Watershed Restoration to Reconcile Fisheries and Habitat Impacts at the Keogh River in Coastal British Columbia

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Abstract.—Reconciling fisheries, climate, and habitat impacts with conservation may be possible with ecosystem restoration. Riparian logging decreased large woody debris in most British Columbia streams, reducing fish cover, overwinter refuges, and bank stability. Salmon survival at sea declined dramatically in the 1990s in southern British Columbia, at some places accompanied by declines in yield from freshwater life stages. Watershed restoration may offset poor survival. At the oligotrophic Keogh River, approximately 500 habitat structures were installed, off-channel ponds developed, nutrients added annually, and logging roads storm proofed and stabilized. Treatment effectiveness was evaluated stepwise by annual monitoring of juvenile fish in stream, and steelhead *Oncorhynchus mykiss* and coho *O. kisutch* salmon smolts, in comparison to the adjacent Waukwaas River. Mean juvenile sizes and densities were highest where treated with nutrients and habitat structures. By 2003, 90% (previous mean, 32%) of steelhead smolts were age-2 or younger with average previous size of age-3 smolts, as found in the nutrient-enriched river in the mid-1980s. Yields exceeded (coho) or approached (steelhead) the average smolt yield of an earlier more productive decade (1980s), despite exceptionally low returns. Steelhead smolt yield per spawner improved substantially in the Keogh River, compared to a pretreatment extirpation trajectory. Regardless, covariance analysis indicated that steelhead smolt recruits per spawner were lower than that of the earlier regime (1980s) and not significantly different from those in the recent (1990s) regime, prior to treatment. The latter was confounded by differing levels of spawners. Nonetheless, based on the density and growth studies in river, earlier age of steelhead smolts (with no change in mean size), and observations on other species, we conclude that populations are in better condition after watershed restoration to respond to low survivals of smolts in the ocean, potential harvest impacts, and climate shifts.

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Introduction

Anadromous salmonids in their southern distribution of North America have undergone substantial declines over the last few decades that have been attributed to lower survival during the marine life stage (Anderson 1999; Smith and Ward 2000; Ward 2000). Reasons for these declines appear coincident with a series of El Niño events, the Pacific decadal oscillation, and global climate warming. Further, climate changes may have affected freshwater habitats for steelhead negatively by increasing summer droughts and winter storms (Ward et al. 2003b). Past habitat impacts of forest land use, particularly historical riparian logging practices, are also considered a significant factor (Slaney and Martin 1997). Moreover, lower productivity of salmonid stocks may, in part, be related to low salmon escapements in the Pacific Northwest and fewer salmon carcasses (i.e., a depletion of marine-derived nutrients transported into oligotrophic freshwater environments; Larkin and Slaney 1997).

Applied strategies of habitat rehabilitation may assist in counteracting these trends of depressed salmonid stocks by increasing stock productivity and capacity in freshwater. Programs of watershed restoration have emerged in northern California, Oregon, Washington, and British Columbia (Slaney and Martin 1997); these recovery initiatives assume improvements in salmonid productivity and capacity in freshwater. Only a few watershed and habitat restoration programs have provided sufficient monitoring and evaluation to confirm their effectiveness. A long-term evaluation of steelhead *Oncorhynchus mykiss* and coho salmon *O. kisutch* smolt yield from 14 km of large wood restoration at Fish Creek, Oregon, was inconclusive (Reeves et al. 1997). However, a well-replicated postrestoration evaluation of salmonid streams in coastal Washing-

ton and Oregon demonstrated greater juvenile abundances in rehabilitated reaches, particularly in winter (Roni and Quinn 2001). Similarly, controlled before and after evaluations of large wood restoration in two small coastal streams in Oregon confirmed improvements in coho salmon, steelhead, and cutthroat trout *O. clarki* smolt yields in response to instream large wood and off-channel alcove restoration (Solazzi et al. 2000). In south coastal British Columbia, experimental whole river addition of nutrients in the mid-1980s increased juvenile salmonid growth and steelhead smolt yield (Johnston et al. 1990; Slaney et al. 2003), and steelhead trout and coho salmon juvenile abundance responded positively to physical habitat manipulation (Ward and Slaney 1981). Thus, past evidence supports habitat recovery measures; yet whole river ecosystem strategies to date have not been evaluated, and their effectiveness is uncertain under the current conditions of low survival of smolts in the ocean (Ward 2000).

More recently, the Keogh River received watershed-level rehabilitative treatments, including large-scale habitat restoration, nutrient additions, and logging road rehabilitation. An increasing trend in densities of juvenile steelhead in the Keogh River was documented from 1998 to 2001, as the stream rehabilitation treatments progressed from 1997 to 2001 (Ward et al. 2003a, 2003b). As a response to marine-derived nutrient replacement, steelhead and coho salmon fry size (mean weight by autumn) exceeded the reference stream by 50% and 38%, respectively (Ward et al. 2003b). By 2000, coho salmon smolt yield increased in the Keogh River to 74,500, or 20% above of the historical average of 62,000 smolts, and steelhead smolt yield increased to 2,338 fish, the highest since 1993, but still well below the historical average of 6,000 smolts (Ward 2000). Moreover, steelhead smolts per spawner, albeit at low spawner den-
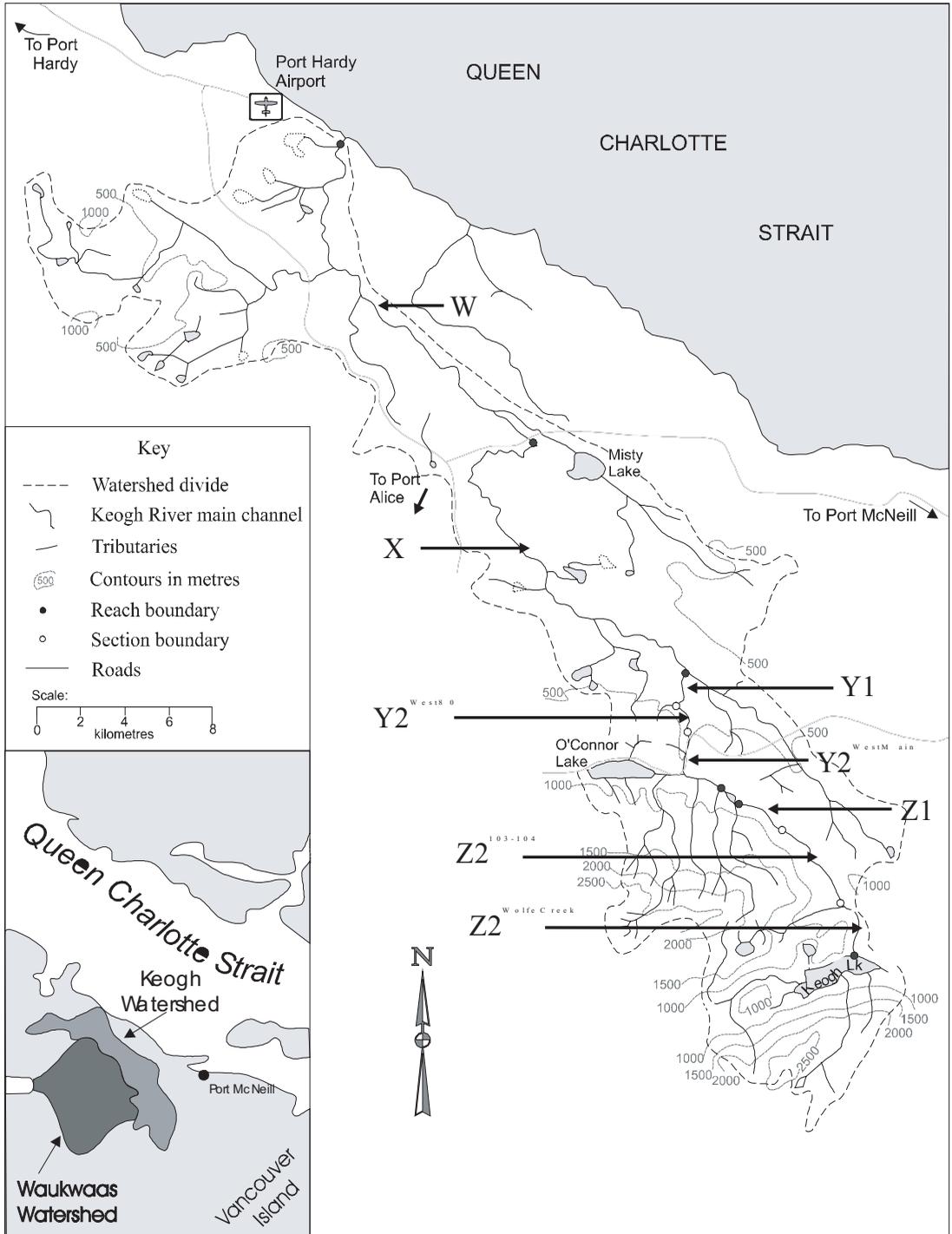
Figure 1. The Keogh River watershed, indicating reach boundaries and section boundaries used in this study, elevations, the watershed divide, and the location on the British Columbia coast (inset), as well as the relative position of the neighboring Waukwaas River, British Columbia.

sity, showed a sharp increase over four brood years up to 1998. Thus, comparisons of juvenile abundance and growth, as well as yields of steelhead in treatment and reference streams, have provided preliminary support for the contention that an extinction trajectory of steelhead may be halted or reversed (Ward et al. 2003a, 2003b).

Our preliminary results suggested that reductions in survival rate at one salmonid life stage (smolt-to-adult) can to be compensated by improvements in another stage (fry-to smolt; Ward et al. 2003a, 2003b). However, several years of additional monitoring of a highly variable juvenile response was required to confirm sustained positive trends in smolt yield, smolt yield per spawner, and returning adults as the ultimate response variables. Herein, we report on two additional years of the response by steelhead and coho salmon smolts, to 2003.

Methods

The Keogh and Waukwaas rivers, two oligotrophic fourth-order streams, are situated at the northern end of Vancouver Island, British Columbia, Canada (Figure 1). The logging history, river size, and fish species present have been described previously (Ward et al. 2003a, 2003b).

The experimental design for instream response involved two treatment types: habitat structures and slow-release nutrient addition. The plan of restoration within the Keogh watershed was adapted to a staircase-like experimental design, with structure placement commencing in the upper reaches, nutrient addition beginning in lower reaches, and both treatments expanding annually over 5 years until the whole watershed was treated (Ward et al. 2003b).

The entire watershed underwent habitat restoration treatments to address historical logging impacts, as part of British Columbia's Watershed Restoration Program (WRP) (Slaney and Martin 1997). Treatments included instream habitat and nutrient addition, rehabilitation of several off-channel ponds as overwinter flood refuges for juvenile fish, and storm-proofing of logging roads. Overall rehabilitation costs, including road deactivation of about Can$200,000, approached Can$1,000,000.

Riparian trees had been removed within about 50% of the basin during 1960–1985, resulting in simple featureless channel segments as remaining in-stream wood decayed over time. From 1996 to 2001, approximately 500 habitat structures were added to 10 km of the main stem where overwinter and summer rearing habitats were most lacking. This included 6.5 km of reaches Z and Y, a 0.5 km segment located midway between reach Y and X, 0.6 km of reach X near the Island Highway, 1 km of reach X near the mainline logging road crossing, and a 1.1 km segment of reach W in the lower river (Figure 1). In stream structures were largely based on natural templates, designed as either boulder clusters (Ward 1997) or boulder-ballasted large woody debris (LWD) structures (Slaney et al. 1997), and reconstructed riffle-pool habitats (Slaney and Zaldokas 1997).

Low-level inorganic nutrients were added as slow-release briquettes of magnesium ammonium phosphate from 1997 to 2003 to compensate for reduced marine-derived influx of nutrients (Larkin and Slaney 1997). Pink *O. gorbuscha* and coho salmon escapements were at historical lows of about 15–25% of average estimated historical abundances (data on file). Initially, the lower half of the river was treated with nutrients, and by 1999, the total length (31 km) of the Keogh River main stem to the

outlet of Keogh Lake was treated every 3–5 km, including ~10 km of small tributaries. The objective was to moderately increase the very low concentration of dissolved inorganic phosphorus from less than 1 or 1 $\mu g \times L^{-1}$ upwards to 3–5 $\mu g \times L^{-1}$ (as soluble reactive phosphorus) during mid to late May to September, as the river was P-limited rather than N-limited (Johnston et al. 1990; Slaney et al. 2003). Details of methods were provided in Ashley and Slaney (1997) and briefly in Ward et al. (2003b), the latter at the Keogh River.

Several off-channel ponds were also rehabilitated to provide additional overwintering refuges for juvenile coho salmon. Between 1997 and 2000, seven ponds were expanded from remnant alcoves to elongated ponds averaging about 200 m in length by 10 m in width or about 0.2 ha in area (range 0.1–0.5 ha). Six of seven sites were connected to small water courses or groundwater inflows to elevate dissolved oxygen and provide fish access (one site had low oxygen concentrations). Ponds were located 0.5, 1.5, 4.0, and 20 km from the mouth of the river, and smolt out-migration was monitored.

Finally, an extensive network of logging roads throughout the watershed was stabilized from 1994 to 2000. About 75% of roads were associated with rolling low-slope forest lands, and about 25% were associated with steeply sloping forest lands in the headwaters (Figure 1). Overall, road segments were storm-proofed to comply with 1995 forest practice regulations to ensure adequate drainage and prevent washouts during large coastal storm events. At hill slope access roads, improved drainage was achieved using cross ditches and water bars. In addition, a small portion of roads (about 20 km), particularly at the base of the steep hill slope, was semipermanently deactivated by removing water course crossings and leaving swales. As well, several kilometers of

roads were permanently deactivated and revegetated. Some stormproofing of logging roads was also undertaken in the reference Waukwaas watershed.

To evaluate the effectiveness of watershed rehabilitation techniques, four methods were utilized. First, the density of salmonid juveniles in freshwater was assessed by mark–recapture, using electroshocking and seine-netting techniques (McCubbing and Ward 1997). Fish were sampled within each reach (100 m except reach W on the Keogh where 200 m were sampled) in proportion to the frequency of occurrence of habitat classes. These results were reported by Ward et al. (2003a, 2003b). Second, steelhead and coho smolt yields were assessed through operation of a full-river counting fence near the mouth of the Keogh River, and by mark–recapture estimates using rotary screw traps on the Waukwaas River as described below and in Ward et al. (2003a, 2003b), here adding two more years to the results. Third, steelhead smolt-age data from scales were used to detect the main response to nutrient addition (age and size), similar to nutrient experiments at the same river in the mid-1980s (Slaney et al. 2003). Further, as a key variable, we analyzed the steelhead smolt yield per spawner as a function of the number of spawners in the Keogh River, in comparison to the historic record.

A permanent counting fence is located at the mouth of the Keogh River, where a total count of coho salmon and steelhead smolts has been conducted each spring from April to June since 1976, including systematic subsampling for size and age. A description of the methodology of fish sampling, smolt enumeration, and estimation of overall capture efficiency by smolt marking is provided in Ward and Slaney (1988). Fence failures during spring floods were rare, lasted only 1–2 d, and numbers

were adjusted either by mark–recapture (partial trapping) or by interpolation between pre- and postflood counts of each species (e.g., McCubbing 2001).

Numbers of adult winter-run steelhead have been estimated at the counting fence by mark–recapture and, since 1997, independently assessed by an electronic counter verified by video records (McCubbing et al. 1999). Methods of population estimation were described in detail elsewhere (Ward and Slaney 1988). Briefly, total numbers of adult male and female steelhead were estimated separately by the adjusted Petersen estimate by marking upstream adults with an opercular punch and examining kelts during their downstream migration. During December to March, commencing in 1998, a Logie 2100C resistivity fish counter was also utilized to enumerate adults. Accuracy was tested on coho salmon adults in the fall and was greater than 90% (McCubbing et al. 1999).

Smolt yields from the nearby Waukwaas River, as an external reference watershed, were estimated from 1996 to 2003 based on mark–recapture estimates derived from operation of two rotary screw traps from mid-April to mid-June. The two 1.50-m traps were spaced approximately 500 m apart, above tidewater, with the upper trap utilized for marking and the lower trap used for recapture and enumeration, and sampling for size and age. Migrant coho salmon greater than 70 mm and migrant steelhead greater than 130 mm were defined as smolts when silver colouring was most evident. Details on marking (mainly caudal fin clipping) and estimation procedure were provided in Ward et al. (2003b).

Steelhead smolt recruitment per spawner was based on the total number of smolts manually counted, their age based on scale analyses, and tabulation by brood year of origin.

These data were utilized to estimate the number of smolts produced per spawner in comparison to the number of spawners contributing to their recruitment, as in Ward et al. (2003a, 2003b). Density, growth, and smolt yield of salmonid juveniles were analyzed by anova and t-tests. Smolt yields and smolts-per-spawner were utilized as the key response variable and tested by covariance analysis as described below because adults were affected by highly variable ocean conditions and, for coho, ocean fishing for salmon.

We tested for differences in smolt production under different watershed production regimes and among years of watershed rehabilitation. Therefore, we performed a statistical analysis to challenge the null hypotheses that the number of smolts produced per spawner did not differ among the four treatment classes (i.e., 1980s regime, fertilizer addition, 1990s regime, and WRP; Ward et al. 2003b). Our analysis structure was based on an initial scrutiny of our data that indicated that the smolt–spawner relationship for the Keogh River followed a Beverton–Holt formulation (Ricker 1975; Ward 2000). However, we modified the fundamental Beverton–Holt relationship to allow the intercepts and slopes of that relationship to potentially differ according to treatment, such that our formulation is

$$\frac{R_y}{S_{y-d}} = \frac{1}{\sum_{t=1}^{4} \beta_t Y_t + \sum_{t=1}^{4} \beta_{4+t} S_{y-d} Y_t} + \varepsilon_y$$

where R_y is the number of smolts leaving the river in year y and S_{y-d} is the number of spawners that produced these smolts d years in the past, where d can be 2 or 3. The Y_y represent the proportional contributions of each treatment effect in each year y. The coefficients to be estimated are the b_ts (units = $\left(\frac{S_{y-d}}{R_y}\right)$) which measure the intercepts for the four treatments, and the β_{4+t}s (units = $\left(\frac{S_{y-d}}{R_y}\right)$) which measure the
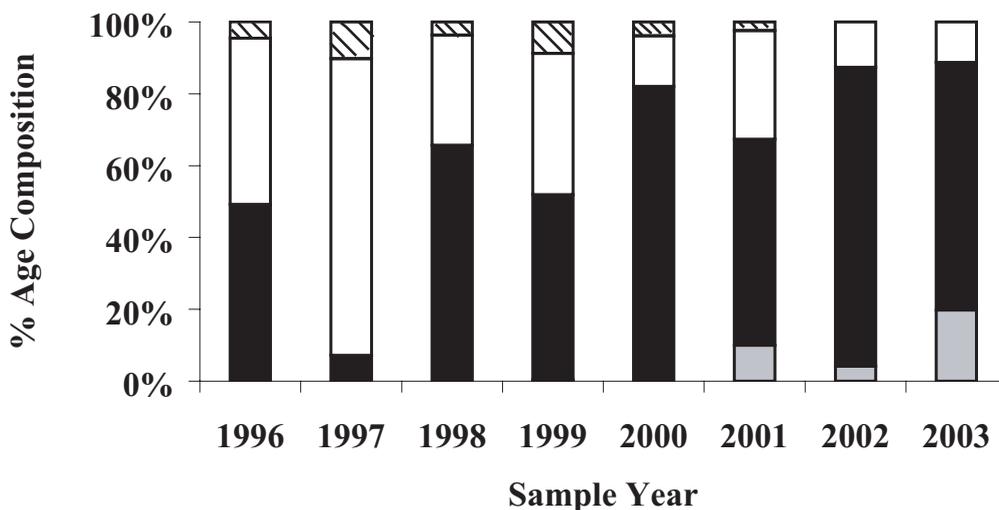
Figure 2. Percent composition of age-1 (gray bar), age-2 (black bar), age-3 (white bar), and age-4 (hatch bar) steelhead smolts in the Keogh River in 1996 and 1997 (no nutrient addition) and from 1998 to 2003 (nutrients added).

slope of the influence of the number of spawners on the number of smolts produced. Scrutiny of our data also indicated that prediction error variance appeared to be proportional to the predicted mean number of smolts per spawner. Given this apparent proportionality, and also that observed values for the number of smolts per spawner cannot be less than zero, we chose to represent the distribution of model error deviates, ε_y, with a gamma distribution. This required an additional model parameter, γ, a variance scalar, such that the variance of prediction error is represented by $\left(\frac{R_y}{S_{y-4}}\right)^2 \gamma$. We used an information–theoretic approach to judge the quality of model fit and selected the best model on the basis of lowest Akaike's Information Criteria corrected (AICc) for sample size (Burnham and Anderson 2002), then used covariance analysis to judge the statistical significance of our estimates of the β_t coefficients.

Results

The age of steelhead smolts was reduced by restoration treatments at the Keogh River while abundance increased. The proportion of younger steelhead smolts was altered in the Keogh River in 2001, with age-1 and age-2 smolts representing over 67% of the smolt yield, compared to an average age-2 composition of 32% in years of no nutrient addition (Figure 2). By 2002 and 2003, age composition showed a marked shift to smolts 1 year younger; 90% were age-1 and age-2. The calculated proportion of age-2 smolts in the Waukwaas River remained similar through the 1997–2001 period (Figure 3). The difference in the proportions of age-2 smolts from the Keogh River versus Waukwaas prior to the impact of nutrient addition (1997–1999) versus after addition (2000–2003) was significant ($p < 0.05$, anova). The proportion of age-3 smolts was significantly lower in Keogh than Waukwaas after 2000 ($p < 0.05$, anova).
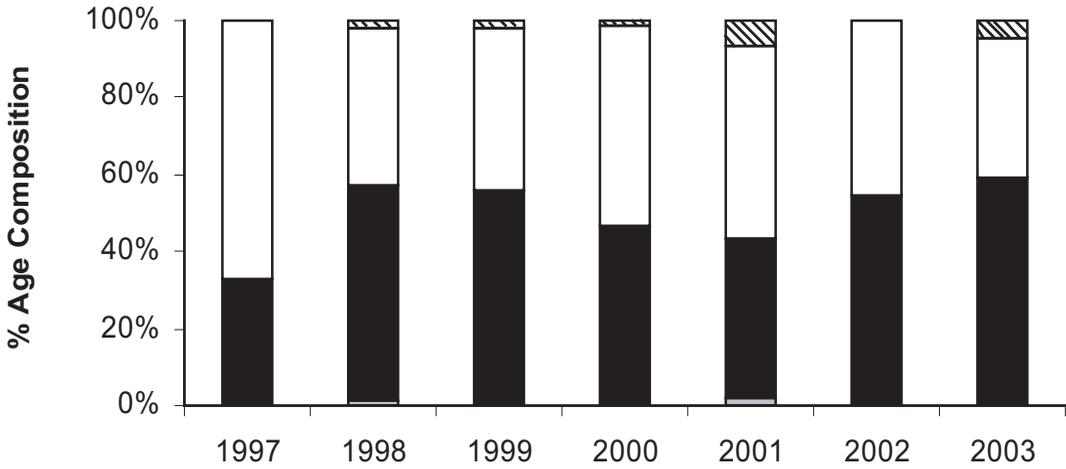
Figure 3. Proportional age composition estimates for Waukwaas River steelhead smolts, 1997–2003. Age-1 (gray bar), age-2 (black bar), age-3 (white bar), and age-4 (hatch bar).
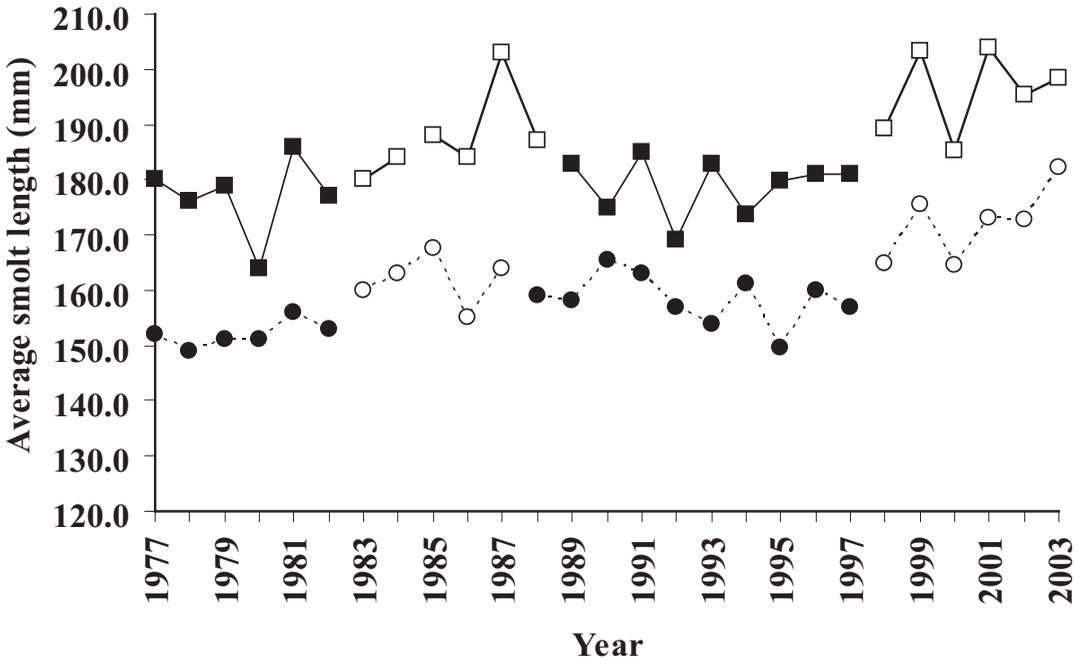

Figure 4. Mean length of 2-year-old (broken line, circles) and 3-year-old (solid line, squares) steelhead smolts. Open markers indicate years affected by nutrient addition at the Keogh River, British Columbia.
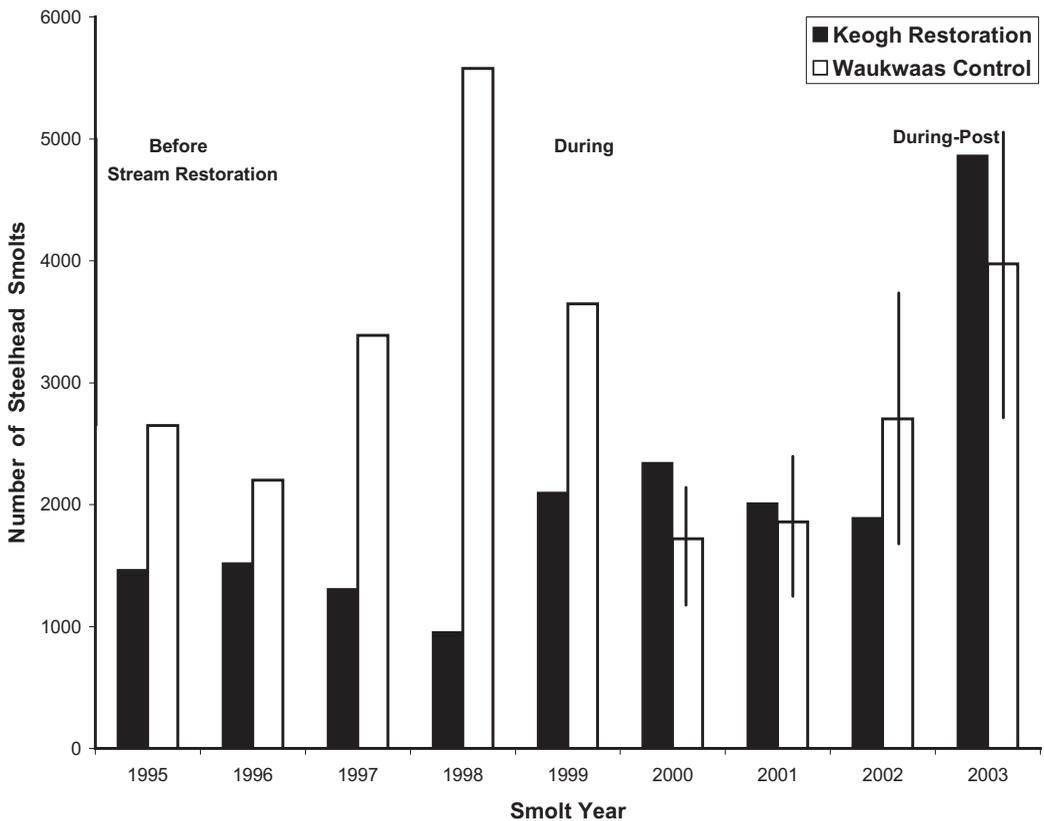
Figure 5. Steelhead smolt yield from the Keogh and Waukwaas rivers, British Columbia, from 1995 to 2003.

In years where partial or full-river fertilizer addition was undertaken on the Keogh River, smolt length-at-age was clearly increased (Figure 4). Age-2 smolts averaged 173 mm and age-3 smolts, 204 mm from 1998 to 2001 (Figure 4). Length-at-age of Waukwaas smolts remained stable through the 4 years; age-2 smolts averaged 165 mm and age-3 smolts, 187 mm, similar to Keogh smolts prior to nutrient addition.

Smolt yield reflected the watershed response of juvenile salmonids (Figures 5 and 6), but also the response to extreme low adult abundance. At the Keogh River, steelhead smolt yield increased in 1999–2001 to about 2,000 smolts after a pretreatment record low yield of less than 1,000 in 1998. Then, smolt yield elevated sharply to almost 5,000 in 2003, close to the historical average. In comparison, estimated yield on the Waukwaas River remained low at 1,859 fish, the second lowest in the six sample years, but developed an increasing trend to 2,800 and 4,000 in 2002 and 2003, respectively (Figure 5). The difference between steelhead smolt yield on the Keogh and Waukwaas rivers was significant ($P < 0.05$, single factor anova) for years when Keogh fish were influenced by restoration treatments (2000–2003). Mean difference in yield was higher by 355 smolts (SD = 907) at Keogh versus years prior to treatment effect (1995–1998) when the mean difference in yield was higher by 2,142 fish at Waukwaas
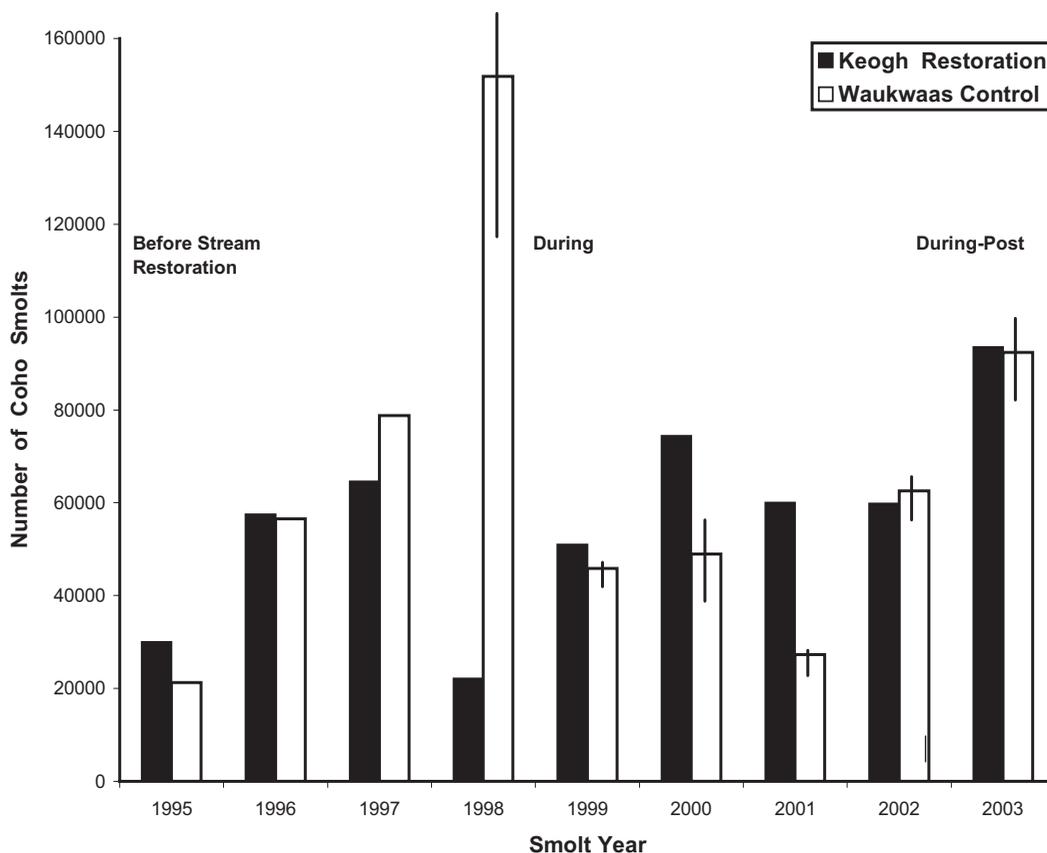
Figure 6. Coho smolt yield from the Keogh and Waukwaas rivers from 1995 to 2003.

(SD = 1,754). Yields from 1999 were treated as transitional and thus omitted from the analysis (i.e., nutrient additions were stepped up annually starting in 1997, thus smolts [majority were 2+] from treated areas were not expected until 1999 and later).

Coho smolt numbers rose steadily for both watersheds through the first 3 years of investigation, but fell sharply in the Keogh River in 1998. Thereafter, an increasing trend developed at Keogh, reaching 94,000 in 2003 or greater than 50% above the historical average (Figure 6). In the Waukwaas River, reductions in coho smolt yield in 1999 and 2000 were followed in 2001 by a further decline, but increased thereafter to a level similar to that of the Keogh River in 2003. On average, pretreatment differences (1995–1997) were

slightly higher at Waukwaas, by 1,514 smolts (SD=11,667). Posttreatment differences (1999–2003) were higher in favor of the Keogh River, by an average 13,585 fish (SD=20,874), but differences were insignificant ($P = 0.3$). Since coho were mainly 1-year-old smolts, the smolt yield in 1998 was considered transitional and omitted from anova.

A substantial shift in steelhead smolt recruitment per spawner in the Keogh River was a key response in the effectiveness evaluation (Figure 7). Pretreatment data from the 1990s indicated very low yield, with less than 2 smolts per spawner. This was rapidly exceeded under even partial treatment, when greater than 14 smolts per spawner were produced from the 1996 brood year. Further increases to 42 smolts per spawner occurred from the
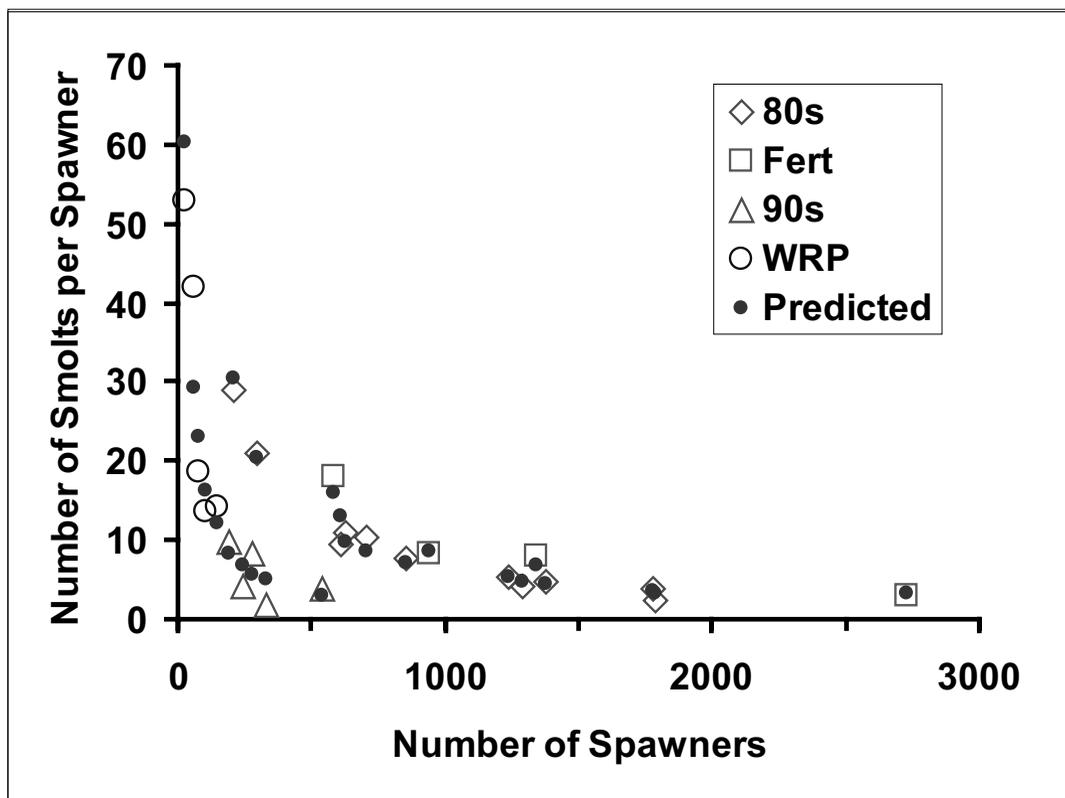
Figure 7. The relationship between the number of the steelhead smolts per spawner and the number of spawners in the Keogh River during the production regimes of the 1980s (diamonds) and the 1990s (triangles), during nutrient experiments in the mid-1980s (squares), and initial results during watershed restoration treatments to 2003 (circles). Our modified Beverton–Holt fit to these data (solid points) statistically distinguishes the 1980s and nutrient experiments from all other treatments, while the 1990s and initial watershed restoration treatments cannot be statistically distinguished from each other.

1997 brood year, and the highest yield in 26 years was recorded from the 1998 brood year (53 smolts per spawner). Coho yield was estimated at 9 and 21.5 smolts per spawner in 1998 and 1999, respectively, assuming 90% of smolts were 1-year-old. By 2002 and 2003, and associated with low adult escapements, coho smolts per spawner were much greater, or 52 and 33, respectively. Comparative data are not available from the Waukwaas River because spawners were not enumerated.

Based on lowest AICc, the best fit of our Beverton–Holt spawner–smolt relationship to our observed steelhead data retained the value

of all four intercept terms (β_t), $t = 1–4$, at zero. This indicates there was no significant difference in the mean level of steelhead smolt yield per spawner, independent of the number of spawners, among treatments. However, there were differences in the relationship between spawner numbers and smolt production among some treatments. During the 1980s, and under the fertilization regime, there was a significant relationship between steelhead spawner numbers and smolt production, with $\beta_5=1.65\times10^{-4}$ (*SE*: 1.47×10^{-5}) and $\beta_6=1.08\times10^{-4}$ (*SE*: 1.58×10^{-5}), respectively. In other words, significantly more

smolts were produced per spawner during years when nutrients were added to the stream in the 1980s. During the 1990s and the WRP regime, this relationship changed and was significantly different from the relationship identified for the 1980s and under the nutrient-addition regime (Figure 7). However, no statistical distinction could be made between the 1990s and the WRP regime, thus, $\beta_7 = \beta_8 = 5.89 \times 10^{-4}$ (*SE*: 5.17×10^{-5}). Note that due to the reciprocal structure of the Beverton–Holt spawner–smolt relationship, larger values of β_t indicate less smolt production per spawner. The model prediction error was approximately 27% (i.e., $100\sqrt{\gamma}$) of the predicted values.

Discussion

Increased smolt yield was attributed to ecosystem rehabilitation treatments. However, statistical comparisons of trends in smolt yields between the two rivers were perhaps weakened by the impact of ongoing climate change and likely differences in adult escapement between the Keogh River, draining to the east and into Queen Charlotte Strait, and the Waukwaas River, which drains into Quatsino Inlet and then to the west coast of northern Vancouver Island. Welch et al. (2000) and Smith and Ward (2000) noted major differences in survival of steelhead stocks from the east versus the west coast of Vancouver Island. As a consequence, adult recruitment to the Keogh River was below capacity as was subsequent steelhead fry recruitment in the Keogh River (Ward et al. 2003a, 2003b). Adult steelhead decreased to less than 100 spawners in the Keogh River by 2001, while two- to threefold this number were required to effectively recruit the entire river length with enough fry to produce the full benefits of the habitat rehabilitation (i.e., at or near capacity smolt yield). Experiments of this nature are best conducted when yields are at or near capacity

production, thus avoiding the statistical difficulties of this study where definition of the recruitment relationship at low spawner levels confounded the analysis.

Trends of instream juvenile abundance and smolt yield in the west coast Waukwaas River likely reflected higher abundances of adult steelhead, based on estimated summer fry abundances and local observational records of adults from catch-and-release angling. The abundance of coho fry and smolts at Keogh appeared to exceed or equal that of the Waukwaas River, despite a reduction in coho adult escapement after 1998 in the Keogh River. Despite low recruitment of steelhead fry at the Keogh River, the abundance of steelhead parr in reaches treated with both restoration techniques were either higher, or at least similar, to those observed in the untreated Waukwaas River (Ward et al. 2003a, 2003b). Thus, Keogh restoration appears to have dramatically and persistently improved fry-to-parr survival rates (perhaps by as much as threefold) of steelhead. By 2003, at the Keogh River, coho and steelhead smolts increased to near and well above their historical averages, respectively.

Trends in fish age in the Keogh River indicated positive effects of watershed restoration that were incrementally increased over 5–6 years, although tempered with changes in fry density related to low and varied adult escapements. Accordingly, there has been a marked shift in dominant smolt age from age 3 to age 2, while increasing average smolt size at age and maintaining the overall average smolt size. The smolt age and size-at-age response to the restoration treatment is unequivocal and was similar to that detected earlier in 1980s after 3 years of experimental whole-stream enrichment, when steelhead smolt yield increased on average by 62% (Slaney et al. 2003).

Length at age trends in steelhead smolts from the Keogh River increased during nutrient addition to 2003, with evidence of an additional marine-derived nutrient signature due to improved pink salmon escapement (highly abundant in even years). Ward and Slaney (1988) suggested this may have been the case in the past, based on annual variation in the shape of the length frequency distribution of steelhead smolts. Steelhead smolt length-at-age increased again in 2001 for both age-2 and age-3 smolts to among the highest recorded in 27 years of study on the Keogh (Ward 2000; Slaney et al. 2003). In 2003, mean length increased even more than in 2001 among age-2 smolts, even though they comprised nearly 90% of the steelhead smolts and neared historic average abundance. An increase in length and weight of juvenile steelhead apparently improved overwinter survival, culminating in sustained increases in smolt yield. Historically, larger steelhead smolts have survived at higher rates in the ocean, producing a greater escapement of adult steelhead upon return than smaller smolts (Ward and Slaney 1988; Ward et al. 1989).

As the key response indicator, smolt yields per spawner have increased substantially up to 2003. Steelhead smolts per spawner in the Keogh River have risen from the dangerously low of less than 3 smolts per spawner from the 1996 brood (i.e., below adult replacement at 4% smolt-to-adult survival) to less than 53 smolts per spawner from the 1998 brood year, the highest production per spawner on record (Ward 2000). Thus, there were continued high levels of production from low adult escapements, as expected in a Beverton–Holt recruitment relationship. While these values were high by Keogh standards, Cramer et al. (2003) reported a range from 8 to 223 smolts-per-spawner for summer-run steelhead of the more productive Yakima River, Washington, a tributary of the Columbia River, for the period of 1985–1997.

Smolt recruits during the 1990s indicated a new recruitment relationship, or lower productivity and capacity within a different climate regime, as Welch et al. (2000) had suggested for adult steelhead returns after 1989. We could not detect a significant statistical difference in smolt recruitment from years of watershed restoration and that obtained in the 1990s regime. However, definition of the shape of the recruitment curve at both very low and high spawner abundance was poor from data of the 1990s, although clearly near the replacement line (Ward 2000). The statistical testing of WRP results (Figure 7) with this data was confounded by comparison of values at different spawner densities. Nonetheless, the most recent WRP values were above recruitment replacement (25 smolts per spawner at 4% smolt-to-adult survival) whereas previous points (1990s) were not. Thus, the restoration work may have provided sufficient recruitment of steelhead smolts to offset poor survival at sea and assist in population viability.

Historically, approximately 90% of coho smolts have migrated seaward at age 1, thus, the 1998 brood year produced about nine smolts per spawner. This increased significantly for the 1999 brood year with an estimate of 19 smolts per spawner. By 2002 and 2003, coho smolts per spawner increased substantially to 52 and 33, respectively. In comparison, coho smolt recruitment in 1999 averaged 83 smolts per female spawner at Black Creek, near Courtney on the east coast of Vancouver Island. The latter is a highly productive stream in an agricultural setting, with abundant coho habitat (K. Simpson, DFO, Nanaimo, personal communication).

Regardless of high variability to date in smolt yields, the magnitude of a recovery trend of

all Keogh salmonid fish stocks, combined with coinciding size and age changes of smolts, suggested that ecosystem recovery was advancing. Although lacking statistical controls, increases were also apparent in Dolly Varden *Salvelinus malma* smolts (sevenfold) and adults (threefold) of the Keogh River (McCubbing and Ward 2003). The apparent recovery trend in smolt and adult yield of Dolly Varden char from 1998 to 2003 provided additive support that recovery was linked to improved freshwater conditions, since this species migrates for only a few months at sea before returning (Smith and Slaney 1980). Thus, negative environmental factors should be buffered, in part, by stream habitat rehabilitation and nutrient replacement. Thereby, restorative watershed treatments, combined with occasional years of improved ocean survival, may sustain salmonid populations in coastal streams against poor ocean conditions. Broader implications are that protection of the spawning stock, habitat protection and rehabilitation, and a better understanding of the limits to production in both the freshwater and the marine environment remain of profound importance. To date, whole-river restoration appears to be a useful tool towards mitigation of logging impact and adaptation to climate change for wild salmonids on the west coast of Canada.

Reconciling fisheries with conservation through ecosystem restoration, now and in the future, will need to incorporate climate considerations, even when fisheries have been temporarily closed. Can we get more fish from habitat rehabilitation in freshwater? Our results suggest it may be possible, but we could not yet confirm recruitment benefits from whole watershed treatments, largely because climate conditions worsened through the course of the work in both freshwater and the ocean, such that the numbers of spawners declined to levels that were far below previous

conditions. There remains uncertainty in the steelhead smolt recruitment we currently may expect at higher levels of spawners. Regardless, the weight of evidence, from work on steelhead and coho abundance and growth in stream, as well as the positive changes in smolt age and results of previous experiments with nutrient addition and habitat alteration studies in the 1980s, suggested that smolt yields would have been much lower otherwise, to the point where the steelhead population would likely now be far below recruitment replacement, and near local extirpation. The hope is that habitat improvements may assist with population viability until climate conditions improve for these salmonids, or these fish adapt effectively.

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