escapements within the range of 5800–14 500 adults (Lestelle et al. 1983). The total abundance of Queets (Clearwater) coho has varied between 1858 and 21 434 ocean-age-3 recruits in the last 20 years (PFMC 2001), so harvest opportunities on this stock have been sporadic. In the late 1970s, terminal returns of Queets (Clearwater) coho began to plummet because of a major harvest in ocean fisheries outside the juridical control of the local USA managers (PFMC 2001), resulting in increasing restrictions on terminal fisheries. During the late 1980s and early 1990s, the escapement levels on this stock continued to decline to the point where natural spawning escapements were insufficient to produce sufficient numbers of juveniles to utilize available habitat to its estimated capacity. The chronically depressed status of Queets (and Clearwater) coho has frequently resulted in severe constraints for management of USA ocean and terminal fisheries since the late 1970s (see Fig. 1). Further reductions in harvest rates were not achievable, as a substantial portion of the fisheries mortality on this stock occurred outside USA jurisdiction. This was the situation when the supplementation program was

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initiated in 1984 to try to increase spawning escapements and the overall recruits of Queets coho. Since 1996, restriction of Canadian fisheries to address domestic conservation concerns for its own coho stocks has substantially reduced the impacts of fisheries on Queets coho.

This paper presents early results of a project designed to evaluate supplementation as a means to address depressed abundance of coho salmon returning to the Queets (Clearwater) River on the Olympic Peninsula of Washington State. The supplementation project we evaluate in this paper focuses on the use of broodstock taken from natural spawners to increase productivity of underutilized spawning and rearing habitat in the Clearwater River, a tributary of the Queets. This is possibly one of the first cases where an evaluation of a program that has used natural spawners as brood stock has been attempted. Results of this study may help address the void identified by Waples et al. (2006).

The Queets (Clearwater) supplementation project was designed to utilize natural spawners (brood stock), rear progeny in a hatchery environment to a pre-smolt stage, acclimate juveniles in a natural, off-channel habitat for a period of 10 weeks in the vicinity of brood stock capture, and allow the smolts to migrate volitionally. Hatchery-reared fish have been found to be more aggressive than wild fish when reared in similar conditions (Swain and Riddell 1990), and these behaviors were heritable traits (Riddell and Swain 1991). As such, these techniques were developed in an attempt to minimize potential deleterious effects of artificial propagation on natural fish during an early life history stage.

The objective of this paper is to evaluate supplementation efforts within the Clearwater River watershed by focussing on the following questions: (*i*) How does the full life history survival rate compare between supplemental and naturally reared coho? (*ii*) Given these differences in life cycle survival, will the addition of a supplemental program cause a net increase in the number of adult coho returning to the Clearwater basin? (*iii*) Will the addition of supplemental coho to the natural population increase the number of naturally produced offspring (smolts and adults) within the Clearwater basin?

To answer these questions, we examined the efficiency of the supplementation program by comparing the return rates of the supplemental and natural smolts. In addition, we estimated the carrying capacity and productivity of the Clearwater River through a subsequent generation analysis, as both supplemental and natural fish spawn in the natural environment. These estimates of productivity and carrying capacity, along with an integrated model analysis, were used to answer the questions identified above.

Materials and methods

Background on the supplementation project

The Queets River drains the western slopes of the Olympic Mountains and flows into the Pacific near the village of Queets on the Quinault Indian Reservation (Fig. 2). The river flows 82.7 km and drains a watershed of approximately 1152 km^2. The Queets River upstream of the Clearwater River lies predominantly within the Olympic National Park and is largely unaffected by anthropogenic habitat disturbances. In contrast, the Clearwater River, which is the largest tributary of the Queets River, with a drainage area of ~400 km^2, has been subjected to intense logging.

Since the Clearwater River has no separate escapement goal for management purposes, we assumed an upper and lower bound to the target escapement goal for the Clearwater to be based on a third of the goal that the Queets system is managed for, as the Clearwater is approximately a third of the Queets in watershed area. From the late 1970s through most of the 1980s (Fig. 1), the Clearwater escapement was consistently below or near the lower end of the range. As a large portion of the ocean harvest of Queets (Clearwater) coho was taken by Canada, the depressed status of this stock became a limiting factor and resulted in increasing restrictions on terminal and marine salmon fisheries in the USA (PFMC 2001).

It was under these conditions that the supplementation program was initiated in 1984 to try to increase spawning escapements, production, and finally the productivity of Queets coho in underutilized spawning and rearing habitats. The project was initiated as a cooperative project between the Quinault Indian Nation (QIN) and the Washington Department of Fisheries (now part of Washington Department of Fish and Wildlife). The first few years (1984–1988) of this project involved experimental fry releases, and only since brood year 1989 were clear protocols for smolt releases established (Lestelle et al. 1992). Since 1995, the project has been managed by the QIN. In this paper, we report only the results of the smolt supplementation program that was conducted on the Clearwater River.

The Queets and Clearwater supplementation project involves (*i*) the collection of natural origin brood stock (adults and jacks (precocious male fish)) from various locations throughout the Queets (Clearwater) watershed; (*ii*) mating, incubation, and rearing of progeny by brood stock location (for Christmas Creek, Miller Creek, and Clearwater River (Fig. 2) have different substock groups that are reared separately); (*iii*) early rearing in hatchery facilities at Salmon River (a tributary of the Queets); (*iv*) 100% marking of supplemental fish initially with a ventral fin clip (this was changed in 1998 to adipose fin clips); (*v*) release of an estimated number of pre-smolts into natural ponds for short-term rearing in the vicinity of the parent brood stock collection with the objective of producing adults that would spawn in underutilized mainstem and tributaries; (*vi*) volitional migration as smolts; (*vii*) estimation of natural smolt production through a mark–recapture experiment on the Clearwater River; (*viii*) monitoring of terminal catches and escapements; and (*ix*) use of only unmarked fish for future brood stock.

Brood stock were collected from six separate areas of the Queets watershed: Miller Creek; Christmas Creek; upper mainstem of the Clearwater; Matheny Creek; middle mainstem of the Queets; and upper mainstem of the Queets (Fig. 2). In this paper, we focused only on the Clearwater streams (Fig. 2). For the Clearwater River, the program targeted the collection of 30 pairs of adult salmon for brood stock (more brood stock than the required amount are typically collected to account for prespawning mortality, 40% based on QIN data, in holding ponds). To reduce the risks of artificial selection and homogenize the genetic composition of the stock, marked fish were excluded from brood stock collection, and a 1:1 sex ratio was generally employed for

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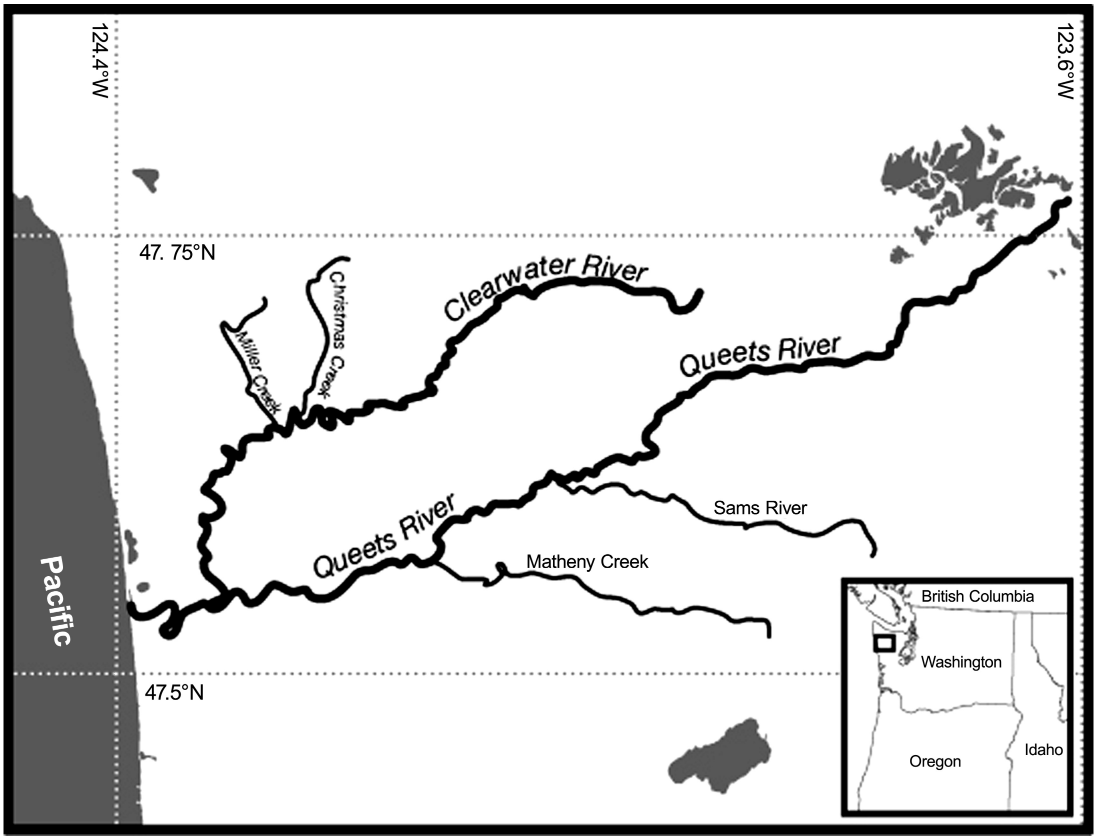
Fig. 2. Wild brood stock locations on the Queets River in western Washington, USA. The inset shows the study location in the Pacific Northwest.



spawning. Although 3-year-old fish were used as primary spawners (Queets (Clearwater) coho spawn primarily as 3 year olds), jacks were also used to increase genetic diversity across brood years (Van Doornik et al. 2002).

For most of our discussion from this point on, we refer to two different groups of fish: the supplemental group are those fish that are from wild brood stock, spend a portion of their life cycle in a hatchery, are then acclimated in a natural environment, smoltify, rear in the ocean, and return to spawn in the natural environment; the natural group live their entire life cycle in the wild, though at the spawner life stage they may interact with supplemental fish and a few hatchery strays. They are termed “natural” and not “wild”, as they are somewhat affected by hatchery and supplemental fish.

Data are provided for the natural origin production and supplemental releases, the estimated supplemental acclimation mortality, the estimated number of outmigrating smolts, and the estimated escapement data for natural and supplemental groups on the Clearwater River (Table 1). For the period covered during supplementation, the number of supplemental coho smolts released into the Clearwater varied from a low of 16 623 for the 1994 brood to 128 493 for the 1990 brood. During the period reported in this paper, natural smolt yield ranged from a low of 28 750 for the 1997 brood to 101 328 for the 1999 brood.

On average, 76 322 supplemental smolts were released annually in natural and semi-natural ponds located in upper areas of the Clearwater River and its tributaries (Christmas and Miller creeks) at age 1+ in early February. During their 6- to 10-week residence in acclimation ponds, hatchery feed was offered in decreasing amounts to facilitate a shift to natural foods and behavior. Eventually these fish were allowed to migrate of their own volition as smolts. While the number of supplemental fish released can be known with relative certainty, the number of supplemental smolts actually leaving these ponds was difficult to estimate. The supplemental smolt estimate is critical in determining accurate return rates from smolt to adult for the supplemental group. The Clearwater River scoop trap recovered both supplemental and natural smolts, and we used mark–recapture techniques on this data to estimate the outmigrating supplemental and natural populations (Table 1). Mortality in acclimation ponds was often greater than 40% (Table 1), which translates into an increase in survival from smolt to adult if adjusted for this mortality. These losses are believed to occur primarily through predators such as river otters that are known to frequent pre-smolt outplant sites. Additionally, the practice of ventral fin-clipping on supplemental fish may have also induced variable mortality rates (ASFEC 1995).

Comparison of production efficiencies of Clearwater coho before and during supplementation

All supplemental releases were fin-clipped (originally ventral-clipped and later adipose-clipped) and wire-tagged with a unique tag code. Natural origin fish were wire-tagged during the mark–recapture experiment. A modified Peterson mark–recapture method (Seber 1982) was used to estimate the number of smolts leaving the Clearwater system annually since 1979, based on fish captured in a smolt trap located near the confluence of the Clearwater and Queets

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Table 1. Estimated escapement of coho salmon (*Oncorhynchus kisutch*) adults of natural and supplementation origin and estimated smolt outmigrants for the Clearwater River (source: Larry Gilbertson, unpublished data).

Brood year	Natural origin escapement	Supplemental escapement	Total natural escapement	Supplemental releases	Supplemental mortality (%)	Supplemental outmigrants*	Natural smolt production
1979	2984	—	2984	—	—	—	52 900
1980	1850	—	1850	—	—	—	42 600
1981	2234	—	2234	—	—	—	99 800
1982	2457	—	2457	—	—	—	60 600
1983	539	—	539	—	—	—	48 200
1984	3683	—	3683	—	—	—	90 800
1985	1563	—	1563	—	—	—	47 500
1986	1556	—	1556	—	—	—	73 600
1987	1894	—	1894	—	—	—	86 000
1988	1913	—	1913	—	—	—	67 800
1989	1160	—	1160	35 000	49§	17 850	52 600
1990	2086	—	2086	128 493	49§	65 831	77 500
1991	1609	—	1609	37 650	40	22 763	61 814
1992	1128	922	2050	49 973	48	26 038	55 105
1993	2342	1120	3462	118 189	67	39 017	43 930
1994	427	86	513	16 623	33	11 212	36 275
1995	1829	204	2033	93 855	57	40 392	80 598
1996	2355	2785	5140	108 658	39	66 676	51 405
1997	636	0††	636	45 321	59	18 355	28 750
1998†	1343	854	2197	129 461	49§	66 025	93 837
1999†	2268	519	2787	—	—	—	101 328
2000	2585	356	2941	—	—	—	—

Note: The mark–recapture data is based on differential marking of adipose versus ventral fin clips along with coded wire tags for the natural and supplemental groups. Recapture occurs at the scoop trap (1/4 mile (1 mile = 1.609 km) before the confluence of the Clearwater River with the Queets River). Some sacrifices are necessary when the same mark is used for both groups (that occurred after 1998).

*Assuming that smolt trap efficiency is the same for both release groups, pre-smolt mortality in acclimatization ponds can be estimated using a simple Peterson-type proportional recoveries model. For the natural group, a simple Peterson with Bailey's correction is used to derive the natural origin outmigrants. For the supplemental outmigrants, we use the scoop trap recovery data to estimate the outmigrating smolts through the following equation:

$$S_{\text{out}} = \frac{R_S}{R_W} W$$

where S_{out} is the supplemental outmigrants, and W the number of natural fish tagged in the streams in the Clearwater River. R_S and R_W are the recoveries of these respective groups (supplemental and natural) at the scoop trap (the recapture event).

†Flood on Salmon River in December of 1999 caused the mixing of all supplemental fish at the hatchery and were thus released directly from the hatchery.

††No carcass or spawning ground samples were available in 1997 because of a high water event; therefore, no estimates were available to distinguish natural or supplemental fish; all fish are pooled in the natural group.

§1989, 1990, and 1998 estimated smolt outmigrants are based on average mortality for the other time series (1991–1997).

rivers (Table 1). We tested average smolt per spawner rates prior to the supplementation program and during supplementation, with a two-tailed t test assuming unequal variances and a nonparametric Wilcoxon test (Zar 1995). Because of the small number of observations and the inability to validate the underlying assumptions of normality for the t test, the Wilcoxon test may be more appropriate. In addition, we also tested overall spawner abundance before and during supplementation.

Comparison of survival rates of natural origin and supplemental groups

Marine survivals were compared using smolt to spawning escapement ratios for fish from supplemental production and natural escapement. It was not necessary to adjust for differences in harvest impacts because both the supplemental and natural fish face the same fishing pressure (PFMC 2001). Spawning escapements for Clearwater coho were estimated from expansion of spawning ground survey data (redd count data). These surveys are conducted by foot (and (or) boat) and cover over 50% of the spawning ground habitat in the tributaries and mainstem (C. Holt, Washington Department of Fish and Wildlife, 48 Devonshire Road, Montesano, WA 98563, USA, unpublished data). The survey area chosen was stratified on the basis of habitat use. The expansion factors were based on the area surveyed, the total area, and the number of fish per redd. We assumed one male and one female per redd based on field studies done on Washington coastal rivers (Washington Department of Fisheries and Quinault Treaty Area Tribes 1982). Total escapements were partitioned into supplemental and natural origin fish based on sampling of terminal fisheries and spawning escapements for ventral clips (Table 1).

The escapement rate (I) per smolt (supplemental or natural) was estimated using eq. 1.

$$(1) \qquad I_{g,t} = E_{g,t} / S_{g,t-1}$$

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where E is the escapement of the particular group (g, either supplemental or natural) in year t, and S is the number of smolts migrating in that same group in year (t – 1). Note that a 40% mortality during acclimation of the supplemental group translates to an increase in survival by a factor of 1.67 from smolt to adult. For each year, we performed a test of proportions using the standard normal curve (Zar 1995). We also performed an analysis of variance (ANOVA) using the overall yearly outmigrants, with release group and year as the main effect. We tested both a linear model (eq. 2) as well as log-transformed model (eq. 3) as suggested by Green and Macdonald (1987). Note that the 1997 data point was not included in the analysis because data were not available to enable the escapement to be partitioned. E is calculated as

$$E_{g,t} = \alpha + \beta_t t + \gamma S_{g,t-1} + \theta_g G + \varepsilon \qquad (2)$$

where t is the year, S is the number of outmigrating smolts from either the supplemental or natural group of the preceding year, and G is the group (supplemental or natural). The parameters associated with these variables are β, γ, and θ, respectively, measuring the effects of their corresponding variables. Note that we investigated the year effect because varying conditions from year to year may be a major influence for the return rate.

Under the null hypothesis, $\beta = \gamma = \theta = 0$. Under the alternative hypothesis, β and (or) γ and (or) $\theta \neq 0$. The most important term to test for is θ (i.e., difference in escapement between supplemental and natural groups, or group effect). We also tested a log-linear model (Green and Macdonald 1987; Cormack and Skalski 1992) because of the multiplicative nature of survival from one life cycle stage to the next.

$$\ln\left(\frac{E_{g,t}}{S_{g,t-1}}\right) = \ln(I_{g,t}) = \alpha + \beta_t t + \theta_g G + \varepsilon \qquad (3)$$

Under the null hypothesis, $\beta = \theta = 0$. Under the alternative hypothesis, β and (or) $\theta \neq 0$.

We also tested both models with adult data; that is, instead of outmigrating smolts (S) being one of the independent variables, we used adult escapement ($E_{g,t-3}$) or supplemental brood stock at time (t – 3) that contributed to escapement in year (t).

$$E_{g,t} = \alpha + \beta_t t + \gamma E_{g,t-3} + \theta_g G + \varepsilon \qquad (4)$$

$$\ln\left(\frac{E_{g,t}}{E_{g,t-3}}\right) = \alpha + \beta_t t + \theta_g G + \varepsilon \qquad (5)$$

Sensitivity analysis of escapement estimates

Annual escapement of the Queets coho salmon has been estimated by redd counts. Possible errors in this method of escapement estimate can come from a variety of sources, including incomplete survey of spawning areas, timing of survey, as well as variation in spawning ground characteristics (e.g., substrate, water flow, and visibility, etc.) and observers' experience level (e.g., capability of distinguishing redds of different species) (Dunham et al. 2001). Errors in the escapement estimates may affect the results of our analyses (eqs. 1 to 5). To investigate the effect of estimating errors in the escapement on our overall conclusions from the previous section, we carried out a simulation study. We allowed natural and supplemental escapement to vary 25% below or above their estimated values. Then we repeated the analyses for eqs. 2 to 5 with the simulated data. We repeated this simulation 1000 times. Results from the simulated data were tabulated.

Estimating productivity and carrying capacity using maximum likelihood techniques

The combined supplemental and natural populations were fit to the modified Beverton–Holt spawner–recruit relationship (Beverton and Holt 1957; Moussali and Hilborn 1986) shown below:

$$S_t = \frac{E_{t-2}}{\frac{1}{p} + \frac{1}{c} E_{t-2}} \qquad (6)$$

where S_t is the number of smolts that were counted in year t, E_{t-2} is the estimated escapement (or aggregate sum of both supplemental and natural spawners) of spawners in year t – 2, p is the initial slope of the line, or productivity (i.e., smolts per spawner at low density), and c is the capacity, or maximum number of smolts that can be produced by the system. We used the Beverton–Holt model because coho production is believed to be constrained by the number of suitable territories (Larkin 1977).

Smolt production from spawning escapement was evaluated as a likelihood function of p and c (eq. 7), assuming that the observations are log-normally distributed. The log-normal assumption reflects the multiplicative nature of survival between egg deposition and smolt counts (Peterman 1981; Hilborn and Walters 1992, p. 264). The likelihood of observing S_t smolts given the predicted value is

$$L(p, c|S_t) = \frac{1}{\sqrt{2\pi\sigma^2}} \frac{1}{(S_t)} \exp\left\{-\frac{[\ln(S_t) - \ln(\hat{S}_t)]^2}{2\sigma^2}\right\} \qquad (7)$$

where $\hat{S}_t$ is the predicted value of smolts from eq. 6 given p, c, and E. Since each data point is assumed to be independent, the total likelihood is simply the product of all the likelihoods. The method of likelihood profile (Hilborn and Mangel 1997) was used to calculate confidence intervals for p and c.

Results

Comparison of before and during supplementation effects on the Clearwater coho population

The mean and variance for the smolt per spawner rate during the presupplementation period (1979–1988 brood) was 38.27 and 431.69, respectively. For the supplementation period (return 1992–1999 broods), the mean and variance for the smolt per spawner rate were 33.37 and 367.82, respectively. We performed a two-tailed t test assuming unequal variances and a nonparametric Wilcoxon test to evaluate average recruits per spawner for the two time periods: presupplementation and during supplementation (1989–1999 brood). Both tests indicate that the average smolt per spawner rates do not differ significantly during the two time periods at a $\alpha = 0.05$ (t test, $p = 0.61$; Wilcoxon test, $p = 0.69$). The analysis on overall spawner abundance also pro-

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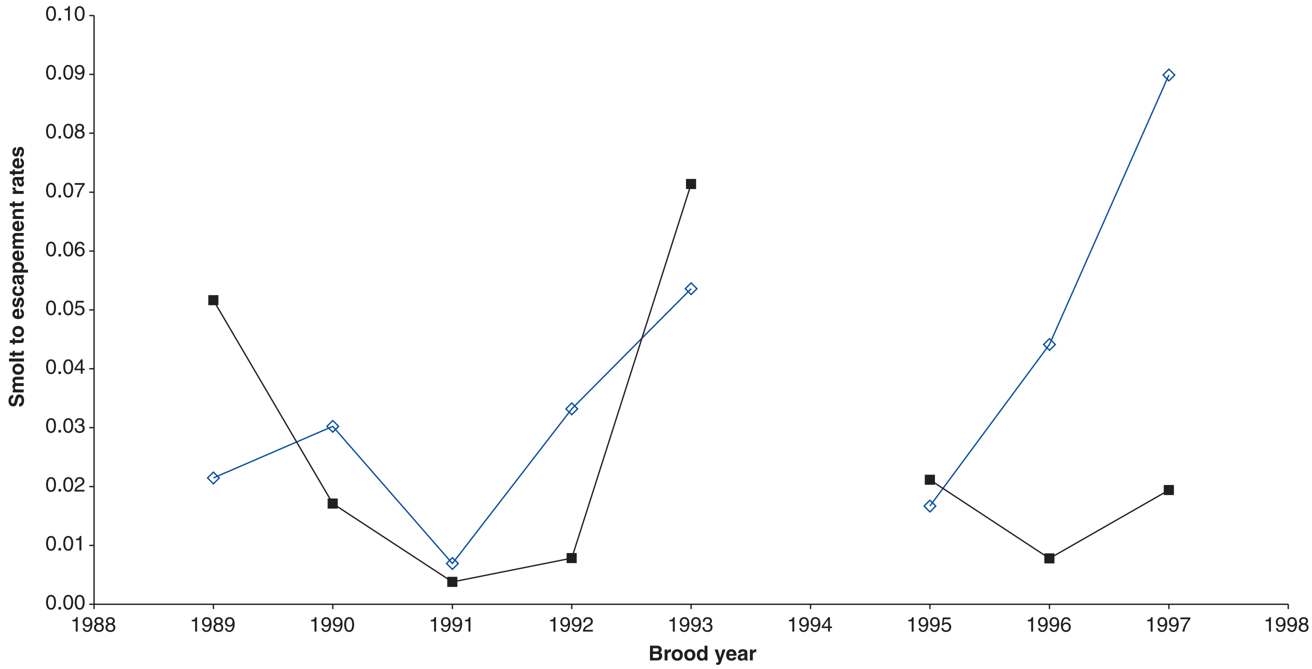
Fig. 3. Estimates of return rates from smolt to spawners for the natural (◇) and supplemental (■) groups by brood year (eq. 1).



duced a nonsignificant result (*t* test, *p* value = 0.47; Wilcoxon test, *p* value = 0.42).

Return rates between groups

A statistical test of proportions for large sample sizes found that survivors of supplemental and natural origin smolts from the Clearwater River differed at $\alpha = 0.05$. However, in 1990, 1991, and 1995 brood years, the survival of the supplemental and natural components were almost identical (Fig. 3). The data (Fig. 3) also indicate that in 1989, 1993, and 1995 broods, the return rate of the supplemental group was higher than that of the natural group, and vice versa in other years. We also compared the overall survival from outmigrating smolts with returning adults over all years (Fig. 3) with an ANOVA using the multiple releases, with release group type and year as the main effects (eqs. 2 and 3). Results indicate that group type is a significant variable, but not year or release size in the linear model (Table 2; eq. 2). With the log-linear model (Table 2; eq. 3), group and year are not significant at a level of 0.1, but are marginally detectable ($p < 0.15$ for both year and group). Assumptions of normality and constant variance appear reasonable based on residual diagnostics of the log-linear model.

Using the adult data and broodstock taken (Tables 1 and 3), supplemental fish have a substantially higher escapement than that of the natural group (Fig. 4). Using the linear model (eq. 4), we only detect escapement as being a significant variable (Table 4). The log-linear model (eq. 5) indicates that group is highly significant ($p = 0.016$, Table 4). Since survival from adult to spawning adult 3 years later is the result of a multiplicative process of survivals during successive life history stages, the log-linear model may be more appropriate for both the juvenile and adult data.

In addition, we analyzed the effect of the proportion of supplemental spawners on the natural smolt per spawner ratio. The result was marginally significant at $\alpha = 0.1$ ($r^2 = 0.4$, $p = 0.09$), which might indicate that supplementation has a negative impact on productivity. However, the data also suggest that spawner escapements increase, as we observe a higher proportion of supplemental spawners (Fig. 5*b*). It is likely that rather than a negative impact of supplemental spawners, the data are simply showing density-dependent relationship between the number of total spawners and productivity (smolts per spawner), as is evident from Fig. 5(*c*). It appears that irrespective of the number of spawners, the number of average smolts for the time period shown here is stable, albeit lower than the estimated carrying capacity (Fig. 6).

Sensitivity analysis of escapement estimates

Results from the simulated data (Table 5) were generally consistent with the results from the estimated data (as shown in Tables 2 and 4 and Figs. 3 and 4). In the case of the smolt to escapement rate estimates, with escapement as our response variable (eq. 2), the group effect is strong and is consistent with results from Table 2. In the case of the log-transformed response (eq. 3), the group and year effects are marginal at best (Table 5). With escapement as our response variable, the adult data indicate a weak group effect (eq. 4). With a log-transformed response variable (eq. 5), the effect of group was always significant (Table 5).

These results suggest that the group effect is marginally significant on juvenile data (eqs. 2 and 3; Table 5) and is significant on adult data (eqs. 4 and 5; Table 5). However, the direction is different, namely the juvenile data suggest that the natural smolts survive at higher rates, and the adult data suggest that the supplemental return rates are higher.

Productivities and capacities of naturally spawning Clearwater coho

Available juvenile and spawning escapement data during the supplementation study period appear to fit a modified

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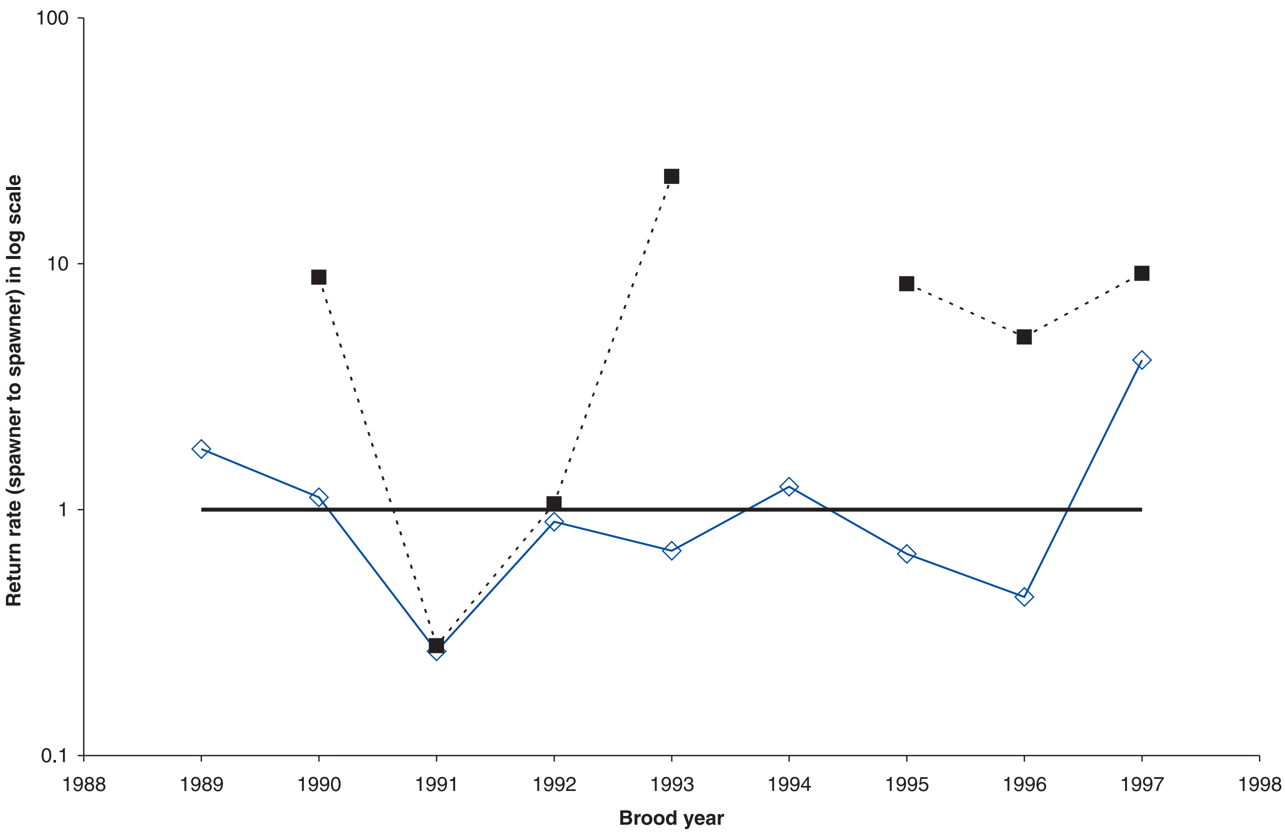
Table 2. Analysis of variance (ANOVA) on fitting linear models to eqs. 2 and 3 with response variables being escapement of either supplemental or natural group (E_g) and natural log of escapement per outmigrating smolt ($\ln(E_{g,t}/S_{g,t-1})$).

Variable	df	SS	MS	*F*	*p* >*F*
Response variable E_g; eq. 2					
Year	7	6 237 410	891 059	2.14	0.186
$S_{g,t-1}$	1	813 861	813 861	1.95	0.212
G	1	3 059 385	3 059 385	7.35	0.035**
Residuals	6	2 498 798	416 466	—	—
Response variable $\ln(E_{g,t}/S_{g,t-1})$; eq. 3					
Year	7	7.87	1.12	2.41	0.1345
G	1	1.26	1.26	2.69	0.145
Residuals	7	3.27	0.47	—	—

Note: df, degrees of freedom; SS, sum of squares; MS, mean square; *G*, group; **, $p = 0.05$.

Fig. 4. Return rates from spawner to spawner for the supplemental (■) and natural (◇) groups by brood year. All values on the *y* axis are on a log scale. The horizontal line shows replacement (i.e., return rate of 1 from spawner to spawner). Note that archived data for brood stock taken in 1989 for the supplemental group is unavailable at this time.



Beverton–Holt model slightly better than a Ricker model (r^2 values for Beverton–Holt and Ricker models were 0.80 and 0.75, repectively). The measure of goodness of fit (r^2) explains the proportion of the variation that can be attributed to natural spawners. At low spawner densities, the productivity of the combined supplemental–natural escapement (the number of smolts produced by supplemental–natural spawners at low spawner abundances) is estimated at 113 smolts·spawner^{-1} (Fig. 6). Parameter uncertainty, derived through likelihood profiles of the parameter estimates for the Beverton–Holt model, is shown (Figs. 6*b*, 6*c*). The method of likelihood profile (Hilborn and Mangel 1997) generated a lower bound for a 95% confidence interval (CI) of 48.62 smolts·spawner^{-1}. Because there are few data points at low spawner abundances, the upper CI is extremely high (2002 smolts·spawner^{-1}) and is unrealistic (see the long tail in the profile shown in Fig. 6(*b*)). The data fit to a Beverton–Holt model indicates that on average, the Clearwater River can at most be expected to produce 83 146 smolts, with a 95% CI for this estimate of 48 728 to 165 000. The CI for the estimate of capacity (Fig. 6*c*) reflects adequate contrast in the data (i.e., we have numerous data points over a range of high spawner abundances).

We also fit the data using the presupplementation period (i.e., from 1979 to 1990 smolt outmigration years, 1977 to

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Table 3. Estimated returns without supplementation in comparison to what was observed.

Brood year	Natural brood stock taken	Estimated escapement without supplementation	Observed escapement with supplementation
1989*	113	—	—
1990	127	—	—
1991	308	—	—
1992	193	1521	2050
1993	123	2608	3462
1994	31	540	513
1995	103	2104	2033
1996	103	2542	5140
1997	39	NA†	636
1998	73	1484	2197
1999	49	2362	2787
2000	97	2841	2941

Note: 1989 to 1991 are not shown, as we do not see the benefit of supplemental brood stock until 1992 (1989 brood returns).

*Brood stock in 1989 is averaged over the entire time series seen (archived data unavailable at this time).

†Do not know the fraction of natural escapement becaus of high flow event that washed all carcasses out.

1988 spawning brood years). Estimates of productivity were centered at 177 smolts·spawner^{-1} and carrying capacity at 82 600 smolts. The estimates of freshwater productivity are not statistically different between these periods, as the confidence intervals overlap (Fig. 7), though the presmolt supplementation's point estimate on productivity is higher than that during the supplementation period by about 57% (Fig. 7). This is an important point, because the climate regimes between these two periods were very different (Mantua et al. 1997), and thus favorable freshwater conditions could possibly explain the higher productivity before the 1990s. However, owing to lack of data at low spawning abundances, uncertainty around this estimate is larger than that shown in Fig. 6, exhibited by the flat likelihood profile.

Comparing derived maximum production goals on the Clearwater River with observed data

Based on estimates of juvenile carrying capacity (83 146 smolts), we estimated the number of spawners required to maximize production at smolt carrying capacity under different freshwater survivals. The number of spawners required to fully seed the available coho habitat on the Clearwater River at high (71 smolts·spawner^{-1} in the 1994 brood; Table 1), average (37 smolts·spawner^{-1}; Table 1), and low (10 smolts·spawner^{-1}; Table 1) freshwater survivals is 1175, 2257, and 8311, respectively. The high number of smolts per spawner represents the best spawner–smolt survival ever seen in the Clearwater River (1994 brood); however, adult returns from that brood were very poor because of low ocean survival and the small numbers of smolts produced. Data are not available to evaluate the survival of supplemental releases for the 1994 brood, since no carcass samples were collected in 1997 owing to extreme flow (Fig. 8). If freshwater conditions are poor, as they were with the 1993 brood, nearly all the potential adult production at average marine survival rates would be required to achieve the smolt carrying capacity of the Clearwater River. If both freshwater and marine survivals are poor, the natural spawning escapement will decline. This unhappy combination of conditions was experienced in the 1990s.

Table 4. Analysis of variance (ANOVA) using adult data fitting linear models to eqs. 4 and 5 with response variables being escapement of either supplemental or natural group (E_g) and natural log of escapement observed 3 years ago of the natural group or supplemental broodstock that contributed to the returns ($\ln(E_{g,t}/E_{g,t-3})$).

Variable	df	SS	MS	*F*	*p* >*F*
Response variable E_g; eq. 4					
Year	7	6 217 984	888 283	1.72	0.3
$E_{g(t-3)}$	1	3 025 211	3 025 211	5.86	0.1*
G	1	616 098	616 098	1.19	0.3
Residuals	6	2 498 798	416 466	—	—
Response variable $\ln(E_{g,t}/E_{g,t-3})$; eq. 5					
Year	7	13.29	1.90	2.18	0.18
G	1	9.55	9.55	10.95	0.02**
Residuals	7	3.27	0.47	—	—

Note: df, degrees of freedom; SS, sum of squares; MS, mean square; *G*, group; **, p = 0.05; *, p = 0.1.

Integrated model evaluating escapement with and without supplementation (a hypothetical scenario)

Based on the data presented in Table 3 and the return rates depicted in Fig. 4, we developed a model that compares the reproductive efficiency of fish taken for supplementation brood stock against the contribution that those fish would have been expected to make had they been permitted to spawn naturally (Table 3). Our assessment indicates that supplementation is consistently more efficient (spawner to spawner return) than natural spawners over the study time period (Table 3) other than brood years 1991 and 1992. These results are similar to those obtained by Salo and Bayliff (1958). Prior to 1993 when the current rearing facility came on line on the Salmon River tributary of the Queets River, supplementation fish experienced relatively high handling mortality because of inadequate hatchery facilities. The Lake Quinault facility, where progeny from supplementation brood stock were reared prior to 1993, was not designed to efficiently handle fish for the supplementation program. Losses due to handling, predation, and disease during rearing were greater at Lake Quinault than at Salmon River for pre-1993 periods.

With the 1991 and 1992 brood years, abnormally high prespawning mortality with supplementation brood stock was observed (Fig. 4; Table 3). However, once the initial problems of rearing were worked out, the premium from supplementation over natural spawning diminished as survivors of the natural origin brood stock improved, as seen in the later brood years (Table 3).

Discussion

The potential value of artificial propagation techniques as a means to reduce extinction risks and rebuild depressed spawning populations is an area that has commanded considerable scientific and policy debate (Waples et al. 2006). The

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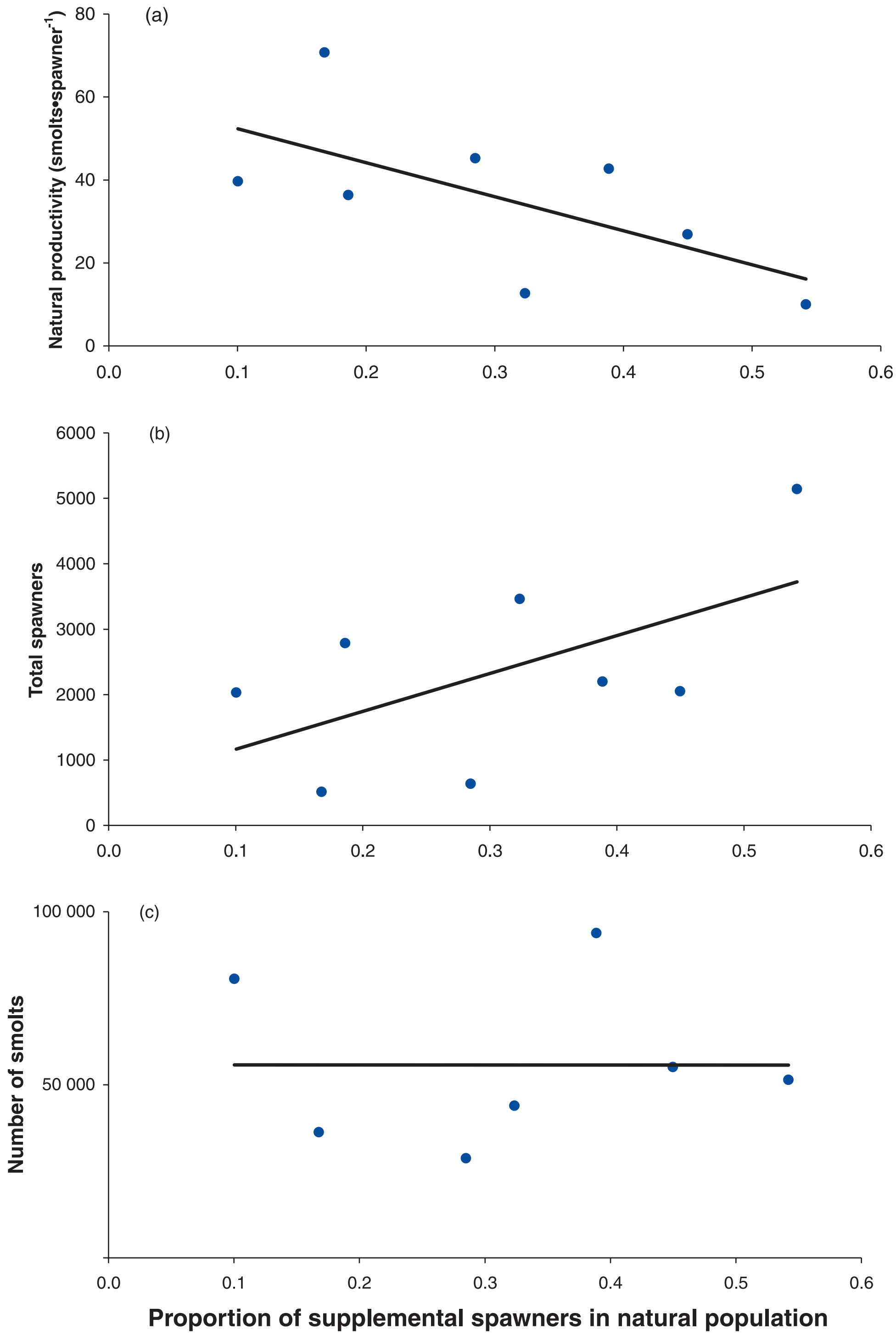
Fig. 5. Numbers of smolts per spawner (*a*), total spawners (*b*), and estimated smolts (*c*) versus the proportion of supplemental spawners in the natural population.



results presented here differ from other studies encountered in the literature primarily because previous scientific research in this area studied hatchery populations that were not intended to supplement natural spawning (e.g., Reisenbichler and McIntyre 1977; Leider et al. 1984). Studies in natural environments, such as those by Nickelson et al. (1986) on Oregon coho, used poorly adapted brood stock for supplementation. Other studies, such as Chilcote et al. (1986), may have had misleading results because of management practices or because of using poorly adapted brood stock with regards to the system being studied (Campton et al. 1991). In contrast, the Queets coho supplementation project was designed from the outset to minimize the deleterious effects reported by Chilcote et al. (1986) and Nickelson et al. (1986). As presented in this study, when supplemental experiments are designed properly, improvements in produc-

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Fig. 6. The Beverton–Holt fit from spawners to smolt on the Clearwater River (*a*). The data in (*a*) is the sum of supplemental and natural spawners for each brood and the corresponding juvenile recruitment for that brood (occurring 2 years after spawning). Panel (*b*) indicates the uncertainty in the productivity parameter, and panel (*c*) indicates the uncertainty in the estimate of freshwater smolt capacity.

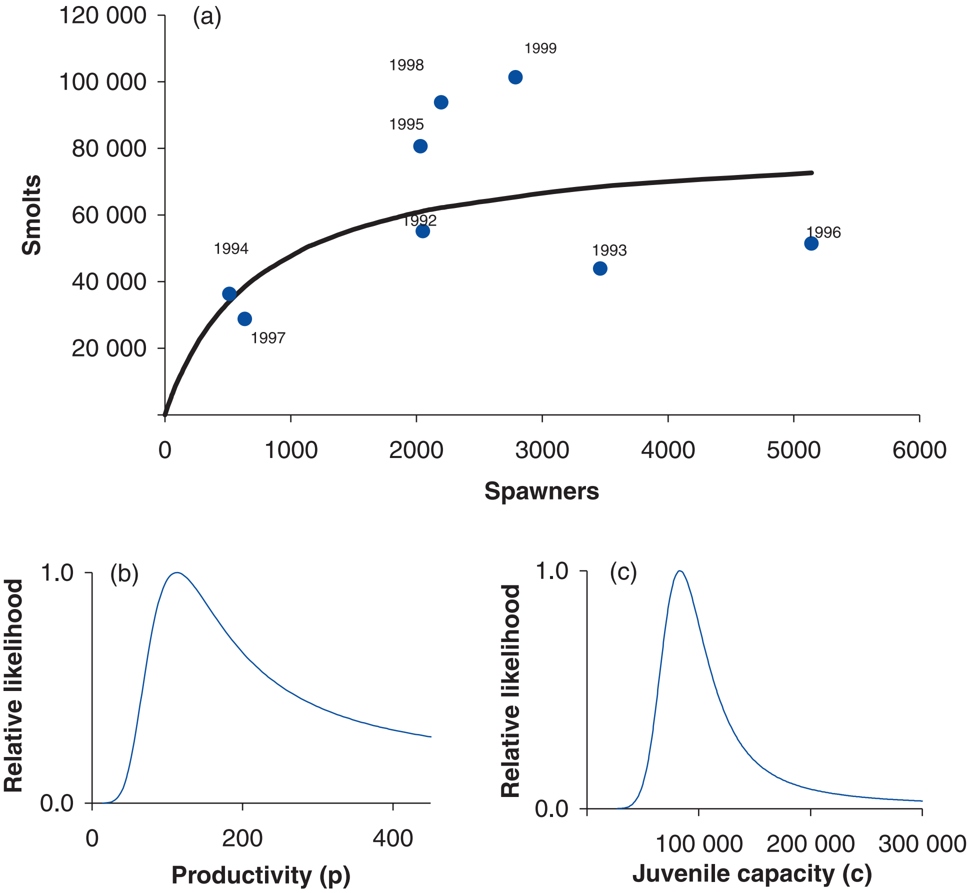

Table 5. Results from simulated data testing sensitivity in escapement estimates.

	Variable			
Equation	Year	Escapement	Smolt	Group
α = 0.05				
2	63	—	16	528
3	6	—	—	3
4	12	36	—	274
5	0	—	—	1000
α = 0.10				
2	236	—	79	829
3	206	—	—	151
4	142	191	—	628
5	0	—	—	1000

Note: The number in each cell is the number of times that *p* value is less than the value of the significance level (α). The number of replications is 1000.

tion efficiency from spawner to returning spawner could be helpful in efforts to restore damaged populations or stabilize declining populations, such as those listed under the Endangered Species Act for an interim period until causes for declines can be addressed.

From a fisheries management perspective, our integrated analysis provides some useful insight into the potential value of supplementation. In our analysis, we assume that the goal of the agencies involved was to seed the available habitat for juvenile production (i.e., have 83 146 smolts from Fig. 6*c*). We assume that periods of low, average, and high freshwater survival were based on the minimum, average, and maximum smolt per spawner ratios observed, respectively, on the Clearwater River between 1989 and 1998 broods. Figure 8 illustrates that it would be problematic to provide sufficient escapements to maximize smolt production from the Clearwater River unless environmental conditions in freshwater and marine areas are conducive to favorable survivals. In regimes of low freshwater and marine survivals, escapements and production would continue to decline on the natural component of the population. Higher efficiencies of supplementation fish suggests that supplementation could potentially be used to slow the rate of decline experienced during periods of low marine survival and low freshwater survival (attributable to degraded habitat condition) and provide increased capacity for recovery when conditions improve. When freshwater survival is low and marine survival is average, nearly all the production would be required to achieve escapements necessary to produce full smolt capacity. This would of course eliminate or severely curtail harvest opportunities in fisheries impacting the stock. Since

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Fig. 7. Uncertainty in productivity estimates (*p*) between presupplementation (broken line) and during supplementation (solid line) periods.

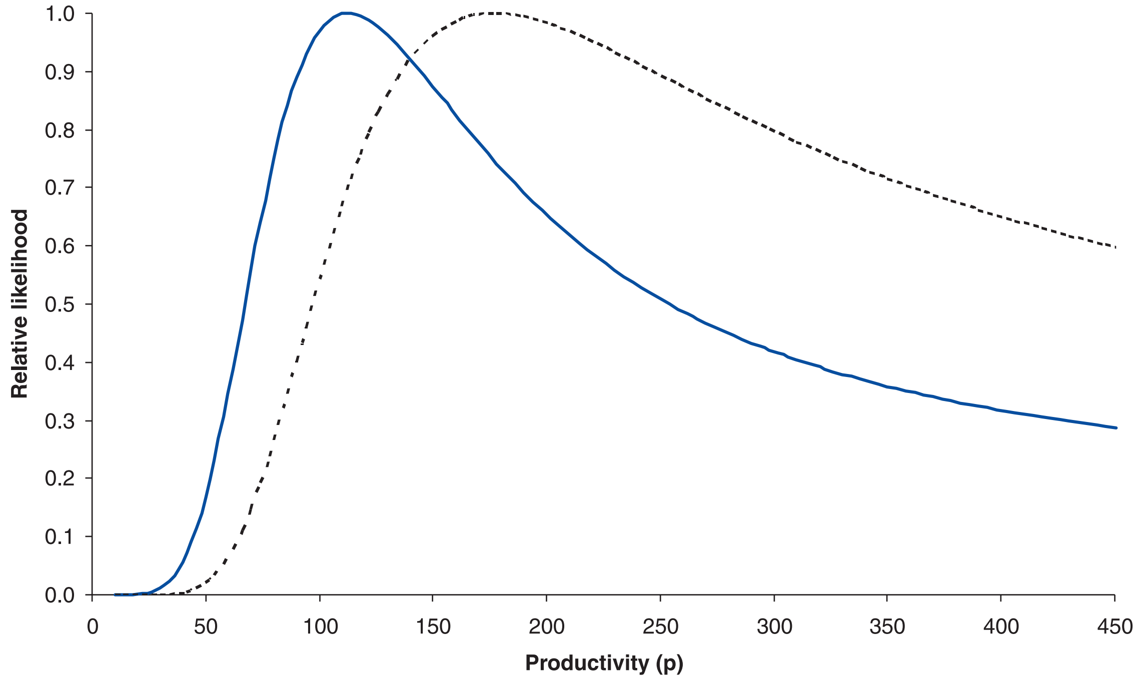
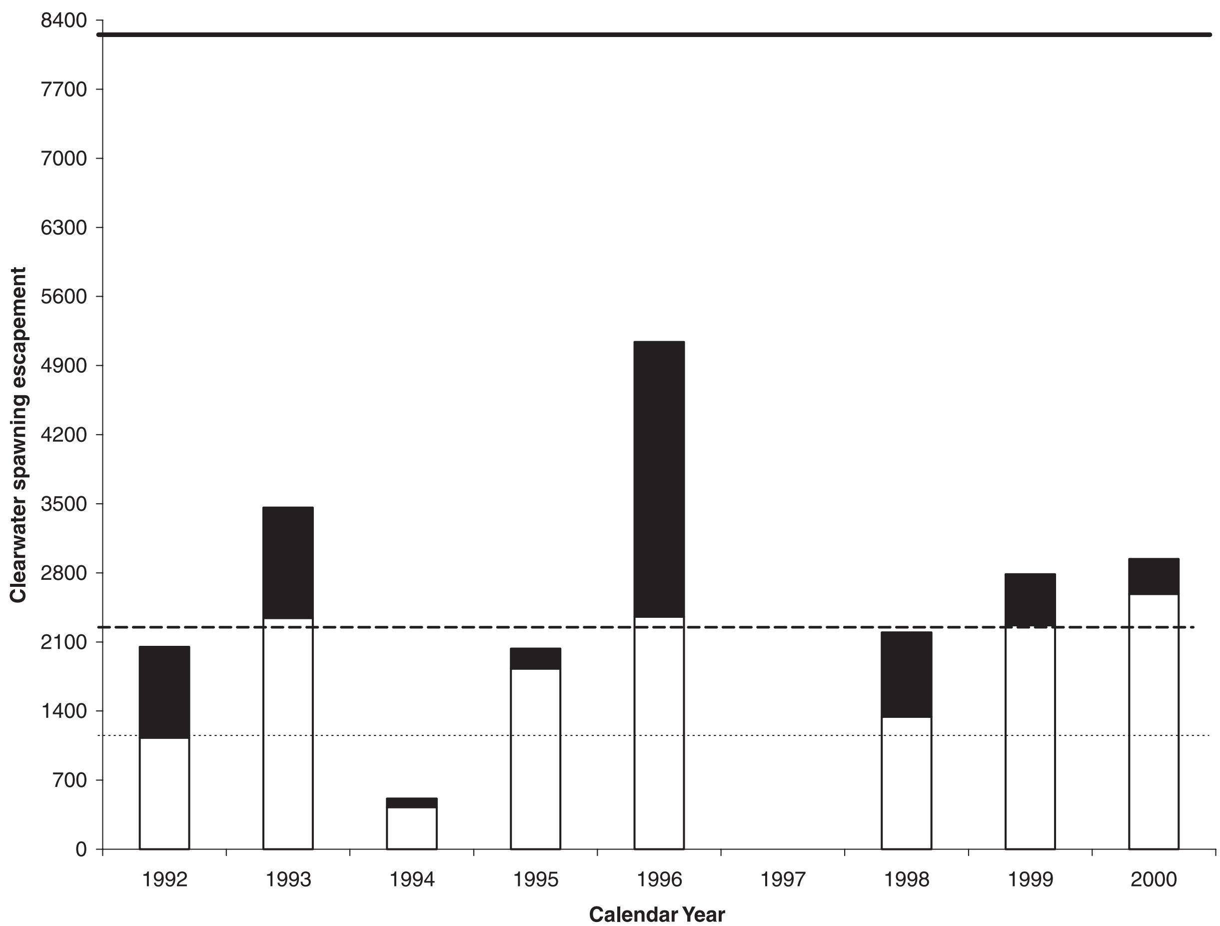


Fig. 8. Target escapement goals given poor (solid line), average (middle broken line), and maximum (lower dotted line) spawner to smolt survival and the contribution of natural (open) and supplemental (solid) fish towards those goals. Goals under maximum, average, and poor conditions in fresh water are 1175, 2257, and 8311 spawners, respectively.



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Queets (Clearwater) coho are caught by highly mixed stock ocean fisheries and more limited mixed stock terminal fisheries (the run timing of Queets coho overlaps the timing of returning runs of Chinook and steelhead), restrictions on Queets (Clearwater) coho harvests would limit the catches of other non-target fish stocks.

This integrated analysis also indicates that smolt to spawner survival must exceed 10% in poor freshwater survival years to provide sufficient spawners to produce the maximum number of smolts from the Clearwater River. For average conditions, smolt to spawner survival must exceed 3%. In 3 of the last 8 years, smolt–spawner return rates for Clearwater coho were below 3%. This is not atypical, as survival from smolt to adult of coastal coho is commonly below 3% (Coronado and Hilborn 1998). Evidence from Francis and Hare (1994) suggests that cyclical climatic and oceanographic phenomena occur in the North Pacific, and if these cycles generate unfavorable ocean conditions, these effects will result in low smolt to spawner survival for a number of years. Restrictions on harvest alone are unlikely to be sufficient to maintain production at desired levels. In the late 1980s, exploitation rates on Queets coho averaged 47% (PFMC 2001). These harvest rates declined substantially (25%) in the mid- to late 1990s, yet escapement levels continued to decline (PFMC 2001). Without the capacity to predict either freshwater or ocean conditions, it may not be prudent to stop supplemental activities in the short term. If one can determine that survivals can be expected to improve a few years in advance, it may be desirable to ramp down the supplementation program (but restarting the program could prove problematic given constraints on the logistics and training of field personnel).

Nonetheless, one should be wary of using these techniques for long-term purposes, as using so few hatchery brood stock for each generation can probably lower effective population size (Ford 2002) and may eventually lead to substantial decreases in natural productivity because of the potential loss of genetic variation (Waples and Do 1994; Wang et al. 2002). Although, the data presented does not suggest such factors have come into play (intrinsic productivity appears to be unchanged), it is premature to claim that they will not have an effect in the future.

Admittedly, our analysis reflects limitations of data collected over the course of the study. Ideally, the Queets study would have involved the creation of an experimental control area as suggested by Waples et al. (2006), but situations in which true controls can be established in a natural environment are rarely encountered. Uncertainties surrounding the accuracy and precision of estimates of spawning escapements and juvenile production, while undesirable, are commonplace when data are collected in a natural environment where observations are affected by a myriad of uncontrollable influences that are virtually impossible to measure. We observed that the supplemental group contributed a large portion of the spawning escapement in some years. Whether or not this turns out to adversely affect the genetic diversity of the natural stock on the Clearwater River as hypothesized by Waples and Do (1994) is uncertain.

In many respects, we have had to rely on indirect inferences rather than on direct samples or measurements. For example, we relied upon results of fitting smolt and escapement data to a Beverton–Holt model to estimate productivity. This was because data were not available to permit us to try to directly trace the genetic history and performance of progeny produced by the combined spawning population of supplemental and naturally produced fish. We evaluated data collected during presupplementation and supplementation periods to try to detect changes in reproductive efficiency over time. However, we were unable to provide information that might be more helpful in directly addressing certain questions related to overall performance of the supplemental group and its contribution to production from natural spawning (Waples et al. 2006).

Our results indicate that the productivity of the naturally spawning population (a composite of both supplemental and natural fish) is very high (113 smolts·spawner^{-1}) for the period in which supplementation occurred. The Clearwater coho supplemented stock has an estimated productivity that is comparable with coho produced by other healthy systems. The south fork of the Skykomish River, one of the healthiest systems in terms of freshwater habitat available for coho, has a juvenile productivity estimate of ~128 smolts·spawner^{-1} (256 smolts·female^{-1}; Sharma and Hilborn 2001). We interpret the productivity estimated through the Beverton–Holt production model as an indicator of reproductive fitness. After three generations (10 years of research with smolt supplementation), there is no evidence that supplementation has negatively affected the fitness of the target population. Conclusive results would require a commitment for continued monitoring over an extensive period of time, perhaps even after supplementation efforts are terminated (Waples et al. 2006).

As an alternative to supplementation, habitat enhancement or restoration is another option. Nickelson et al. (1992*a*) reported that annual variations in flow, water temperature, overwintering, and summer rearing habitat affect the overall smolt to spawner survival and carrying capacity. Some habitat restoration activities, such as building side-channel habitat (Nickelson et al. 1992*b*), might be of value in improving productivity and increasing the capacity of coho in the Clearwater River. Some of this work has already been performed by Cederholm and Scarlett (1991) with some positive results. Although habitat restoration is ultimately the best way for improving the overall productivity and survival in the freshwater lifecycle of coho, it is expensive, time consuming, and results are often not observed for decades (Lichatowich et al. 1995). Habitat modification is difficult to achieve in the context of the Clearwater River,as much of the habitat utilized by coho lies on land owned or managed by different government and private entities. In addition, the fish produced by habitat restoration or enhancement efforts would still be subject to high interannual variability in survivals.

In conclusion, this study demonstrates that a supplementation (hatchery) program, in this case following new and innovative operational protocols, can produce smolts that have nearly the same survival rate to adults as that of wild smolts and can result in more adult coho returning to the Clearwater basin. This benefit appears possible without short-term adverse impacts to either intrinsic productivity or the number

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of naturally produced smolts. However, the long-term outlook is uncertain and cannot be inferred from the data generated during the first 10 years of this program.

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