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ARTICLE

Watershed-scale effectiveness of floodplain habitat restoration for juvenile coho salmon in the Chilliwack River, British Columbia

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Abstract: Although billions of dollars have been spent restoring degraded watersheds worldwide, watershed-scale studies evaluating their effectiveness are rare. To mitigate damage from past logging activities, the floodplain of the upper Chilliwack River watershed (~600 km²) was extensively restored from 1996 to 2000 through off-channel habitat restoration. The contribution of restored habitat to watershed-scale production of wild coho (*Oncorhynchus kisutch*) smolts was estimated through an extensive mark–recapture program in 2002. 27%–34% of the production of the estimated 247 200 out-migrating coho smolts could be attributed to the 157 000 m² of newly created habitat. Area-based habitat models from the literature performed reasonably well in predicting smolt production from restored habitat, providing an acceptable first-order approach for evaluating production benefits of restoration. The costs of smolt production integrated over 30 years ranged from US$0.69–US$10.05 per smolt, falling within the range of hatchery production costs reported elsewhere (typical cost of ~US$1.00 per smolt) at the most cost-effective restoration sites. This study demonstrates that large-scale habitat restoration can effectively enhance fish production at a watershed scale, at a cost that may be comparable to hatchery smolt production.

Résumé : Bien que des milliards de dollars aient été dépensés à restaurer des bassins versants dégradés dans le monde entier, les études à l'échelle du bassin versant qui s'intéressent à l'efficacité de ces actions sont rares. Afin d'atténuer les dommages causés par les activités de coupe de bois passées, la plaine inondable du bassin versant du cours supérieur de la rivière Chilliwack (~600 km²) a fait l'objet d'une vaste restauration de 1996 à 2000 reposant sur la restauration d'habitats à l'extérieur du chenal. La contribution des habitats restaurés à la production de saumoneaux sauvages de saumons cohos (*Oncorhynchus kisutch*) à l'échelle du bassin versant a été estimée dans le cadre d'un vaste programme de marquage–recapture en 2002. De 27 % à 34 % de la production d'un total estimé de 247 200 saumoneaux cohos ayant migré vers la mer peut être attribuée aux 157 000 m² de nouveaux habitats créés. Les modèles d'habitat reposant sur la superficie recensés dans la littérature prédisent raisonnablement bien la production de saumoneaux d'habitats restaurés, fournissant une approche de premier ordre acceptable pour évaluer les avantages de la restauration en ce qui concerne la production. Les coûts de la production de saumoneaux intégrés sur 30 ans allaient de 0,69 $US à 10,05 $US par saumoneau, soit dans la fourchette des coûts de production en écloserie rapportés dans d'autres ouvrages (coût typique de 1,00 $US par saumoneau) pour les sites restaurés les plus efficaces en terme de coûts. L'étude démontre que la restauration d'habitats à grande échelle peut accroître efficacement la production de poissons à l'échelle du bassin versant à un coût qui pourrait se comparer à la production de saumoneaux en écloserie. [Traduit par la Rédaction]

Introduction

Conservation concerns over declining fish populations (e.g., Slaney et al. 1996) and widespread degradation of aquatic habitats throughout the world have led to increased recovery efforts for fish populations (Roni et al. 2005, 2008). Pacific salmon species are of particular interest in western North America because of their commercial, ecological, and cultural value (Slaney et al. 1996; Cederholm et al. 1999; Gende et al. 2002). Salmon populations have declined severely since the 1800s as a consequence of overharvest, dams, and widespread habitat degradation from land use activities, including mining, logging, and agriculture, resulting in many runs being listed as threatened or endangered (Nehlsen et al. 1991; Ruckelshaus et al. 2002; Lackey et al. 2006). To address widespread population declines, habitat restoration efforts have become popular throughout the globe as a strategy to mitigate the negative effects of habitat degradation (National Research Council 1992; Cowx and Welcomme 1998). An estimated US$14 to US$15 billion has been spent on freshwater habitat restoration in the USA alone since 1990, averaging roughly US$1 billion a year (Bernhardt et al. 2005).

Despite the billions of dollars spent annually on watershed restoration, the benefits of this investment are poorly documented in terms of the biological response to habitat change (e.g., increases in fish biomass or production). Credible large-scale studies examining the effectiveness of restoration are rare (Paulsen and Fisher 2005), and many restoration projects keep poor records of construction and maintenance costs (Bernhardt et al. 2005). With the lack of statistically rigorous evidence, there has been a dependence on models and expert opinion for effectiveness evaluation (Sutherland et al. 2004), which makes it challenging to assess the benefits of any investment or competing recovery techniques. Consequently, there has been recognition of an acute need for

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effective postconstruction assessment and monitoring (Bash and Ryan 2002; Downs and Kondolf 2002).

Development on river floodplains is a widespread land use impact that has greatly reduced the abundance and complexity of riverine habitat worldwide (Beechie et al. 1994; Sparks 1995). Roads, levees, channel straightening and hardening, and cumulative impacts from urban and agricultural development all tend to isolate seasonally or permanently wetted floodplain habitats from the main channel. Floodplain (off-channel) habitats encompass sloughs, side channels, beaver ponds, and other permanently or seasonally flooded areas and represent important rearing habitat for juvenile salmonids and other fish and amphibian species (Beechie et al. 1994; Blackwell et al. 1999; Pollock et al. 2004). This relatively slow-water habitat is especially important for juvenile coho salmon (*Oncorhynchus kisutch*), as they typically use it for both rearing and overwintering (Morley et al. 2005). Consequently, off-channel habitat is now regularly constructed to increase productivity for juvenile coho salmon throughout western North America (Slaney and Zaldokas 1997; Saldi-Caromile et al. 2004; Roni et al. 2006). Although various studies have documented the use of these restored habitats by juvenile coho or trout (e.g., Cederholm et al. 1988; Picard et al. 1998; Roni et al. 2010), the overall contribution of restored habitat to total production in a watershed, particularly the production of out-migrating smolts, is rarely known (with some notable exceptions, e.g., Solazzi et al. 2000).

This study evaluates the effectiveness of habitat restoration in the Chilliwack River watershed in coastal British Columbia, Canada, which is broadly representative of coastal rivers in that much of the valley bottom has been impacted by extensive historic and contemporary logging activities, resulting in reduced channel complexity and extensive loss of off-channel habitat. As a consequence, Fisheries and Oceans Canada in conjunction with the BC Ministry of Environment Watershed Restoration Program initiated construction of seven major off-channel habitat restoration projects in the upper Chilliwack River watershed between 1996 and 2000, creating a total of 157 000 m² of new habitat. Each project involved construction and reconnection of floodplain habitat to the main stem, intended primarily to restore rearing habitat for juvenile coho salmon; however, two of the restoration sites also included construction of extensive spawning habitat for pink salmon (*Oncorhynchus gorbuscha*), and all sites were used by various life stages of coho, steelhead (*Oncorhynchus mykiss*), or Dolly Varden char (*Salvelinus malma*). In spring of 2002 an extensive marking program was carried out using smolt weir traps installed at the outlets of five of the restoration sites, with smolt recapture at a rotary screw trap located downstream on the main stem to estimate the contribution of fish produced in restored habitat to total wild coho smolt production.

Objectives were to determine production from restored habitat and to examine the degree to which this large-scale restoration increased overall production of coho salmon smolts at the watershed scale. Given the difficulty and considerable effort involved in a watershed-scale effectiveness assessment like this, our second objective was to compare the accuracy of existing area-based habitat capacity models for predicting coho smolt production with empirical estimates of production from restored habitat, so as to validate simpler and more cost-effective approaches for assessing restoration effectiveness. Our final objective was to use estimates of the costs of habitat construction to compare the costs of smolt production between restored habitat and hatcheries, so as to evaluate the cost-effectiveness of habitat restoration relative to hatchery production.

Methods

Study area

The study was conducted in the upper watershed of the Chilliwack River, British Columbia, upstream of the Chilliwack River Hatchery (Fig. 1). The upper watershed includes Chilliwack Lake (12 km²) and a total of 69 linear kilometres of accessible mainstem and tributary habitat in both the United States and Canada. The Chilliwack River originates in Washington State, where the majority of the first 20.5 km of anadromous main stem upstream of Chillwack Lake is pristine old-growth forest within the North Cascades National Park. Much of the habitat downstream of Chilliwack Lake on the Canadian side is second-growth forest that has been heavily impacted by past logging activities, resulting in reduced woody debris recruitment, increased sediment inputs, and decreased channel complexity (Cleary 2001). Road building and logging on the floodplain has also contributed to isolation of off-channel habitat (Picard et al. 1998; Blackwell et al. 1999). The mainstem Chilliwack between the hatchery and lake is a relatively high power boulder–cobble channel ranging from 40 to 80 m bankfull width in a variably confined valley bottom, with a mean annual discharge of 66 $m^3 \cdot s^{-1}$. The entire watershed is an important producer of all seven species of Pacific salmon and supports an intensive freshwater sport fishery. Considerable angler effort is directed toward coho salmon, which are sustained in large part by production from the Chilliwack River Hatchery.

This study focused on production of wild fish in the upper watershed (fish are not stocked upstream of the hatchery; the "upper watershed" refers to the area upstream of the hatchery, where the downstream screw trap was located; Fig. 1). Like most anadromous salmon, adult coho spawn in freshwater streams and rivers in the fall, and fry emerge from the gravel in late spring; juvenile coho typically rear for a summer in fresh water, overwinter in suitable habitat, and then migrate to the ocean as smolts the following spring before returning to spawn as 3-year-old fish. Although there is suitable mainstem spawning habitat downstream of the hatchery, there is limited mainstem coho spawning habitat in the 14 km reach between the hatchery and the lake (Fig. 1), where the main stem is a fast-flowing boulder–cobble channel with a high velocity thalweg (Fedorenko 2002). Aside from several natural side channels and the lake outlet, most spawning in this reach of the upper watershed is confined to tributaries or constructed off-channel habitat (Fedorenko 2002).

Habitat restoration became a focus in the watershed during the early 1990s as part of the BC Watershed Restoration Program, a partnership between the provincial Ministry of Environment, Ministry of Forests, and Fisheries and Oceans Canada (Cleary 2001). Much of the restoration involved building or reconnecting off-channel habitat on the river floodplain, and this study focuses on determining the specific cumulative production benefits from the seven major side-channel habitats constructed in the upper watershed during this period.

Side channels were constructed by diverting river water into a series of interconnected stream and pond complexes at suitable sites on the river floodplain (Fig. 2; Picard et al. 1998; Cleary 2001). Upper Bulbeard, Lower Bulbeard, Angelwing, Millenium, and Centre Creek Camp sites were designed to be primarily rearing habitat for juvenile coho, with inclusion of spawning habitat sufficient to saturate constructed rearing habitat (Table 1). The Centennial and Yukalap complexes were designed to be mostly spawning channels for pink salmon, with less than 50% of total wetted area considered to be good quality rearing habitat for juvenile coho. All of the sites represented newly constructed habitat, with the exception of Millenium Ponds, where a preexisting beaver pond complex was greatly enlarged. Restored habitat was characterized by two habitat extremes: slow-water ponds, or flowing channels suitable for spawning as well as rearing (Cleary 2001; Rosenfeld et al. 2008), although most sites contained a mixture of both. Most large ponds were created by enlarging existing ponds through the addition of downstream berms, although some ponds were created through excavation, primarily at Centennial Channel. All side channels incorporated deeper pond habitat (maximum depths in excess of 2 m) suitable for overwintering. Constructed habitat generally

Fig. 1. Chilliwack River watershed showing locations of restored off-channel sites (1–5) and the location of the downstream screw trap (ST) for catching out-migrating smolts in the mainstem. The broken line indicates the watershed boundary. 1, Angelwing side channel; 2, Millenium Ponds side channel; 3, Centennial and Upper and Lower Bulbeard side channels; 4, Centre Creek Camp side channel; 5, Yukalup side channel.

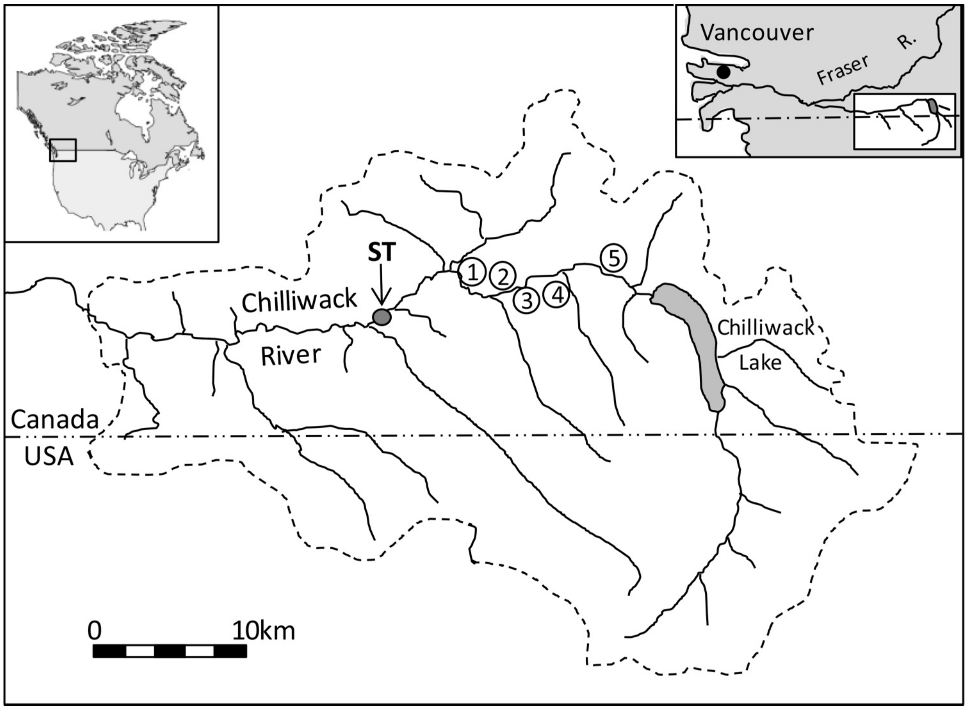
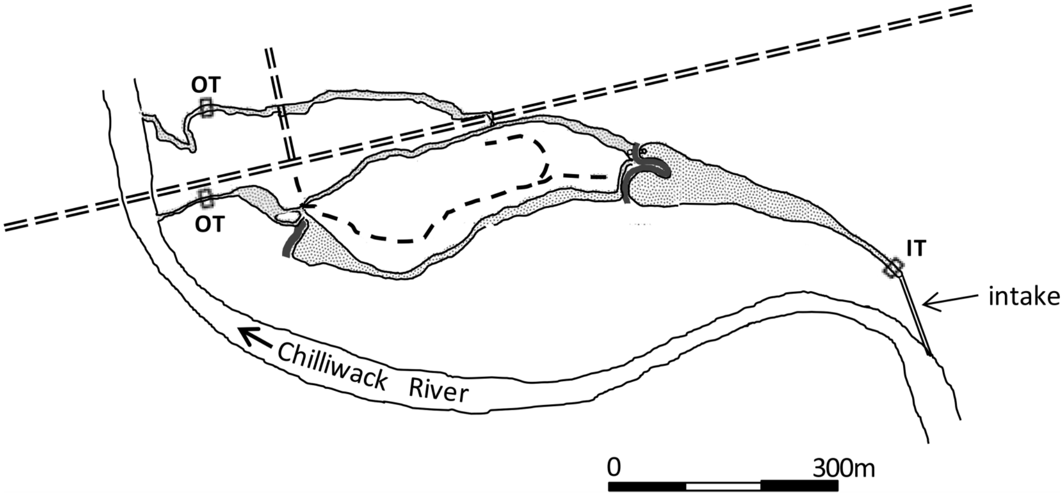


Fig. 2. Plan view of a typical side channel (Angelwing). Grey stippled area indicates side-channel habitat, and thick lines downstream of ponds represent berms. Parallel broken lines are main roads, and the single broken line is an old skid road. The location of the inlet smolt trap immediately below the 60 cm diameter intake pipe is indicated by IT; OT indicates the locations of the two outlet traps, which were placed some distance above the mainstem Chilliwack River confluence to prevent back-flooding of traps during high water.



followed natural drainage patterns and abandoned side channels on the floodplain or historical floodplain (benches).

Coho smolt production estimates from restored habitat using downstream weir counts

To determine the number of out-migrating smolts produced from restored habitat, converging downstream weir traps were used at Upper Bulbeard, Lower Bulbeard, Angelwing, Millenium, and Centennial restoration sites. Each downstream weir trap consisted of 1 m by 2.5 m wooden panels screened with 0.5 cm × 0.5 cm galvanized wire mesh grid, a 15 cm diameter plastic entrance pipe, and a welded aluminum trap box with screened sides. Weirs were installed during 25 March to 8 April 2002; two weirs were placed at the Angelwing site as there were two outlets. All traps were operational from 9 April to 14 June. Weirs were thoroughly cleaned and inspected for damage each day and repaired as necessary.

All captured fish were identified to species and fork length measured to the nearest millimetre. Out-migrating fish were classified as smolts using a 70 mm length threshold (i.e., fish less than 70 mm were considered to be parr that were redistributing in the watershed rather than smolting in their first year, thereby supporting conservative estimates of smolt production). The inlet flows at Upper Bulbeard, Lower Bulbeard, and Millennium were

Table 1. Characteristics of restoration sites in the upper Chilliwack River valley, including the year when restoration was completed, site length, area, mean female adult spawner returns from trap counts from 1998 to 2000, and predicted female spawners needed to fully seed juvenile rearing habitat (after Reeves et al. 1989).

Site	Date of construction	Length (km)	Total area (m^2)	Spawning area (m^2)	Observed spawners	Predicted saturated spawners
Centennial	1996	2.1	30 100	4 300[a]	—	—
Upper Bulbeard	1996	1.8	17 500	2 500[a]	360[b]	431[b]
Lower Bulbeard	1998	3.7	58 000	8 200[a]		
Angelwing	1998	2.1	11 200	2 050	157	64
Millennium	2000	3.1	42 000	2 000	302	240
Yukalap	1997	0.5	4 400	2 000	64	25
Centre Creek Camp	2000	1.2	6 500	1 100	30	37

[a] Prorated based on a combined estimate of spawning habitat area for Centennial and Upper and Lower Bulbeard channels.

[b] Spawner counts for Upper and Lower Bullbeard are combined.

screened during the smolt out-migration to prevent downstream migrants produced in the upper (natural or mainstem) habitat from mixing with those from the restored site and inflating smolt production estimates. Because of the large number of smolt traps that had to be maintained during the spring of 2002, it was not possible to install similar traps to exclude smolts from water flowing into Centennial and Angelwing side channels. Instead, smolt counts from traps installed at these side-channel intakes in 1999 and 2000 (Fisheries and Oceans Canada, unpublished data) were used to correct production estimates (i.e., by subtracting the mean number of smolts entering the side channels through the river intakes based on the previous year's data). Cumulative smolt counts at side-channel intakes were generally low (i.e., on the order of ~4% of total out-migrating smolts).

Coho smolt production estimates from restored habitat using minnow trap mark–recapture

Because the logistic demands of operating multiple traps limited the number that could be installed, and marking all out-migrating fish is not essential for a stratified population estimate (Arnason et al. 1996), we estimated coho presmolt abundance in Yukalap and Centre Creek Camp sites using mark–recapture rather than smolt traps. Smolts were initially captured at Center Creek Camp on 12–13 March 2002 and at Yukalap on 26–27 March using wire mesh minnow traps baited with 2 g of preserved roe and set for 24 h. Smolts were anesthetized with dilute clove oil dissolved in ethanol, counted, and marked by clipping a very small portion of the upper caudal fin. Fish were allowed to recover, then released uniformly throughout each restored habitat. Smolts were recaptured using 50 wire mesh minnow traps on 25 and 26 March at Centre Creek Camp and 3 and 4 April at Yukalap. The Peterson formula (Seber 1982) was used to estimate population size and 95% confidence intervals. We assumed that the very small upper caudal fin clip had regrown by the time the rotary screw trap (for capturing all downstream migrants) was operational (16 April to 7 June). This assumption is supported by the observation that upper caudal fin clip marks do not appear in the rotary screw trap until 14 May, after smolts from the other sites had been marked with this tag (refer to online supplementary data, Tables S1 to S3[1]). Because production from Yukalup and Centre Creek Camp side channel was small compared with the other sites, smolts from these two sites were not marked for the stratified population estimate (where marking of fish serves the function of providing an estimate of the downstream screw trap capture efficiency).

Marking fish from restored habitat

The mark–recapture design was stratified by time (a different mark was use on fish captured at all weirs over approximately weekly time intervals); stratification allows for more precise population estimates because it permits both capture probability and the proportion of fish marked to vary over time (Arnason et al. 1996). Out-migrating smolts trapped at weirs were batch-marked with a different mark approximately every week (Tables S1 to S3[1]) by applying a subdermal tattoo with a Pan-Jet dental inoculator (Herbinger et al. 1990) or a small fin clip on either the upper or lower lobe of the caudal fin. Tattoos were used for the first two marking periods. Upper and then lower caudal clips were used at the peak of migration for ease of application and identification. Upper then lower tattoos were used again for the last two batches. To mark smolts, fish were anesthetized with a bath of dilute clove oil dissolved in ethanol, marked, placed in a recovery bucket that was aerated with a battery operated pump, and released after they had recovered from the marking process. Fish that showed signs of injury during handling (through trapping, dip-netting, etc.) were not marked to prevent mortality en route to the downstream screw trap from inflating the population estimate.

Recovery of marked fish to estimate total smolt production

Recovery of marked smolts at a downstream rotary screw trap was used to estimate trap capture efficiency, and in conjunction with capture of unmarked smolts provided an estimate of the population size of outmigrants from the entire upper watershed (restored and unrestored habitat combined). The 2.0 m diameter rotary screw trap was installed in the upper Chilliwack River main stem (54.6391°N, 59.8917°E) adjacent to the intake for the Chilliwack River Hatchery (Fig. 1) and was operational from 16 April to 7 June. The rotary screw trap was suspended in the main river flow from a welded aluminum boom bolted to the deck of the hatchery intake. A pulley system using high tension climbing rope was used to winch the trap into place for fishing or cleaning. All captured fish were identified to species, juvenile coho were counted and recorded as unmarked or marked smolts, and the type of mark was identified. From the downstream weir trap counts it was known that 9% of the marked smolts migrated out either before or after the rotary screw trap was in place, necessitating an adjustment for this sampling bias (described below).

Data analysis

Mark–recapture data from the rotary screw trap were analyzed using the Stratified Population Analysis System (SPAS; Arnason

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0189.

et al. 1996; available from www.cs.umanitoba.ca/~popan/ using six (~weekly) temporal strata. SPAS provides a likelihood-based mark–recapture population estimate, but allows the user to divide (stratify) marks and recaptures by different time intervals, allowing for the detection of temporal variation in recapture probability (Arnason et al. 1996). Because the data were stratified by time, a maximum likelihood Darroch estimate was used to calculate the population of the entire watershed (i.e., from both natural and restored habitat). Direct counts from the five downstream weir traps and the minnow trap mark–recapture estimates from Yukalup and Centre Creek Camp side channels were combined to estimate total smolt production from restored habitat. This number was then divided by the stratified population estimate for the entire watershed to calculate the proportion of coho smolts produced from restored habitat within the upper Chilliwack watershed.

The mark–recapture population estimation approach involved several key assumptions. First, it was assumed that marking does not affect the capture probability of fish at the downstream screw trap. This is reasonable, since marks were small and minimally invasive, only visibly healthy or uninjured fish were marked, and fish were generally not recaptured for several days after marking, providing adequate time for recovery from handling. Tag loss between marking and recapture was also assumed to be minimal, which is realistic since most fish were recovered within 10 days. It was further assumed that mortality was minimal en route to the downstream screw trap. Some unknown level of mortality and tag loss were likely present, but this would contribute to an underestimate of trap efficiency, resulting in an overestimate of the wild smolt population and therefore ensuring a conservative estimate of the proportion of smolts from restored habitat (which was estimated independently based on counts from outlet traps and minnow trapping). Finally, equal capture probability of smolts from natural and restored habitat is also implicit.

Accounting for the potential contribution of mainstem fish to off-channel smolt production

Because side-channel habitats are open to immigration, some of the smolts captured in side-channel outflow traps could represent mainstem production (i.e., individuals that reared in the main stem but overwintered in off-channel habitat). The most robust study design for documenting changes in production following watershed restoration is a before–after control–impact (BACI) design, where watershed-scale smolt production is measured before and after restoration (e.g., Solazzi et al. 2000). Measuring annual smolt out-migration in the main stem before and after upstream restoration would eliminate concerns about how movement from the main stem into side channels might bias interpretation of side-channel out-migration. However, resource limitations precluded a multiyear before–after assessment in this study. Consequently, the assumptions underlying our smolt trap data need to be carefully assessed if production is to be attributed to newly created habitat with confidence. In this section we consider the potential for movement of fish into restored habitat to inflate estimates of production from restored habitat. We then describe approaches used to estimate the proportion of smolt production of potential mainstem origin, to provide a more robust assessment of the likely contribution of restored habitat to total watershed-scale production.

Skeptics rightly question the reliability of observed use of restored habitat as evidence of increased productive capacity, since colonization of new or restored habitat may indicate redistribution of fish rather than a reach-scale population increase (Gowan et al. 1994; Riley and Fausch 1995; White et al. 2011). This is a reasonable criticism in terms of rigorous effectiveness assessment; however, the assumptions implicit in this scenario warrant careful consideration. Movement of fish into newly created habitat indicates that the new habitat has higher intrinsic quality than vacated habitat (e.g., Hansen and Closs 2009) or lower density-dependent limitation of growth (i.e., competition). Colonization of new habitat may represent a loss of production from vacated habitat, but only if the previously occupied habitat is under-recruited. In other words, an increase in rearing habitat will have no population response if the overall population is recruitment-limited (e.g., through insufficient spawning habitat or poor marine survival; Reeves et al. 1989). This is primarily a concern for restoration that creates rearing habitat but not spawning habitat and should not be an issue if restoration includes sufficient spawning habitat to saturate newly constructed rearing habitat.

If newly created off-channel habitat is saturated with juvenile recruits from in situ spawning within constructed side channels, then high juvenile abundance in off-channel habitat will reduce realized habitat quality (sensu Kramer et al. 1997) and act as a partial barrier to mainstem immigrants for summer rearing (but not for fall immigrants seeking overwintering habitat, which may be largely density-independent in deep off-channel pond habitat). All off-channel habitats were designed to have sufficient spawning habitat to fully recruit available rearing habitat (Table 1). However, to infer with confidence that smolt production from constructed side-channel habitats represents an increase in overall system productivity (rather than a redistribution of fish), it is important to demonstrate that in situ spawning is sufficient to fully recruit newly constructed side channels.

To evaluate whether side-channel habitat was likely saturated, we compared observed spawner counts in constructed habitat with the estimated number of adult female coho spawners required to saturate (fully seed) juvenile habitat using the formula from Reeves et al. (1989), where the optimum number of female coho per kilometre of stream equals [total rearing area / (linear kilometres of stream × area per smolt × egg–smolt survival × fecundity)]. Area per smolt, egg–smolt survival, and fecundity were set at 3–3.5 smolts·m^{-2}, 0.02, and 2500 eggs per female, respectively, after Reeves et al. (1989).

Precisely estimating the proportion of off-channel parr and smolt production that is of mainstem origin would require operating fish traps at side-channel inlets and outlets throughout the year, which was not feasible at multiple sites. However, the mean number of juvenile recruits of mainstem origin can be estimated based on smolt production in the first year of side-channel operation, before the progeny of the first spawning fish have matured. Because spawning takes place in the first year of side-channel operation, parr that colonize in the first year are of mainstem origin, and recruits from in situ spawning only appear in smolt traps in the second year after construction. Consequently, we estimated the proportion of smolts of mainstem origin based on the observed increase in smolt production in the second year following side-channel construction, for the limited subset of side-channel habitats where this data was available. We were able to obtain suitable serial annual data on smolt out-migration from four side-channel habitats in British Columbia: Worth Creek side channel (Norrish Creek basin), Upper Paradise side channel (Cheakamus River), Mamquam side channel (Mamquam River; Sheng et al. 1990), and Upper Bulbeard side channel (Chilliwack River). The percentage of smolts of mainstem origin was calculated as the first year outmigrant count divided by the mean outmigrant count in subsequent years when offspring from in situ spawners were present (Table 2). We adjusted estimates of side-channel production to account for mainstem recruits by reducing observed outmigrant numbers by the maximum observed proportion of mainstem recruits, thereby generating a conservative lower bound to smolt production from side-channel habitats. An upper bound to estimated smolt production was generated by assuming that all outmigrants recruited from side-channel habitat (i.e., no mainstem recruitment).

Because overwinter survival in off-channel habitats is generally much higher than that in hydraulically harsh coastal river main

Table 2. Proportion of smolts recruiting from the main stem, based on the assumption that smolt out-migration the year after channel construction is based entirely on mainstem recruits (i.e., that smolts from in situ spawning only appear in traps 2 years postconstruction).

Project	River	Area (m^2)	Brood year	Smolt recruitment from the main stem	Smolt recruitment from in situ reproduction and the main stem	Recruits from main stem (%)
Worth Creek	Norrish Creek	850	1978	81		21%
			1980		87	
			1981		120	
			1982		120	
			1984		285	
			1985		856	
			1987		877	
			Avg.		**391**	
Upper Paradise	Cheakamus River	2 625	1981	1 580		30%
			1982		8 240	
			1983		6 228	
			1984		4 453	
			1985		5 483	
			1986		4 923	
			1987		2 355	
			Avg.		**5 280**	
Mamquam	Mamquam River	2 000	1983	157		3.6%
			1984		5 813	
			1985		1 126	
			1987		6 265	
			Avg.		**4 401**	
Upper Bulbeard	Chilliwack River	17 500	1997	568		6.6%
			1998		8 750	
			1999		7 350	
			2000		9 385	
			Avg.		**8 562**	

stems that experience sustained winter flooding (Quinn and Peterson 1996; Solazzi et al. 2000), any increased overwinter survival in side-channel habitats for fish of mainstem origin can reasonably be attributed to side-channel production. We therefore reviewed the literature on overwinter survival of coho in mainstem versus side-channel habitats to estimate a survival differential between habitats and multiplied the proportion of smolts of mainstem origin by this factor to determine the proportion of their production that could be attributed to occupancy of restored habitat.

Evaluation of existing smolt production models

To compare the accuracy of existing habitat capacity models for predicting coho production from restored habitat, we estimated smolt production from each of the seven restored sites using three area- and one length-based habitat models from the literature: (1) smolt production = $0.37 \times \text{area}\ (\text{m}^2)$, from Roni et al. (2010); (2) smolt production = $8.05 \times \text{area}^{0.61}\ (\text{m}^2) - 145$, from Rosenfeld et al. (2008); (3) smolt production = $2951 \times \text{area}^{0.51}$ (ha), from Keeley et al. (1996); and (4) watershed smolt production = $992 \times \text{total stream length}^{0.97}$ (km), from figure 1 in Bradford et al. (1997) and also assuming a mean smolt production of 2060 smolts·km^{-1} based on mean smolt abundance reported by Bradford et al. (1997, their table 4) for streams between 48°N and 50°N latitude. Production was calculated using the total area of each individual restoration site for the first three models, and watershed-scale smolt production was estimated from the Bradford et al. (1997) model using total stream length for all mainstem and tributary habitat in the upper watershed (69 km), as well as an additional 20 km of shoreline on Chilliwack Lake. Model fit was evaluated based on the mean deviation of observed and predicted smolt production for each model.

Costs of habitat restoration and smolt production

The costs of restoration for each site were recorded at the time of construction, and the total costs of all restoration activity was determined by the costs of supporting grants and matching funds (e.g., Fisheries and Oceans Canada labour). Annual maintenance and minor upkeep expenses were also recorded following construction. The mean restoration cost for the sites was compared with the mean restoration cost for a typical Puget Sound, Washington, habitat as reported in Roni et al. (2010) and earlier studies. To place the costs and benefits of restoration in a broader management context, we also compared the mean costs of smolt production from restored habitat with hatchery production (both amortized over a 30-year period). We used the lower bound on estimated smolt production (assuming maximal mainstem recruitment) to provide a liberal estimate of smolt production costs from restored habitat.

Estimates of hatchery productions costs for coho were obtained from Radtke and Carter (2009) and National Marine Fisheries Service (2014) for state and federal hatcheries from the Pacific Northwest United States (Washington, Oregon, and Idaho). Estimates included annual hatchery operation costs reported by state and federal agencies, agency administration costs, fixed capital infrastructure costs, and costs of smolt acclimation and release (see Radtke and Cater 2009 and National Marine Fisheries Service 2014 for details). Mean reported coho smolt production costs reported by Radtke and Carter (2009) and National Marine Fisheries Service (2014) were, respectively, US$1.10 and US$0.90 (in 2009 dollars). We assumed that hatchery costs for coho smolt production in coastal British Columbia were similar to those reported for the Pacific Northwest United States.

Results

Smolt out-migration from each of the restored sites ranged from 740 to 53 840 smolts, and smolt density ranged from 0.17 to 0.75 smolts·m^{-2} (Table 3), with a mean smolt density of 0.48 smolts·m^{-2}. Yukalap had the lowest smolt density and production because of the habitat design for use primarily as spawning channels. The

Table 3. Coho smolt production from restored sites in 2002, including population estimation method, estimated production over 30 years, and smolt density for individual restored sites in the upper Chilliwack River valley.

Site	Estimation method	No. of smolts	Smolt density (smolts·m^{-2})	Smolt production over 30 years
Centennial	Count	12 210	0.41	366 300
Upper Bulbeard	Count	9 590	0.55	287 700
Lower Bulbeard	Count	32 050	0.55	961 500
Angelwing	Count	8 350	0.75	250 500
Millenium	Count	16 350	0.39	490 500
Yukalap	PPE	740±390	0.17	22 200
Centre Creek Camp	PPE	3 560±1 010	0.55	106 800
Total restored habitat		82 840±1 140		2 485 200

Note: Smolt production was calculated by either weir trap counts (Count) or a pooled Peterson estimate (PPE) using mark–recapture data. Smolt production over 30 years was calculated assuming that production remained constant at 2002 levels.

total number of smolts from restored habitat was 82 840 (±1.7%) (Table 3). Smolt production in 2002 was broadly similar to production in other years for the subset of Chilliwack valley side channels where data were available across multiple years (Table 4), indicating that 2002 smolt production is likely representative of long-term mean production.

A stratified maximum-likelihood Darroch estimate of coho smolt production from the entire upper Chilliwack watershed of 226 800 (±3.8%) fish was generated using SPAS (Arnason et al. 1996). Based on downstream weir counts at the restored sites, it was known that 9% of the total marked coho smolts out-migrated before or after the mainstem rotary screw trap was in place. The watershed population estimate was therefore adjusted upward by a factor of 9% to 247 200 (±3.8%) to include migration outside of the screw trap mark–recapture period. The ratio of smolts produced from restored habitat to total smolt out-migration (82 800 / 247 200) provides an upper bound of 34% on the contribution of constructed habitat to total watershed-scale smolt production (i.e., assuming that 100% of side-channel smolt out-migration is from side-channel production with no contribution from mainstem recruits).

Accounting for the potential contribution of mainstem fish to off-channel smolt production

Observed female coho spawner returns to side channels are similar to those required to fully seed juvenile rearing habitat (Table 1; calculated after Reeves et al. 1989, as described above), indicating that off-channel rearing habitat was at or near capacity from in situ reproduction in constructed habitat.

Comparison of smolt production in the year following construction (mainstem recruits only) with production in subsequent years (which includes in situ spawning in side channels) generated estimates of mainstem recruitment ranging from 3.6% to 30% (Table 2). A relatively low proportion of mainstem recruits may be expected when the area of the side channel is particularly large (e.g., Upper Bulbeard; Table 2), as is the case for most of the Chilliwack River side channels (e.g., Fig. 2; Table 1), since a large area would tend to dilute the potential contribution from any fixed pool of local mainstem recruits.

Thirteen estimates of stream overwinter survival and five estimates of pond overwinter survival were extracted from the literature (Table 5). This literature indicates significantly lower overwinter survival in mainstem versus side-channel habitat (24% versus 68%, respectively; t test, $t_{[16]} = 6.5$; $P < 0.0001$; Table 5), with a survival differential of approximately 40% between habitats (mean stream survival = 24.4%; mean pond survival = 68.4%). This is broadly consistent with observations of increased winter survival in several before–after studies where restoration involved creation of deeper pond habitat (e.g., Cederholm et al. 1988; Solazzi et al. 2000).

Table 4. Smolt production data (outmigrants per square metre of habitat area) from off-channel habitats in the Chilliwack drainage for which data measured across multiple years were available.

Site	1997[a]	1998[b]	1999[b]	2002[c]
Upper Bulbeard	0.03	0.50	0.42	0.55
Lower Bulbeard	—	1.63	0.75	0.55
Millenium (14 Mile)	0.36	—	—	0.39
Thurston	0.14	0.21	—	—
R4	0.3	0.08	—	—
Anderson	0.48	0.21	0.07	—

Note: Interannual variation is moderate, suggesting habitat saturation and limited variation in productive capacity across years. 2002 smolt production reported in the present study appears broadly representative of production in other years, with the notable exception of very low smolt production in Upper Bulbeard in 1997. Upper Bulbeard was constructed in 1996, so that reduced smolt outmigrants in 1997 reflect, in part, an absence of in situ recruitment from spawning within the side channel.

[a] Data from Blackwell et al. (1999).

[b] Unpublished monitoring and assessment data, Fisheries and Oceans Canada, Pacific Region, Resource Restoration Division.

[c] This study.

The maximum likely proportion of side-channel smolt outmigration attributable to mainstem production was therefore calculated as 0.3 (assuming 30% mainstem recruitment; Table 2) multiplied by 0.6 (assuming that 40% of production from mainstem recruits could be attributed to off-channel production through higher overwinter survival), yielding a final proportion of 0.18. Reducing smolt production attributable to off-channel production by 18% yields a conservative lower bound to smolt production from side-channel habitats of 67 900 / 247 200 = 27.5%. Therefore the percentage of total coho smolt production supported by restored habitat was in the range of 27%–34%, indicating a substantial contribution of restored habitat to smolt production at a watershed scale. Even in the extremely conservative (and unrealistic) scenario of all side-channel smolts recruiting from mainstem habitat, an overwinter survival differential of 40% would still mean that 13.4% (82 840 × 0.4 / 247 250) of watershed-scale smolt production was attributable to restored habitat.

Evaluation of existing smolt production models

Of the three published area-based smolt production models, Roni et al. (2010) provided the most accurate predictions of smolt production (Table 6), with a mean 25% error compared with up to 76% for the other models. Surprisingly, the simple production formula from Roni et al. 2010 (assuming a fixed production of 0.37 smolts·m^{-2}) provided better production estimates than models generated using data sets that included smolt production from the actual study sites (e.g., Rosenfeld et al. 2008). The stream length-based regression production model (Bradford et al. 1997)

Table 5. Overwinter survival estimates extracted from the literature for coho parr in mainstem versus off-channel pond habitats.

Study	Stream	Habitat[b]	Survival (%)	Region	Study duration (years)
Hauer 2013	Freshwater Creek[a]	Stream	32	Calif.	2
Roni et al. 2012	East Twin Creek[a]	Stream	23	Wash.	3
	West Twin Creek[a]		22	Wash.	3
Brakensiek and Hankin 2007	Prairie Creek	Stream	46	Calif.	1
Crone and Bond 1976	Sashin Creek	Stream	35	Alaska	3
Solazzi et al. 2000	East Fork Lobster Creek[b]	Stream	19	Ore.	7
	Upper Lobster Creek[c]		13	Ore.	3
	Moon Creek[b]		15	Ore.	7
	East Creek[c]		11	Ore.	2
Quinn and Peterson 1996	Big Beef Creek	Stream	36	Wash.	2
Ebersole et al. 2009	West Fork Smith River[d]	Stream	10	Ore.	3
Nickelson 1998	Five unidentified streams[e]	Stream	22	Ore.	—
Bustard and Narver 1975	Carnation Creek	Steam	35	B.C.	—
Bustard and Narver 1975	Carnation Creek	Pond	68	B.C.	1
Nickelson 1998	Five unidentified streams[e]	Pond	49	Ore.	—
Peterson 1982	Clearwater River[f]	Pond	78	Wash.	1
Cederholm et al. 1988	Clearwater River	Pond	56	Wash.	2
Dekker 1999	Coquitlam River[g]	Pond	91	B.C.	1

Note: A single value was calculated for each stream or pond based on the mean of reported annual survival for multiyear studies.

[a] Mean of apparent survival and summed proportion survival (which counts fall outmigrants as survivals rather than mortalities; see Roni et al. 2012 and Hauer 2013).

[b] Control stream in BACI restoration experiment.

[c] Treatment stream, including pretreatment years only from the BACI restoration experiment.

[d] Data extracted from figure 3 of Ebersole et al. (2009), under the conservative assumption that survival in the Chilliwack River main stem (700+ km^2 watershed) is equivalent to the maximum basin area in their figure 3.

[e] Data extracted from figure 2 of Nickelson (1998), including two beaver ponds.

[f] For deep ponds with a maximum depth well in excess of 1.3 m, which includes all those in this study.

[g] Mean value for two ponds; see table 3.5 of Dekker (1999).

Table 6. Comparison of observed coho smolt production with estimated production from published habitat models for individual restored sites and the total watershed (natural and restored habitat combined) in the upper Chilliwack River valley.

Site	This study	Roni et al. 2010	Rosenfeld et al. 2008	Keeley et al. 1996	Bradford et al. 1997
Centennial	12 200	11 140	4 200	5 180	—
Upper Bulbeard	9 590	6 480	3 110	3 930	—
Lower Bulbeard	32 050	21 460	6 330	7 230	—
Angelwing	8 350	4 140	2 230	3 130	—
Millenium	16 350	15 540	5 180	6 140	—
Yukalap	740	1 630	1 200	1 940	—
Centre Creek Camp	3 560	2 410	1 560	2 370	—
Total watershed[a]	247 250				77 250[b] / 183 550[c]
Mean error (%)		25%	72%	40%	76% / 26%

Note: Mean error is calculated as the mean deviation of predicted values from observed.

[a] The maximum likelihood Darroch estimate of 226 830 is adjusted upwards by 9% to account for truncated duration of the screw trap set relative to the out-migration window (see text for details).

[b] Estimate based on the smolt production versus stream length regression from Bradford et al. (1997; their figure 1, smolt production = 992 × total stream length$^{0.97}$ (km)).

[c] Estimate based on a mean smolt production of 2060 smolts·km^{-1}, the mean reported for streams between latitudes 48°N and 50°N (see Bradford et al. 1997, their table 4).

performed poorly at the watershed scale, but the mean value of 2060 smolts·km^{-1} for midlatitude smolt production reported by Bradford et al. (1997; Table 4) produced much better estimates when scaled up to the entire watershed.

Costs of habitat restoration and smolt production

The initial cost of restoration ranged from $\text{CAN\$}7.65\cdot\text{m}^{-2}$ to $\text{CAN\$}25.45\cdot\text{m}^{-2}$, and the cost of maintenance over a 30-year period (Table S4[1]) ranged from $\text{CAN\$}0.77\cdot\text{m}^{-2}$ to $\text{CAN\$}18.41\cdot\text{m}^{-2}$, for a combined range of $\text{CAN\$}8.58\cdot\text{m}^{-2}$ to $\text{CAN\$}41.14\cdot\text{m}^{-2}$ to construct and maintain each site for 30 years (Table 7; cost in 2002 dollars). Sites that had a higher proportion of spawning habitat tended to be more expensive, indicating that creation of primarily rearing habitat is most cost-effective for coho smolt production. Based on the coho smolt production estimates for 2002 (adjusted down to account for potential mainstem recruitment as described above), the initial cost per smolt ranged from CAN\$16.79 to CAN\$164.13 per smolt. Yukalap was the most expensive site because of its relatively large proportion of spawning habitat focused on pink salmon. Cost per smolt for all sites decreased greatly if prorated over 30 years (assuming constant smolt production), decreasing to US\$0.69 to US\$10.05 per smolt (Table 7). Both the initial mean cost of construction ($\text{CAN\$}16.11\cdot\text{m}^{-2}$) and combined mean initial cost plus 30-year maintenance cost ($\text{CAN\$}24.44\cdot\text{m}^{-2}$) were substantially lower than the mean floodplain construction and reconnection

Table 7. Characteristics and costs for each restoration site in the upper Chilliwack River Valley, in 2002 Canadian dollars.

Site	Initial cost ($\$\cdot m^{-2}$)	Cost of 30 years maintenance ($\$\cdot m^{-2}$)	Total cost ($\$\cdot m^{-2}$)	Percent spawning habitat	Initial cost per smolt ($\$\cdot smolt^{-1}$)	Cost per smolt over 30 years ($\$\cdot smolt^{-1}$)	Cost per smolt (2009 CAN$)	Cost per smolt (2009 US$)
Centennial–Bulbeard	7.81	0.77	8.58	14	18.69	0.68	0.79	0.69
Angelwing	25.45	7.23	32.68	18	41.62	1.78	2.06	1.81
Millenium	7.65	2.76	10.41	5	16.79	0.76	0.88	0.77
Yukalap	22.73	18.41	41.14	45	164.13	9.90	11.48	10.05
Centre Creek Camp	16.92	12.46	29.38	17	37.73	2.18	2.53	2.21

Note: Costs are calculated from the maintenance and construction costs in Table S4[1] and are calculated based on conservative estimates of smolt production attributable to created habitat (i.e., total out-migration reduced by 18% to account for potential mainstem recruitment). The last two columns show costs per smolt in 2009 Canadian and US dollars, respectively, to allow comparison with published hatchery production costs.

costs recently reported elsewhere (US\$85–US\$150·m^{-2}; Roni et al. 2010).

Discussion

The effectiveness of stream habitat restoration has proven somewhat controversial (Stewart et al. 2009; Bernhardt and Palmer 2011), with researchers expressing contrasting views on its costs and benefits (Thompson 2006; Whiteway et al. 2010). This controversy is partly driven by a lack of thorough assessments of the biological consequences and economic costs of restoring stream habitats (Bernhardt et al. 2005; White et al. 2011), which allows critics to legitimately question the benefits of investing in restoration. Studies that do demonstrate a positive response of fish to habitat restoration often show an increase in abundance at a relatively small spatial scale, supporting concerns that changes in abundance may reflect short-term redistribution rather than increased productive capacity (Gowan and Fausch 1996; Whiteway et al. 2010). Few studies have demonstrated fish production benefits of habitat restoration at a larger spatial scale distributed throughout a watershed, in part because of the substantial costs of both restoration and monitoring at larger scales (but see Solazzi et al. 2000 for a good large-scale BACI restoration experiment).

Generally speaking, the most rigorous study design for assessing restoration effectiveness is a replicated BACI experiment (Solazzi et al. 2000; although BACI is not without its shortcomings, see Johnson et al. 2005). Resource limitations prevented a BACI on the Upper Chilliwack River, where we directly measured smolt emigration from newly constructed habitat as an index of restoration effectiveness. Interpretation of our data is therefore subject to the same criticism as many postrestoration assessments: that fish use of restored habitat may simply represent redistribution, rather than an increase in production (implying recruitment rather than habitat limitation). In general, it needs to be demonstrated that the life stage targeted by restoration is in fact habitat-limited (i.e., that there are sufficient recruits in the population to saturate both existing and newly created habitat). The exception to this rule is when restoration increases both spawning and rearing habitat simultaneously, or if new habitat is expected to increase survival of the targeted life stage, in which case habitat restoration will result in a population response even if the population remains recruitment-limited (Greene and Beechie 2004; Einum and Nislow 2011). Demonstrating (or at least providing strong inference for) population limitation by habitat quantity (area) or quality (realized survival) should be a key aspect of habitat restoration planning and a precondition for restoration itself.

In the upper Chilliwack River, constructed habitat was designed to include sufficient spawning habitat to fully seed rearing habitat, and habitat capacity models and spawner counts indicate that side-channel habitats were likely fully recruited with juveniles from in situ spawning, indicating that movement of mainstem fish into side-channel habitats was unlikely to contribute overwhelmingly to side-channel production. Further, measured smolt out-migration in the absence of in situ side-channel spawning was available to inform a realistic upper bound on mainstem recruitment to side-channel habitats (i.e., a maximum 30% mainstem origin); this allowed correction of observed side-channel smolt production for potential mainstem subsidies, thereby generating realistic lower bounds on smolt production from restored habitat. Thus, observed habitat use, if conservatively interpreted with consideration of the potential for fish redistribution to bias results, can be used to make reasonable inferences about the effectiveness of habitat restoration.

Population-level effects of increased habitat quality, even under recruitment limitation (i.e., excess habitat), are exemplified by the mean 40% higher coho overwinter survival in deeper off-channel pond habitat (relative to the main stem) identified in the literature review. This implies that increased survival associated with better overwintering habitat in side channels should result in increased smolt production, even if juvenile coho were strongly recruitment-limited. In the Chilliwack River, even if all smolts out-migrating from side channels were of mainstem origin, increased survival from simply overwintering in the newly constructed side channels could in principle create an estimated watershed-scale increase in smolt production of 13%.

Distinguishing between limitation by habitat quantity versus habitat quality (Greene and Beechie 2004; Rosenfeld and Hatfield 2006; Einum and Nislow 2011) is a key consideration in the recovery planning and restoration process, since restoring habitat quality versus quantity have different population implications. At very low adult spawner population size increasing the quantity of juvenile rearing habitat quality will have no effect on juvenile abundance. Increasing the available rearing habitat capacity (i.e., the asymptote of the stock–recruitment curve) will only elicit a population response at large adult population sizes. In contrast, increasing habitat quality (e.g., overwinter survival) will increase stage-specific survival (particularly at low abundance) and therefore result in a population increase even at low adult numbers (i.e., by increasing the maximum slope of the stock–recruitment curve; Sharma and Hilborn 2001). Restoration such as side-channel construction that increases both rearing habitat quantity and quality (e.g., though increased area and overwinter survival in deep pool sections) represents the most robust type of intervention, since it increases both the slope and asymptote of the stock–recruitment curve (Sharma and Hilborn 2001; Bradford et al. 2005), providing production benefits at both high and low population sizes.

This study demonstrates that construction of off-channel habitat at multiple sites throughout the floodplain of a large river increased total coho smolt out-migration by anywhere from 27% to 34%. This represents a considerable increase, given the large size of the watershed (~600 km² upstream of the screw trap) and total smolt production (247 200 smolts). Detecting system-wide incremental effects of restoring individual sites in a watershed may be very difficult (Paulsen and Fisher 2005; Roni et al. 2010); the response to restoration in the upper Chilliwack drainage shows that the cumulative effect of individual restoration projects on system production can be substantial and supports the inference of incremental benefits from individual restoration projects within a watershed, even if their individual effects may be difficult to detect.

The paucity of studies that rigorously evaluate the benefits of restoration is influenced by the high costs of project monitoring, a general desire by restoration practitioners to spend funds on habitat improvement rather than project evaluation, and a willingness of field biologists to consider observed use of restored habitat as adequate evidence of a positive biological response. While labour-intensive evaluations are necessary to assess the outcomes of habitat restoration, habitat capacity models that predict the consequences of habitat restoration can be a good substitute, provided there is confidence in model predictions and sufficient juvenile recruitment to fully saturate rearing habitat. We assessed the ability of several published models to predict observed smolt production from our off-channel habitats. The production models that included the Chilliwack River restoration sites as part of their calibration data sets (Keeley et al. 1996; Rosenfeld et al. 2008) performed relatively poorly (Table 6), generally underestimating production by a factor of four. The Bradford et al. (1997) average regression model that assumed a constant smolt production per linear kilometre of anadromous channel also underestimated production by a factor of about three, although their midlatitude coho smolt production estimate of 2060 smolts·km^{-1} performed much better. Surprisingly, the model that best predicted the biological response to habitat change was the simplest (Roni et al. 2010), based on a constant production of 0.37 smolts·m^{-2} of restored habitat. Given that the present watershed-scale assessment supports the accuracy of predictions from this model in a novel watershed, we suggest that it can be used as a simple approach for estimating the approximate production benefits of off-channel habitat restoration for juvenile coho, provided productivity of constructed habitat does not degrade over time.

While validated habitat capacity models provide a good first-order approach for estimating production from restored habitat, there is no substitute for direct measurement of smolt production to generate credible estimates of the costs of production from restored habitat. The range of estimated production costs per smolt from restored habitat (US$0.69–US$10.05, including capital costs over a 30-year period) overlapped with reported mean hatchery production costs (~US$1.00 per smolt; Radtke and Carter 2009; National Marine Fisheries Service 2014), and production costs from two of five restored sites were below this mean reported value for hatchery production (Table 7). This indicates that off-channel habitat restoration in the Chilliwack River was, at some sites, as cost-effective as hatchery coho production, provided that restored habitats are maintained without any loss of production over time (which requires a long-term commitment by agency staff or local stewards). Note also that our maintenance costs do not include potential future expenses associated with renewing spawning gravel, which will eventually be required at some sites. Smolt production costs from restored habitat will also be sensitive to changes in marine survival, particularly if low adult returns cause rearing habitat to become under-recruited. On the other hand, this simple comparison of production costs tends to undervalue the relative benefits of production from restored habitat. Wild-reared juveniles from restored habitat arguably have higher value than hatchery-reared fishes, because they survive better in the wild and have higher reproductive success (Araki et al. 2007); similarly, production from restored habitat does not incur the potential risk of negative impacts on wild stocks sometimes associated with hatchery production (Meffe 1992; Araki and Schmid 2010). Constructed side-channel habitats also offer considerable production benefits to salmonids other than coho, including steelhead, Dolly Varden, and pink salmon, all of which were observed to spawn, rear, or overwinter in the restored habitats (Blackwell et al. 1999; Rosenfeld et al. 2008). Finally, the restored channel and pond complexes provide habitat complexity on the floodplain that also benefits other wildlife (waterfowl, diving birds, etc.).

Our cost estimates for habitat construction were considerably lower than those recently reported elsewhere in the primary literature (e.g., Roni et al. 2010). We suspect that this is partly due to our use of local logging contractors and equipment for much of the work, and because most of the upper watershed is public land (provincial forest) where we were able to select from a wide variety of sites to optimize biological and cost-effectiveness; a more restricted suite of suitable sites (e.g., in a more urbanized watershed) might have constrained options and inflated costs. The presence of old logging roads from earlier forest harvesting also facilitated site access. There were also efficiencies that were realized by the scale of restoration that took place, including the ability to use liabilities from some projects as assets for others. For example, excavated fill from some sites was transported to a nearby site (Millenium) for constructing berms on the downstream end of natural beaver ponds to increase their depth and wetted surface area. Enlarging ponds in this way was among the most cost-effective form of habitat restoration; in contrast, the most expensive restoration site was Yukalup (Table 7), almost half of which was built as pink salmon spawning habitat, which both reduced mean coho production and greatly increased construction costs. Although our construction costs are low relative to those reported in Roni et al. (2010), they are comparable to reported smolt production costs associated with habitat restoration in earlier studies (e.g., ~US$1.23·smolt^{-1} from Solazzi et al. 2000; based on their reported costs and postrestoration smolt production, in 2009 dollars with values amortized over 30 years of smolt production, excluding maintenance costs).

Ideally, the primary goal of restoration is to reestablish the natural processes that generate and maintain habitat (Beechie et al. 2010). Although side-channel habitats were broadly designed after the natural side channels typically found on coastal river floodplains, intakes were generally engineered as hardened structures to resist erosion, and intake capacity was restricted to prevent scouring flows that could potentially alter or degrade constructed habitat. In contrast, natural side channels are stochastically subject to scouring flow, which removes fines and maintains substrate quality; unfortunately, their dynamic nature may also disrupt connection to the main stem through channel migration or avulsion, and relying on random stochastic events to create and maintain this habitat may leave much of it unproductive at any given time. The benefits of an engineered channel with a fixed intake structure regulating maximum flow include stable fish access and habitat capacity, even though this comes at the cost of a commitment to long-term maintenance to ensure that water intakes (and access for spawning adults) do not become blocked. While hard engineered restoration structures are more durable (stable) than natural side channels, they also have major limitations. For instance, one consequence of increased side-channel stability is that fine sediment drawn in from the main stem is not exported by the scouring flows that periodically remove sediment from natural floodplain habitats, resulting in a tendency for substrate quality to degrade over time in artificial side channels, necessitating the periodic removal of fines or addition of spawning gravel. Although fully restored natural processes are maintenance free, the benefits of stable production from engineered side channels may partly compensate for inputs of fines and the requirements of ongoing maintenance. However, future designs should consider the possibility of intakes that provide some potential for natural gravel recruitment or the ability to accommodate flows that can flush fine sediments without degrading engineered habitat structures.

With billions of dollars being spent on stream restoration worldwide (Roni et al. 2002; Bernhardt et al. 2005), it is important to assess whether or not these efforts are effective. This study demonstrates that floodplain restoration for coho is not only effective in producing smolts at a watershed scale, but can be comparable in cost-effectiveness to hatchery production. Our study also strongly supports the inference that incremental restoration work within a drainage has cumulative production benefits even though the effects of minor projects may be difficult to detect. While intensive project evaluations like that presented here may not always be practical or even necessary, strategically chosen assessments of this nature are essential for understanding the effectiveness of ecosystem restoration.

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References

Araki, H., and Schmid, C. 2010. Is hatchery stocking a help or harm? Evidence, limitations and future direction in ecological and genetic surveys. Aquaculture, **308**: 2–11. doi:10.1016/j.aquaculture.2010.05.036.

Araki, H., Cooper, B., and Blouin, M.S. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science, **318**: 100–103. doi:10.1126/science.1145621. PMID:17916734.

Arnason, A., Kirby, C., Schwarz, C., and Irvine, J. 1996. Computer analysis of data from stratified mark–recovery experiments for estimation of salmon escapements and other populations [online]. Can. Tech. Rep. Fish. Aquat. Sci. 2106. Available from www.cs.umanitoba.ca/~popan/pdf/spasman.pdf.

Bash, J.S., and Ryan, C.M. 2002. Stream restoration and enhancement projects: is anyone monitoring? Environ. Manage. **29**: 877–885. doi:10.1007/s00267-001-0066-3. PMID:11992178.

Beechie, T., Beamer, E., and Wasserman, L. 1994. Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration. N. Am. J. Fish. Manage. **14**: 797–811. doi:10.1577/1548-8675(1994)014<0797:ECSRHA>2.3.CO;2.

Beechie, T.J., Sear, D.A., Olden, J.D., Pess, G.R., Buffington, J.M., Moir, H., Roni, P., and Pollock, M.M. 2010. Process-based principles for restoring river ecosystems. BioScience, **60**: 209–222. doi:10.1525/bio.2010.60.3.7.

Bernhardt, E., and Palmer, M. 2011. River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. Ecol. Appl. **21**: 1926–1931. doi:10.1890/10-1574.1. PMID:21939034.

Bernhardt, E., Palmer, M., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-Shah, J., Galat, D., Gloss, S., Goodwin, P., Hart, D., Hassett, B., Jenkinson, R., Katz, S., Kondolf, G.M., Lake, P.S., Lave, R., Meyer, J.L., O'Donnell, T.K., Pagano, L., Powell, B., and Sudduth, E. 2005. Synthesizing US river restoration efforts. Science, **308**: 636–637. doi:10.1126/science.1109769. PMID:15860611.

Blackwell, C.N., Picard, C.R., and Foy, M.P. 1999. Smolt productivity of off-channel habitat in the Chilliwack River watershed. Watershed Restoration Project Report No. 14.

Bradford, M.J., Taylor, G.C., and Allan, J.A. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. Trans. Am. Fish. Soc. **126**: 49–64. doi:10.1577/1548-8659(1997)126<0049:EROCSS>2.3.CO;2.

Bradford, M.J., Korman, J., and Higgins, P.S. 2005. Using confidence intervals to estimate the response of salmon populations (*Oncorhynchus* spp.) to experimental habitat alterations. Can. J. Fish. Aquat. Sci. **62**(12): 2716–2726. doi:10.1139/f05-179.

Brakensiek, K.E., and Hankin, D.G. 2007. Estimating overwinter survival of juvenile coho salmon in a northern California stream: accounting for effects of passive integrated transponder tagging mortality and size-dependent survival. Trans. Am. Fish. Soc. **136**: 1423–1437. doi:10.1577/T06-211.1.

Bustard, D.R., and Narver, D.W. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. **32**(5): 667–680. doi:10.1139/f75-086.

Cederholm, C.J., Scarlett, W.J., and Peterson, N.P. 1988. Low-cost enhancement technique for winter habitat of juvenile coho salmon. N. Am. J. Fish. Manage. **8**: 438–441. doi:10.1577/1548-8675(1988)008<0438:LCETFW>2.3.CO;2.

Cederholm, C.J., Kunze, M.D., Murota, T., and Sibatani, A. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries, **24**: 6–15. doi:10.1577/1548-8446(1999)024<0006:PSC>2.0.CO;2.

Cleary, J.S. 2001. Increasing coho productivity in the Chilliwack River watershed [online]. Streamline, **6**: 1–7. Available from http://www.forrex.org/sites/default/files/publications/articles/streamline_vol6_no1_art1.pdf.

Cowx, I., and Welcomme, R. 1998. Rehabilitation of rivers for fish: a study undertaken by the European Inland Fisheries Advisory Commission of FAO. Wiley-Blackwell, Oxford, UK.

Crone, R.A., and Bond, C. 1976. Life history of Coho salmon, *Oncoryhnchus kisutch*, in Sashin Creek, southeastern Alaska [online]. Fish. Bull. **74**: 897–923. Available from http://fishbull.noaa.gov/74-4/crone.pdf.

Dekker, A.S. 1999. Effects of primary production and other factors on the size and abundance of juvenile coho salmon in artificial off-channel habitat [online]. The University of British Columbia. Available from https://circle.ubc.ca/bitstream/handle/2429/9267/ubc_1999-0340.pdf?sequence=1.

Downs, P.W., and Kondolf, G.M. 2002. Post-project appraisals in adaptive management of river channel restoration. Environ. Manage. **29**: 477–496. doi:10.1007/s00267-001-0035-X. PMID:12071499.

Ebersole, J.L., Colvin, M.E., Wigington, P.J., Leibowitz, S.G., Baker, J.P., Church, M.R., Compton, J.E., Miller, B.A., Cairns, M.A., Hansen, B.P., and La Vigne, H.R. 2009. Modeling stream network-scale variation in Coho salmon overwinter survival and smolt size. Trans. Am. Fish. Soc. **138**: 564–580. doi:10.1577/T08-047.1.

Einum, S., and Nislow, K.H. 2011. Variation in population size through time and space: theory and recent empirical advances from Atlantic salmon. *In* Atlantic salmon ecology. *Edited by* O. Aas, S. Einum, A. Klemetsen, and J. Skurdal. John Wiley and Sons, Oxford, UK. pp. 277–298.

Fedorenko, A.Y. 2002. Comparison of estimated enhanced contribution to Chilliwack River Coho escapement using two methods of estimation: adipse-CWTs and asipose CWTs plus adipose-only. Fisheries and Oceans Canada.

Gende, S.M., Edwards, R.T., Willson, M.F., and Wipfli, M.S. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience, **52**: 917–928. doi:10.1641/0006-3568(2002)052[0917:PSIAAT]2.0.CO;2.

Gowan, C., and Fausch, K.D. 1996. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecol. Appl. **6**: 931–946. doi:10.2307/2269496.

Gowan, C., Young, M.K., Fausch, K.D., and Riley, S.C. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Can. J. Fish. Aquat. Sci. **51**(11): 2626–2637. doi:10.1139/f94-262.

Greene, C.M., and Beechie, T.J. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **61**(4): 590–602. doi:10.1139/f04-024.

Hansen, E.A., and Closs, G.P. 2009. Long-term growth and movement in relation to food supply and social status in a stream fish. Behav. Ecol. **20**: 616–623. doi:10.1093/beheco/arp039.

Hauer, J.J. 2013. Overwinter survival and growth of juvenile coho salmon, *Onchorhynchus kisutch*, in Freshwater Creek, California. M.Sc. thesis, Department of Fisheries Biology, Humbolt State University.

Herbinger, C.M., Newkirk, G.F., and Lanes, S.T. 1990. Individual marking of Atlantic salmon: evaluation of cold branding and jet injection of Alcian Blue in several fin locations. J. Fish Biol. **36**: 99–101. doi:10.1111/j.1095-8649.1990.tb03524.x.

Johnson, S.L., Rodgers, J.D., Solazzi, M.F., and Nickelson, T.E. 2005. Effects of an increase in large wood on abundance and survival of juvenile salmonids (*Oncorhynchus* spp.) in an Oregon coastal stream. Can. J. Fish. Aquat. Sci. **62**(2): 412–424. doi:10.1139/f04-222.

Keeley, E.R., Slaney, P., and Zaldokas, D. 1996. Estimates of production benefits for salmonid fishes from stream restoration initiatives. Province of British Columbia, Ministry of Environment, Lands and Parks, and Ministry of Forests. Watershed Restoration Management Report No. 4.

Kramer, D., Rangely, R., and Chapman, L. 1997. Habitat selection: patterns of spatial distribution from behavioural decisions. *In* Behavioural ecology of teleost fishes. *Edited by* J. Godin. Oxford University Press, New York. pp. 37–80.

Lackey, R.T., Lach, D.H., and Duncan, S.L. 2006. Policy options to reverse the decline of wild Pacific salmon. Fisheries, **31**: 344–351.

Meffe, G.K. 1992. Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific coast of North America. Conserv. Biol. **6**: 350–354. doi:10.1046/j.1523-1739.1992.06030350.x.

Morley, S.A., Garcia, P.S., Bennett, T.R., and Roni, P. 2005. Juvenile salmonid (*Oncorhynchus* spp.) use of constructed and natural side channels in Pacific Northwest rivers. Can. J. Fish. Aquat. Sci. **62**(12): 2811–2821. doi:10.1139/f05-185.

National Marine Fisheries Service. 2014. Final environmental impact statement to inform Columbia River basin hatchery operations and the funding of Mitchell Act hatchery programs [online]. Seattle, Washington. Available from http://www.westcoast.fisheries.noaa.gov/publications/hatchery/mitchellact_feis/mitchell_act_hatcheries_feis_final.pdf.

National Research Council. 1992. Restoration of aquatic ecosystems. National Academy Press, Washington.

Nehlsen, W., Williams, J.E., and Lichatowich, J.A. 1991. Pacific salmon at the crossroads — stocks at risk from California, Oregon, Idaho, and Washington. Fisheries, **16**: 4–21. doi:10.1577/1548-8446(1991)016<0004:PSATCS>2.0.CO;2.

Nickelson, T.E. 1998. A habitat-based assessment of Coho salmon production potential and spawner escapement needs for Oregon coastal streams [online]. Oregon Department of Fish and Wildlife, Information Report No. 98-4. Available from http://library.state.or.us/repository/2011/201108261007475/index.pdf.

Paulsen, C.M., and Fisher, T.R. 2005. Do habitat actions affect juvenile survival? An information-theoretic approach applied to endangered Snake River Chinook salmon. Trans. Am. Fish. Soc. **134**: 68–85. doi:10.1577/FT03-220.1.

Peterson, N.P. 1982. Population characteristics of juvenile Coho salmon (*Oncorhynehus kisutch*) overwintering in riverine ponds. Can. J. Fish. Aquat. Sci. **39**(9): 1303–1307. doi:10.1139/f82-172.

Picard, C.R., Blackwell, C.N., and Foy, M.P. 1998. Coho smolt production from restored and natural off-channel habitats in the Chilliwack River watershed [online]. Streamline, **3**: 9–15. Available from http://www.forrex.org/sites/default/files/publications/articles/streamline_vol3_no2_art2.pdf.

Pollock, M., Pess, G., Beechie, T.J., and Montgomery, D.R. 2004. The importance of beaver ponds to coho salmon production in the Stillaguamish River basin, Washington, USA. N. Am. J. Fish. Manage. **24**: 749–760. doi:10.1577/M03-156.1.

Quinn, T.P., and Peterson, N.P. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Can. J. Fish. Aquat. Sci. **53**(7): 1555–1564. doi:10.1139/f96-092.

Radtke, H.D., and Carter, C.N. 2009. Economic effects and social implications from federal Mitchell Act funded hatcheries [online]. Oregon City, Ore. Available from http://www.nativefishsociety.org/documents/Radtke_Ec_Effects_and_So_]Impl.pdf.

Reeves, G., Everest, F., and Nickelson, T. 1989. Identification of physical habitats limiting the production of Coho salmon in western Oregon and Washington [online]. US Department of Agriculture, Forest Service, Pacific Northwest Research Station., Gen. Tech. Rep. PNW-GTR-245. Available from http://www.krisweb.com/biblio/gen_usfs_reevesetal_1989_gtr245.pdf.

Riley, S.C., and Fausch, K.D. 1995. Trout population response to habitat enhancement in six northern Colorado streams. Can. J. Fish. Aquat. Sci. **52**(1): 34–53. doi:10.1139/f95-004.

Roni, P., Beechie, T., Bilby, R., Leonetti, F., Pollock, M., and Pess, G. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. N. Am. J. Fish. Manage. **22**: 1–20. doi:10.1577/1548-8675(2002)022<0001:AROSRT>2.0.CO;2.

Roni, P., Hanson, K., Beechie, T., Pess, G., Pollock, M., and Bartley, D. 2005. Habitat rehabilitation for inland fisheries Global review of effectiveness and guidance. FAO Fisheries Technical Paper 484.

Roni, P., Morley, S.A., Garcia, P., Detrick, C., King, D., and Beamer, E. 2006. Coho salmon smolt production from constructed and natural floodplain habitats. Trans. Am. Fish. Soc. **135**: 1398–1408. doi:10.1577/T05-296.1.

Roni, P., Hanson, K., and Beechie, T. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. N. Am. J. Fish. Manage. **28**: 856–890. doi:10.1577/M06-169.1.

Roni, P., Pess, G., Beechie, T., and Morley, S. 2010. Estimating changes in coho salmon and steelhead abundance from watershed restoration: how much restoration is needed to measurably increase smolt production? N. Am. J. Fish. Manage. **30**: 1469–1484. doi:10.1577/M09-162.1.

Roni, P., Bennett, T., Holland, R., Pess, G., Hanson, K., Moses, R., McHenry, M., Ehinger, W., and Walter, J. 2012. Factors affecting migration timing, growth, and survival of juvenile coho salmon in two coastal Washington watersheds. Trans. Am. Fish. Soc. **141**: 890–906. doi:10.1080/00028487.2012.675895.

Rosenfeld, J.S., and Hatfield, T. 2006. Information needs for assessing critical habitat of freshwater fish. **63**(3): 683–698. doi:10.1139/F05-242.

Rosenfeld, J.S., Raeburn, E., Carrier, P.C., and Johnson, R. 2008. Effects of side channel structure on productivity of floodplain habitats for juvenile Coho salmon. N. Am. J. Fish. Manage. **28**: 1108–1119. doi:10.1577/M07-027.1.

Ruckelshaus, M.H., Levin, P., Johnson, J.B., and Kareiva, P.M. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annu. Rev. Ecol. Syst. **33**: 665–706. doi:10.1146/annurev.ecolsys.33.010802.150504.

Saldi-Caromile, K.K., Bates, K., Skidmore, P., Barenti, J., and Pineo, D. 2004. Stream habitat restoration guidelines [online]. Olympia, Washington. Available from http://wdfw.wa.gov/publications/00043/wdfw00043.pdf.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Edward Arnold, London, UK.

Sharma, R., and Hilborn, R. 2001. Empirical relationships between watershed characteristics and Coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams. Can. J. Fish. Aquat. Sci. **58**(7): 1453–1463. doi:10.1139/f01-091.

Sheng, M., Foy, M., and Fedorenko, A.Y. 1990. Coho salmon enhancement in British Columbia using improved groundwater-fed side channels. Can. Manusc. Rep. Fish. Aquat. Sci. 2071.

Slaney, P., and Zaldokas, D. 1997. Fish habitat rehabilitation procedures [online]. Watershed Restoration Technical Circular No. 9. Available from http://www.env.gov.bc.ca/wld/documents/wrp/wrtc_9.pdf.

Slaney, T.L., Hyatt, K.D., Northcote, T.G., and Fielden, R.J. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries, **21**: 20–35. doi:10.1577/1548-8446(1996)021<0020:SOASAT>2.0.CO;2.

Solazzi, M.F., Nickelson, T.E., Johnson, S.L., and Rodgers, J.D. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Can. J. Fish. Aquat. Sci. **57**(5): 906–914. doi:10.1139/f00-030.

Sparks, R.E. 1995. Need for ecosystem management of large rivers and their floodplains. BioScience, **45**: 168–182. doi:10.2307/1312556.

Stewart, G.B., Bayliss, H.R., Showler, D.A, Sutherland, W.J., and Pullin, A.S. 2009. Effectiveness of engineered in-stream structure mitigation measures to increase salmonid abundance: a systematic review. Ecol. Appl. **19**: 931–941. doi:10.1890/07-1311.1. PMID:19544735.

Sutherland, W.J., Pullin, A.S., Dolman, P.M., and Knight, T.M. 2004. The need for evidence-based conservation. Trends Ecol. Evol. **19**: 305–308. doi:10.1016/j.tree.2004.03.018. PMID:16701275.

Thompson, D.M. 2006. Did the pre-1980 use of in-stream structures improve streams? A reanalysis of historical data. Ecol. Appl. **16**: 784–796. doi:10.1890/1051-0761(2006)016%5B0784:DTPUOI%5D2.0.CO;2.

White, S.L., Gowan, C., Fausch, K.D., Harris, J.G., and Saunders, W.C. 2011. Response of trout populations in five Colorado streams two decades after habitat manipulation. Can. J. Fish. Aquat. Sci. **68**(12): 2057–2063. doi:10.1139/f2011-125.

Whiteway, S.L., Biron, P.M., Zimmermann, A., Venter, O., and Grant, J.W.A. 2010. Do in-stream restoration structures enhance salmonid abundance? A meta-analysis. Can. J. Fish. Aquat. Sci. **67**(5): 831–841. doi:10.1139/F10-021.