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[Article]

Effects of Side Channel Structure on Productivity of Floodplain Habitats for Juvenile Coho Salmon

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Abstract.—Numerous artificial side channels have been constructed in British Columbia and the Pacific Northwest to compensate for habitat loss from floodplain development. We reviewed data from published studies on natural and restored side channel habitats to determine how design features influence productive capacity for juvenile coho salmon *Oncorhynchus kisutch*. Average density and biomass of coho salmon parr were significantly higher in stream-type side channels (3.4 parr/m^2 and 8.01 g/m^2, respectively) than in pond-type side channels (0.8 parr/m^2 and 2.37 g/m^2). Although total parr biomass was three times higher in stream-type side channels, average parr weight was 47% lower, suggesting greater density-dependent limitation of growth from higher recruitment of juveniles to stream-type habitats. Parr abundance declined from late summer to early spring in both side channel types but appeared to decrease more quickly in stream-type side channels, suggesting greater self-thinning in stream-type habitat from mortality or immigration to slower pond or main-stem habitat as fish sought lower velocities for overwintering. Fish density in a single off-channel complex that contained both stream and pond habitats (fish were able to move between habitats) was also higher in stream habitats, although fish were significantly larger in pond habitats than in stream habitats. Parr density in stream-type side channels was constant with increasing channel size, whereas density in pond-type side channels was a decreasing function of side channel area. Smolt production data were more limited and variable, and production was not significantly different between stream- and pond-type side channels. Smolt density (smolts produced/m^2 of channel habitat) was also a decreasing function of total side channel area, indicating that the optimal side channel habitat size (or pond size within a side channel complex) was below 5,000–10,000 m^2. Side channels that incorporate a diversity of flowing- and standing-water areas are most likely to provide the variety of habitats (i.e., spawning, summer rearing, and overwintering) required by salmonids to complete their life cycle.

The basinwide distribution of productive habitat for juvenile salmonids is strongly influenced by downstream gradients in physical habitat structure along the river continuum (Rosenfeld et al. 2007). Densities of juvenile salmon tend to be highest in smaller, intermediate-gradient streams (e.g., Rosenfeld et al. 2000) than in larger river main stems, where higher water velocity may create less suitable conditions for smaller fish, particularly at high flows (McMahon and Hartman 1989). Downstream river reaches would be relatively inhospitable for smaller fish without the natural development of off-channel habitat on river floodplains, which may greatly increase juvenile rearing capacity (Beechie et al. 1994) and stock size (Sharma and Hilborn 2001). Seasonal or permanently wetted side channels consist of old river channels formed by channel avulsion or migration, ponds created by American beavers *Castor canadensis* on floodplain side channels or tributary streams, and slough habitat (Beechie et al. 1994; Pollock et al. 2004). Side channels and ponds are natural features of most undisturbed river floodplains (Collins and Montgomery 2002) and provide suitable rearing habitat for many juvenile salmonids farther downstream than would otherwise be expected.

Industrial, urban, and agricultural development on river floodplains has greatly reduced the abundance and complexity of off-channel habitats throughout Europe and North America (Sedell and Froggatt 1984; Beechie et al. 1994; Sparks 1995); in many cases,

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habitat is reduced to a single-braid channel with marginal suitability as rearing habitat for juvenile fish. Although some of the first groundwater-fed side channels in North America were originally constructed as spawning channels for chum salmon *Oncorhynchus keta* (Lister et al. 1980; Sheng et al. 1990; Morley et al. 2005), biologists soon recognized the importance of side channel habitat to other species (particularly juvenile coho salmon *O. kisutch* and trout) and began constructing artificial side channels to address this habitat deficit. Both groundwater and surface-fed side channels are now regularly constructed to increase habitat capacity for juvenile salmonids, particularly coho salmon, in western North America (Saldi-Caromile et al. 2004; Morley et al. 2005; Roni et al. 2006).

Although numerous side channels have been constructed and the effectiveness of individual restoration projects has been widely reported, there has been little retrospective analysis of the effect of channel design on productive capacity or stock size (but see Morley et al. [2005] and Roni et al. [2006] for recent reviews). This is unfortunate because the wholesale construction of artificial side channels can be treated as an adaptive management experiment to provide insight into the effect of channel design on productive capacity as well as the natural drivers of productive capacity at a watershed scale (Sharma and Hilborn 2001; Jansson et al. 2005). Lotic versus lentic habitats (streams versus ponds or lakes) represent one of the most fundamental dichotomies in freshwater ecosystems, and meta-analysis suggests that lotic freshwaters support higher biomass and production of fish than do lentic freshwaters (Randall et al. 1995). Comparison of production from pond- versus stream-type side channel habitats provides an opportunity to evaluate this hypothesis and its relevance to river restoration.

Our objectives were to determine how design features of side channel habitats affect productive capacity for juvenile salmonids based on a retrospective analysis of published studies of natural and artificial side channels. Specifically, we used the design extremes of pond- versus stream-type side channels as the major habitat contrast to assess whether the two types have different capacities, with the null hypothesis that stream-type habitats in freshwater support a higher biomass and density of fish than pond-type habitats (after Randall et al. 1995; but see Nash et al. [1999] for a divergent view). We also include available data on side channel complexes with combined stream and pond habitats to evaluate additional design features, such as the effect of side channel size (area) on productive capacity and the potential effects of nutrient enrichment from spawner carcasses in stream-type side channels. Because the observed density and biomass of fish in stream- versus pond-type side channel habitats could be confounded by underrecruitment in pond-type side channels with limited spawning habitat (Roni et al. 2006), we also compared fish size and abundance between adjacent pond and stream habitats within a single off-channel complex where fish were capable of moving between habitats, thereby partly controlling for recruitment effects.

Methods

Literature review: design effects on juvenile coho salmon abundance.—We performed a literature search to identify studies in primary journals or technical reports that reported biomass or density of fish (either parr abundance or smolt output) from natural or constructed side channel habitats in British Columbia and the Pacific Northwest (Tables 1, 2). We used the Web of Science to search primary aquatic ecology journals to identify articles with keywords related to juvenile salmonid production in side channel and off-channel habitats. Older articles that were not listed in electronic databases were identified based on citations in later publications. We focused our analysis on side channel habitats and excluded studies that reported estimates of juvenile salmonid density from main-stem habitats (i.e., pools, riffles, or main-stem lakes and ponds) because definitive studies of main-stem habitat use by juvenile coho salmon already exist (e.g., Nickleson et al. 1992a). We also excluded studies, sites, or sample years in studies where authors explicitly stated that habitats were underrecruited because of insufficient spawning adults (e.g., in years immediately after side channel construction). For studies in which density estimates were reported (e.g., from depletion electroshocking removal), we estimated population size in a side channel by multiplying density by total side channel area. For studies in which total populations were estimated (e.g., Petersen mark–recapture estimates in ponds), we calculated density as population size divided by total habitat area.

We focused our literature review and analysis on coho salmon, which were the most abundant species examined in all studies. Steelhead *O. mykiss* were the second most abundant species, and juvenile steelhead use of side channel habitats was analyzed separately for the smaller subset of studies in which steelhead abundance was reported. Side channel habitats were classified as pond type, stream type, combined (complexes with both pond- and stream-type habitats), intermittent, or ephemeral (Tables 1, 2). Stream-type channels were either constructed, groundwater-fed side

TABLE 1.—Summary of habitat origin (C = constructed; N = natural), habitat area (m^2), presence of hatcheries, presence of chum salmon spawners, sampling month, and coho salmon parr abundance (total number) and density (fish/m^2) reported for stream-type, ephemeral, intermittent, and pond-type side channel habitats of British Columbia and the Pacific Northwest.

Habitat type	Habitat origin	Area (m^2)	Hatchery presence	Chum salmon presence	Month	Coho salmon parr abundance	Coho salmon density (fish/m^2)	Reference
Stream	C	2,340	No	Yes	Sep	9,477	4.1	Decker 1999
	C	2,214	No	Yes	Sep	11,513	5.2	Decker 1999
	C	1,488	No	Yes	Sep	5,282	3.5	Decker 1999
	C	1,890	No	Yes	Sep	7,560	4.0	Decker 1999
	C	1,830	No	Yes	Sep	3,386	1.9	Decker 1999
	C	2,478	No	Yes	Nov	7,434	3.0	Giannico and Hinch 2003
	C	2,225	No	Yes	Nov	10,569	4.8	Giannico and Hinch 2003
	C	850	No	Yes	Sep	11,978	14.1	Sheng et al. 1990
	C	1,753	No	Yes	Dec	3,868	2.2	Sheng et al. 1990
	N	500	No	No	Jan	1,397	2.8	Swales et al. 1986
	N	500	No	No	Mar	1,188	2.4	Swales et al. 1986
Ephemeral	N	259	No	No	Nov	227	0.9	Brown and Hartman 1988
	N	327	No	No	Nov	23	0.1	Brown and Hartman 1988
	N	243	No	No	Nov	110	0.5	Brown and Hartman 1988
	N	395	No	No	Nov	360	0.9	Brown and Hartman 1988
	N	185	No	No	Nov	159	0.9	Brown and Hartman 1988
	N	115	No	No	Nov	62	0.5	Brown and Hartman 1988
Intermittent	N	405	No	No	Nov	393	1.0	Brown and Hartman 1988
	N	553	No	No	Nov	356	0.6	Brown and Hartman 1988
Pond	C	3,936	No	Yes	Sep	2,539	0.6	Decker 1999
	C	3,300	No	Yes	Sep	1,997	0.6	Decker 1999
	C	630	Yes	Yes	Jul	1,230	2.0	This study
	N	9,700	No	No	Sep	4,300	0.4	Swales et al. 1986
	N	600	No	No	Oct	920	1.5	Swales et al. 1986
	N	10,000	Yes	No	Nov	1,092	0.1	Swales and Levings 1989
	N	1,000	Yes	No	Nov	243	0.2	Swales and Levings 1989
	N	1,300	Yes	No	Nov	1,305	1.0	Swales and Levings 1989

channels (n = 9; Sheng et al. 1990; Dekker 1999; Giannico and Hinch 2003) or natural stream-type side channels ($n = 2$; Swales et al. 1986). Pond-type habitats included ponds created by American beavers, sloughs, abandoned side channels, and constructed ponds. Ephemeral and intermittent habitats included natural floodplain tributaries, swamps, and abandoned American beaver ponds (Brown and Hartman 1988). To

TABLE 2.—Habitat area (m^2), coho salmon and steelhead smolt abundances, coho salmon smolt weight (g) and density (fish/m^2), and steelhead smolt density reported for stream-type, pond-type, and combined side channel habitats of British Columbia and the Pacific Northwest.

Habitat type	Area (m^2)	Coho salmon smolts	Steelhead smolts	Coho salmon smolt weight (g)	Coho salmon density (fish/m^2)	Steelhead density (fish/m^2)	Reference
Stream	2,639	1,351	2	7.6	0.511936	0.00076	Blackwell et al. 1999
	12,251	2,171	110	14.7	0.17721	0.0090	Blackwell et al. 1999
	2,478	2,528		10.59	1.020178		Giannico and Hinch 2003
	2,225	1,202		4.99	0.540225		Giannico and Hinch 2003
	2,000	6,500		7.2	3.25		Sheng et al. 1990
	850	241		16.6	0.283529		Sheng et al. 1990
	5,000	2,162		19.2	0.4324		Cederholm et al. 1988
	13,320	324			0.024324		Lister et al. 1980
	2,040	215			0.105392		Lister et al. 1980
	840	81			0.096429		Lister et al. 1980
	770	11			0.014286		Lister et al. 1980
Combined	4,882	1,736	1	7.9	0.355592	0.00021	Blackwell et al. 1999
	6,955	2,106	52	6.9	0.302804	0.0075	Blackwell et al. 1999
Pond	15,000	5,133	132	8.5	0.3422	0.0088	Blackwell et al. 1999
	6,000	818	2	14.5	0.136333	0.00033	Blackwell et al. 1999
	17,500	7,869		20.6	0.449657		Blackwell et al. 1999
	10,000	1,257	62		0.1257	0.0062	Swales and Levings 1989
	8,500	3,613		13	0.425059		Peterson 1982
	1,200	1,534		18.3	1.278333		Peterson 1982
	565	11			0.019469		Lister et al. 1980
	1,675	175			0.104478		Lister et al. 1980

ensure a clear contrast between lotic and lentic off-channel habitats, we included as pond- or stream-type habitat only those side channels that were clearly described either as deeper, slow-water ponds or as stream-type channels (i.e., flowing water habitat). When a study reported fish abundance or average weight over multiple years, we used an average value to avoid pseudoreplication.

Comparison of fish abundance in stream and pond habitats within a combined side channel complex.—Comparison of fish size and abundance in pond- versus stream-type side channels is confounded by differences in fish density between watersheds and the possibility that some habitats may be systematically over- or underrecruited (e.g., spawning in channels may lead to overrecruitment, whereas juvenile fish may have poor recruitment or access to pond habitats). To get a better understanding of differences in fish size and abundance between stream- and pond-type side channel habitats, we compared density of fish between adjacent stream and pond habitats within a single side channel habitat complex. We assumed that if fish could move freely between adjacent habitats, then realized fish density (under ideal free distribution assumptions) would reflect both habitat capacity and fish preferences.

The off-channel complex was built on the floodplain of the Chilliwack River in southwestern British Columbia (Blackwell et al. 1999) and consisted of a series of three ponds linked by 100-m-long spawning streams on an old floodplain terrace. The ponds were originally shallow American beaver ponds that were enlarged by constructing berms at their downstream ends. We sampled fish in the middle pond as well as the pond's inlet and outlet streams (Figure 1). This pond was naturally subdivided into a shallow upper section and a deep lower section by an old American beaver dam. We sampled the shallow and deep sections separately to assess whether habitat depth influenced size and density of juvenile salmonids along a depth gradient from shallow inlet stream to deep pond. Maximum depths in the shallow and deep pond sections were 1.3 and 3.0 m, respectively. The shallow pond section had measurable flow; average velocities at the thalweg in the shallow and deep sections were 3 and 0 cm/s, respectively. Area was 1,940 m^2 for the shallow section and 4,900 m^2 for the deep section. Although the inlet and outlet streams were constructed, habitat features were complex and represented typical stream habitat with distinct riffle, run, glide, and pool habitat units. Substrate ranged from sand to boulders, and most channel units contained abundant submerged stumps, rootwads, logs, or undercuts. Width was 2.5 m and maximum depth was 30 cm for the inlet stream; the outlet stream was 4.2 m wide and had a maximum depth of 35 cm. The outlet stream reach consisted of regular pool–riffle sequences. The inlet stream consisted of a predominantly glide–pool reach and a long riffle reach that was too shallow to be used by fish. We therefore sampled fish from the glide–pool reach in the inlet stream and from the pool–riffle reach in the outlet stream.

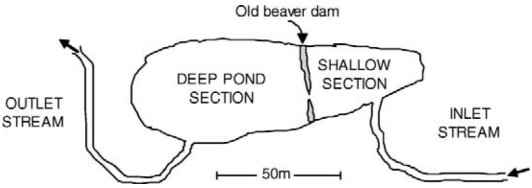

FIGURE 1.—Schematic diagram of a side channel habitat complex used to assess differences in juvenile coho salmon size and density between adjacent pond- and stream-type side channel habitats in the Chilliwack River, British Columbia.

We measured fish density separately in the shallow and deep sections of the pond using mark–recapture. On August 28, 2006, minnow traps ($N = 118$) were each baited with 2 g of salmon roe (Swales 1987) and were set for 2–3 h. Captured fish were identified, measured to the nearest millimeter (fork length), weighed to the nearest 0.01 g, given a small identifying clip on the caudal fin, and released. Fish were recaptured the next day using the same minnow trapping protocol, and fish abundance was estimated using a Petersen mark–recapture estimate (Krebs 1999). Fish abundance was determined by triple-pass removal electrofishing within the representative 20-m (inlet stream; July 7, 2006) or 25-m (outlet stream; September 6, 2006) reach described above. We used block nets (7-mm mesh) to isolate the sample reach during fish removal with a Smith-Root Model LR24 backpack electroshocker. Fish abundance was estimated from removal data using a depletion estimator described by Schnute (1983).

Data analysis.—Because fish size increases over the growing season and many studies in the literature review provided serial measures of fish length and density over time, we selected size and density data reported for November or for the month closest to November in each study to control for seasonal sampling effects. Fall was chosen because most studies sampled abundance in the very late summer or fall. Our analysis focused on coho salmon, since most studies reported coho salmon abundance (the dominant species present), and trends for total juvenile salmonid abundance were similar to those of coho salmon abundance.

We used single-factor analysis of variance (ANOVA) to test for habitat effects (pond [$n = 8$], stream [n

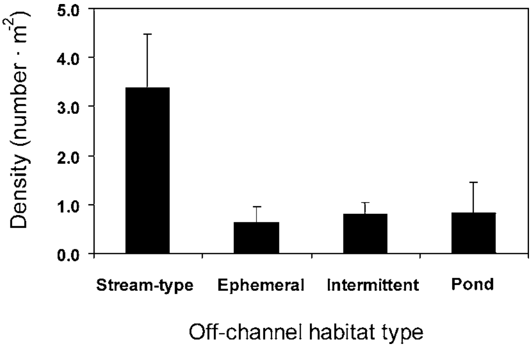

FIGURE 2.—Mean (±SD) density (fish/m^2) of juvenile coho salmon parr in stream-type, pond-type, intermittent, and ephemeral side channel habitats of British Columbia and the Pacific Northwest (see Tables 1, 2 for data sources).

$= 11$], ephemeral [$n = 6$], and intermittent [$n = 2$]) on average coho salmon parr density, size, and biomass. Tukey's test was used to evaluate a posteriori differences in mean density between channel types. We also tested for habitat effects on total biomass for the subset of studies that provided this information. Dependent variables in ANOVA or regression were $\log_{10}(x + a)$ transformed where necessary to meet assumptions of normality and equal variance. The constant a in $\log_{10}(x + a)$ transformation was selected based on the criteria of maximizing normality and minimizing skewness and kurtosis of regression residuals (Berry 1987), which were assessed using the Shapiro–Wilk statistic (SAS Institute 1989) and a frequency histogram of residuals. The assumption of homogeneity of variance in multiple regression was evaluated by testing for a significant correlation between the absolute value of residuals and predicted values. All final analyses met assumptions of normality and homogeneity of variance at a significance level of 0.05.

To evaluate whether changes in parr density over time differed between pond- and stream-type side channels, we regressed parr density on calendar day and tested for a habitat × time interaction (i.e., using analysis of covariance [ANCOVA] to test for differences in slope between pond- and stream-type habitats). To avoid pseudoreplication in assessment of seasonal effects, we randomly chose a single density observation from studies that reported multiple (i.e., seasonal or monthly) density estimates.

We evaluated the effect of off-channel habitat size and morphology (pond versus stream) on total parr production by regressing $\log_{10}$(parr abundance) against $\log_{10}$(total side channel area). A slope for this log–log relationship that is not significantly different from 1.0 indicates that fish density is constant as channel size increases; a slope less than 1.0 indicates that fish density declines with increasing side channel area. We also regressed $\log_{10}$(total smolt out-migrants) on $\log_{10}$(side channel area) to evaluate the effect of side channel size on total smolt production based on data from our review alone ($n = 21$ measurements) and for a combined data set that included smolt output data from Roni et al. (2006; total $n = 51$ measurements). We used a $\log_{10}$(smolt out-migrants + 145) transformation to normalize residuals.

Because nutrient enrichment from chum salmon eggs, fry, or spawner carcasses has the potential to affect abundance of other juvenile salmonids, we used a t-test to determine whether parr density differed between side channels with and without spawning chum salmon.

To evaluate whether fish size differed between pond- and stream-type side channel habitats when fish were free to move between habitats, we used ANOVA to compare weights between fish collected in the shallow and deep pond sections and those collected in inlet and outlet streams within the combined off-channel habitat complex. We compared density between habitats based on overlap of 95% confidence intervals (CIs) calculated from Petersen mark–recapture estimates (pond samples) or electroshocking depletion estimates (inlet and outlet streams). Fish biomass (g/m^2) was calculated as the product of density and average fish weight and was also compared based on overlap of 95% CIs.

Results

Habitat Effects on Parr Abundance

Coho salmon parr density was approximately four times higher in stream-type side channels than in pond, ephemeral, or intermittent side channels (ANOVA: $F_{3,23} = 5.48$, $P < 0.0001$; Figure 2). Density remained higher in stream-type side channels even when an extremely high-density outlier (Worth Creek, 14 parr/m^2; Sheng et al. 1990) was dropped from the analysis (ANOVA: $F_{3,22} = 21.3$, $P < 0.0001$; a posteriori Tukey's tests showed no overlap of 95% CIs between stream-type side channels and the other three habitat types (pond-type, ephemeral, and intermittent side channels, which were not significantly different from one another). Average parr weight (reported for only 16 of 27 studies) was higher in pond-type (mean ± SD $= 5.98 \pm 2.88$ g) than in stream-type side channels (3.14 ± 1.13 g; $t_{0.05,14} = 2.59$, $P < 0.029$). Parr biomass (density × average weight) remained significantly higher in stream-type (8.01 g/m^2) than in pond-type side channels (2.37 g/m^2; $t_{1,12} = 4.28$, $P < 0.001$) despite the higher average coho salmon weight in ponds.

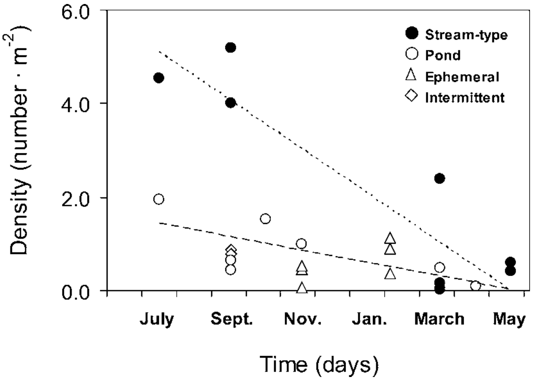

FIGURE 3.—Seasonal changes in coho salmon parr density (fish/m^2) within pond-type (open circles, dashed line), stream-type (shaded circles, dotted line), ephemeral (triangles), and intermittent (diamonds) side channel habitats of British Columbia and the Pacific Northwest (see Tables 1, 2 for data sources).

Coho salmon parr density was higher in side channels where spawning chum salmon were present (4.0 fish/m^2) than in side channels where chum salmon were absent (1.0 fish/m^2; $t_{0.05,25} = 2.8$, $P < 0.017$). However, presence of chum salmon was highly correlated with habitat type (9 of 12 chum salmon sites were stream-type side channels), so this apparent chum salmon spawner effect was confounded by a habitat effect. To determine whether higher parr densities in stream-type side channels were due to the presence of chum salmon (rather than a habitat effect), we compared densities between stream- and pond-type side channels where chum salmon were absent. Parr density in stream-type side channel sites that lacked spawning chum salmon (mean ± SD = 2.6 ± 0.3 fish/m^2) was still higher than parr density in pond-type sites (ANOVA: $F_{1,17} = 8.1$, $P < 0.002$; Tukey's test: $P < 0.05$), suggesting that any chum salmon effect was largely a habitat effect.

The difference in parr density between stream- and pond-type side channels was most pronounced in summer (July); densities appeared to decrease overwinter in both habitats and converged in the spring just before smolt out-migration (Figure 3). The decline in density from summer to spring was greater in stream-type habitat than in pond-type habitat (i.e., the habitat × time interaction, time effect, and habitat effect were significant; ANCOVA: interaction $F_{1,16} = 10.7$, $P < 0.006$, time $F_{1,16} = 33.9$, $P < 0.0001$, habitat $F_{1,16} = 23.9$, $P < 0.0003$; Figure 3). Parr densities in seasonally wetted (fall and winter) ephemeral and intermittent side channels were similar to densities in pond-type channels (Figure 3).

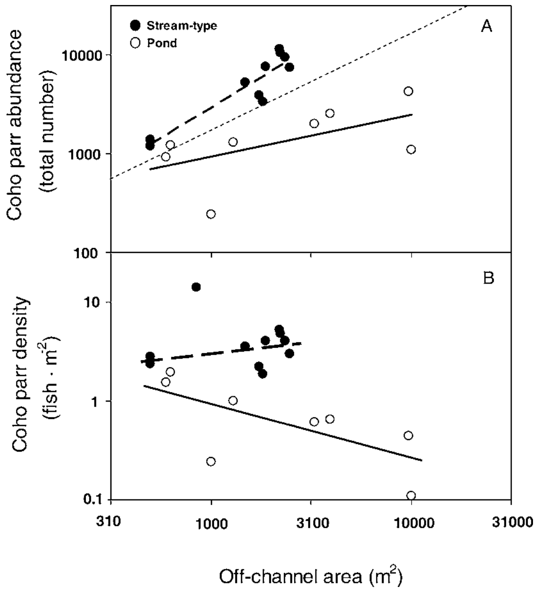

FIGURE 4.—Regressions describing coho salmon use of stream-type (shaded circles, dashed line) and pond-type (open circles, solid line) side channel habitats of British Columbia and the Pacific Northwest (see Tables 1, 2 for data sources): **(A)** slope of the regression of $\log_{10}$ (total parr abundance) on $\log_{10}$ (side channel area) is close to 1.0 for stream-type habitat (slope of 1.0 is represented by the fine dashed line), indicating relatively constant fish density with increasing side channel area; and **(B)** slope is less than 1.0 for pond-type side channels, indicating a decline in parr density with increasing area of pond-type side channels.

Estimates of total parr abundance were positively correlated with side channel area for both pond- and stream-type side channels, but there was a habitat × area interaction when the high-density stream outlier (Worth Creek, 14 fish/m^2; Sheng et al. 1990) was dropped from the analysis (ANCOVA: interaction $F_{1,17} = 5.2$, $P < 0.038$, habitat $F_{1,17} = 2.8$, $P < 0.11$, area $F_{1,17} = 22.2$, $P < 0.0003$; Figure 4A). The slope of the regression of $\log_{10}$(parr abundance) on $\log_{10}$(side channel area) did not differ from 1.0 (mean ± SE = 1.24 ± 0.35), indicating that parr density in stream-type side channels was approximately constant with increasing channel size. The regression slope for pond-type side channels was significantly less than 1.0 (0.43 ± 0.18), indicating that parr density declined with increasing area (Figure 4B).

Habitat Effects on Smolt Production

Based on data from our literature review, coho salmon smolt out-migration was positively correlated with side channel area ($\log_{10}$[smolt out-migrants] = 1.2 $\log_{10}$[area] − 1.36; $F_{1,19} = 17.9$, $r^2 = 0.48$, $P < 0.0005$;

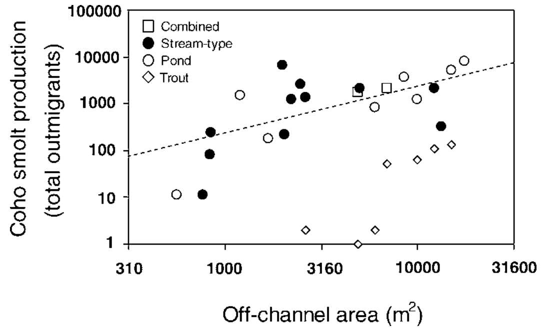

FIGURE 5.—Relation between $\log_{10}$(number of coho salmon out-migrants; i.e., smolt production) and $\log_{10}$(side channel area, m^2) for pond-type (open circles), stream-type (shaded circles), and combined (open squares) side channel habitats of British Columbia and the Pacific Northwest (see Tables 1, 2 for data sources). Steelhead smolt production data (open diamonds) are also presented. Dashed line represents the best-fit regression line for coho salmon production versus area for all habitat types (no significant difference between pond- and stream-type habitats).

Figure 5). The slope of the regression of $\log_{10}$(smolt out-migrants) on $\log_{10}$(area) for all habitats combined (mean ± SE = 1.20 ± 0.29) did not differ from 1.0, indicating that smolt density (smolts produced/m^2) did not change with side channel area (maximum area in the data set was approximately 17,500 m^2). There was also no detectable effect of side channel type (pond, stream, or combined) on smolt density (ANCOVA: $F_{2,17} = 0.09$, $P < 0.92$). When the coho salmon smolt production data set from our literature review was combined with data from Roni et al. (2006; including a larger maximum off-channel area of 140,000 m^2), total smolt production increased with side channel area (Figure 6A) and the slope (mean ± SE = 0.61 ± 0.10) of the relationship ($\log_{10}$[smolt out-migrants + 145] = $0.61 \cdot \log_{10}$[area] + 0.91; $F_{1,49} = 36.9$, $r^2 = 0.43$, $P <$ 0.0001) was significantly less than 1.0. Coho salmon smolt density was consequently a declining function of channel area ($\log_{10}\{$[smolt out-migrants + 145]/area$\}$ = $-0.39 \cdot \log_{10}$[area] + 0.91; $F_{1,49} = 15.0$, $r^2 = 0.23$, $P <$ 0.0003; Figure 6B). Steelhead smolt out-migration was linearly related to channel area (smolt out-migrants = [0.012 × area] − 46; $F_{1,5} = 57.3$, $P < 0.0006$), but steelhead smolt abundance was over an order of magnitude lower than coho salmon smolt abundance (Figure 5).

Fish Abundance in Stream- versus Pond-Type Habitats within a Side Channel Complex

Consistent with observations from our meta-analysis, fish density within the side channel complex was higher in stream-type habitat than in pond-type habitat (Figure 7A), although there was some overlap of 95% CIs (i.e., between density estimates for the outlet stream and the shallow pond section). There was a consistent trend of decreasing fish density as habitat depth increased (i.e., ascending order of depth: inlet stream, outlet stream, upper pond section, and lower pond section). There was also a concurrent increase in average fish size along the same depth gradient (ANOVA: $F_{3,375} = 26.0$, $P < 0.0001$); a posteriori Tukey's tests showed no overlap in 95% CIs except between shallow and deep pond sections, whereas all other pairwise comparisons of habitats indicated significant differences (Figure 7B). Total fish biomass tended to be higher in stream-type habitat than in pond-type habitat (Figure 7C), although differences in biomass between habitat types were not significant.

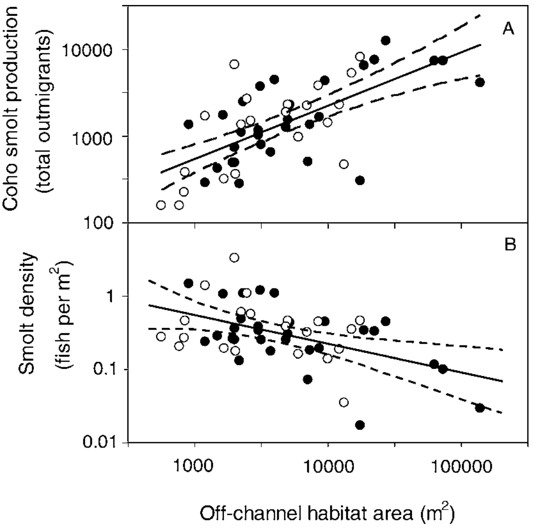

FIGURE 6.—Comparison of data describing coho salmon abundance in pond-type, stream-type, and combined side channel habitats of British Columbia and the Pacific Northwest (open circles; see Tables 1, 2 for data sources) and additional data reported by Roni et al. (2006; shaded circles): (**A**) $\log_{10}$(number of out-migrants) (i.e., smolt production) versus $\log_{10}$(side channel area, m^2) and (**B**) $\log_{10}$(smolt density, fish/m^2) versus $\log_{10}$(side channel area). In each panel, the solid line represents average trend and dashed lines represent 95% confidence intervals.

Discussion

When juvenile rearing habitat is limiting a population, creation of new habitat will elicit a population response by increasing the quantity or quality of available habitat, or both quantity and quality (Nickleson et al. 1992b; Rosenfeld and Hatfield 2006). For example, Sharma and Hilborn (2001) showed that total coho salmon smolt production was strongly correlated with the area of pond habitat across 14 western Washington streams, but areal smolt production from pond habitat (0.07 smolts/m^2) was much lower than production from main-stem pool habitat (0.39 smolts/m^2) . Their analysis suggests that the positive effect of pond habitat on smolt production at a catchment scale results from an increase in total area available for smolt production (i.e., habitat quantity) rather than an increase in extremely high-quality habitat (although smolts from ponds tend to be larger than those from stream-type side channels; Roni et al. 2006). While the Sharma and Hilborn (2001) analysis demonstrates that increasing habitat area alone will generally be beneficial to habitat-limited populations, designs that optimize both the quality and quantity of habitat will maximize the benefits provided by a restoration project.

Flowing (stream-type) and standing water (pond-type) side channels represent the design extremes of side channel habitats as well as the most fundamental dichotomy in freshwater environments (i.e., lotic versus lentic habitats). In a meta-analysis of fish production from lakes and streams, Randall et al. (1995) found that average fish biomass in streams was double that in lakes and production in streams was triple that in lakes. This pattern is in part associated with smaller average size and higher production : biomass ratio of stream fish (Randall et al. 1995) but nevertheless supports the expectation of higher productivity in lotic habitats. The mechanisms underlying these productivity differences remain unclear, but higher production in streams may be caused by relatively higher terrestrial subsidies (Baxter et al. 2005) associated with a larger riparian interface (ratio of perimeter : surface area) or a relatively large euphotic zone in shallow lotic habitats.

Applying this logic to off-channel habitats generates the expectation of higher parr and smolt production in stream-type side channels. This prediction was partly supported by our literature review and field observations. Density and biomass of coho salmon parr in published studies were higher in stream-type side channels than in pond-type side channels, and our comparison of abundance in stream- and pond-type habitats within the side channel complex showed a similar pattern. These differences may reflect the ecological role of stream habitats in the salmonid life cycle; because salmonids spawn in riffles, stream habitats are more likely to be fully seeded than ponds, resulting in higher stream density and areal production. Densities in stream- and pond-type side channels exhibited the greatest difference during summer and appeared to converge overwinter, supporting the inference of ontogenic habitat shifts into deeper areas.

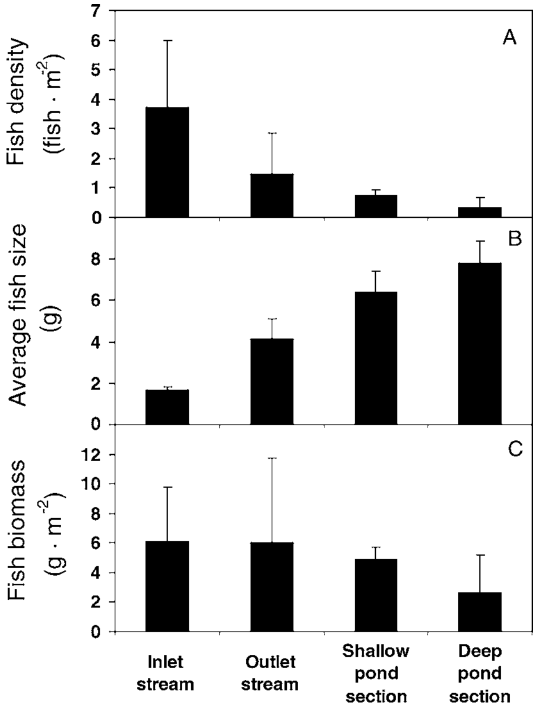

FIGURE 7.—Coho salmon (**A**) density (fish/m^2; with 95% confidence interval [CI]), (**B**) average weight (g; with SD), and (**C**) total biomass (g/m^2; with 95% CI) in different habitat types (inlet and outlet streams; shallow upper and deep lower pond sections) within a single side channel habitat complex of the Chilliwack River, British Columbia, 2006 (see Figure 1).

Greater risk of predation by larger fish may be an additional factor contributing to avoidance of deeper habitats by smaller conspecifics (Schlosser 1987; Biro et al. 2003).

Nutrient enrichment from spawner carcasses or direct consumption of carcass tissue (Bilby et al. 1998; Gende et al. 2002) or chum salmon fry (Sheng et al. 1990) may also contribute to the higher observed productivity in stream-type side channels. However, densities in stream-type side channels were higher than those in pond-type habitats even when spawning chum salmon were absent, suggesting that carcass enrichment is a contributing factor to higher productivity rather than the causative factor.

While a comparison of productivity in lotic and lentic habitats provides some insight into the effects of channel design on fish production, the treatment of streams and ponds as competing habitat types in restoration is simplistic. Stream and pond habitats are better viewed as complementary since they probably play different roles in the life history of salmonids. Stream habitat is essential for spawning and may be more productive for juvenile rearing, but pond habitat may be a better (more energetically benign) area for overwintering once a sufficient size has been attained to reduce mortality risk (e.g., Bustard and Narver 1975). Side channel complexes that are intended as stand-alone habitats for production of juvenile fish should therefore include both lotic (spawning and rearing) and lentic (rearing and overwintering) habitats (Lister and Finnigan 1997), whereas simple pond designs might be more appropriate for side channels intended to provide overwintering habitat in streams with abundant spawning and rearing habitat.

It is important to note that higher parr density and biomass in stream-type side channels did not translate into higher smolt production. This apparent failure to generate higher smolt production could be real or could be a consequence of low power to detect differences in smolt production because of excessive variation in the data (e.g., Figure 5). Alternatively, spring smolt output could also include juveniles that migrated from main-stem habitats into side channels, so that smolt out-migration from a side channel may poorly represent in situ production (i.e., when production is subsidized to an unknown degree by individuals reared in the main stem). Movement of fish into side channels in the fall is common (e.g., Brown and Hartman 1988), and fish may also redistribute from stream-type side channel habitats to lower-velocity overwintering habitats, such as ponds. Again, this highlights the multiple functions of side channel habitats in salmonid life history requirements (i.e., summer rearing versus overwintering habitat).

Our observation of declining smolt density with increasing side channel size (i.e., total smolt production increased with area but at a declining rate) was also documented in an earlier analysis (Keeley et al. 1996). Although we did not find a difference in smolt output between stream- and pond-type side channels, Keeley et al. (1996) observed a slope of 0.51 for their regression of $\log_{10}$(smolt production) on $\log_{10}$(pond area) and a slope of 1.62 for stream-type side channels, indicating that smolt density declined with increasing area in pond-type side channels but not in stream-type side channels. Keeley et al. (1996) suggested that ponds smaller than 10,000 m^2 (1 ha) were optimal; Reeves et al. (1989) also indicated that American beaver ponds less than 500 m^2 provided better overwintering habitat than larger ponds. Pollock et al. (2004) suggested that smaller American beaver ponds have higher areal production, which is consistent with our observation of higher fish density and biomass in the smaller pond section of our intensively sampled side channel complex (Figure 7). The model predicting that the highest smolt density will occur in smaller side channels (Figure 6B) is continuous rather than a step function, so it is difficult to clearly identify an optimum maximum channel size. However, we found no decline in $\log_{10}$(smolt density) with increasing $\log_{10}$(area) (i.e., the slope was not significantly different from 1.0) for our reduced data set with a maximum side channel area of 17,500 m^2 (i.e., data from Roni et al. [2006] excluded). Thus, an optimal side channel size threshold below 5,000–10,000 m^2 (which corresponds with the inflection point in the negative power function of smolt density [Figure 6B] plotted on nonlogarithmic axes) seems to be a reasonable rule of thumb.

Higher fish production per unit area in smaller side channels is likely due to adequate flow at the thalweg to permit drift feeding; even though our smaller pond section was almost 2,000 m^2, we observed drift feeding by fish and measurable velocity at the thalweg. A lower perimeter : area ratio (Pollock et al. 2004) will also cause energy subsidies from both the riparian forest (terrestrial insects and detritus; Baxter et al. 2005) and the inlet stream to become diluted in larger ponds. Zarnowitz and Raedeke (1984) concluded that optimal pond size was less than 10,000 m^2 but did so based on the inference that larger ponds were more likely to attract and support avian and terrestrial predators, rather than based on dilution of terrestrial inputs.

Our observation of larger parr in pond-type side channels is consistent with the larger size of smolts from pond habitats reported elsewhere (e.g., Roni et al. 2006) and is likely caused by lower fish density in ponds rather than differences in productivity between stream- and pond-type habitats. Density-dependent effects on growth may be less pronounced in ponds because they are more likely to be underrecruited (Roni et al. 2006); that is, inadequate spawning habitat in ponds (or inadequate colonization from the main stem) may result in lower pond densities, while abundant spawning habitat in stream-type side channels ensures habitat saturation. Roni et al. (2006) inferred that larger smolt size from ponds indicated better habitat quality, since smolt size was correlated with greater ocean survival during unfavorable marine conditions (Quinn and Peterson 1996). However, the benefits of larger size have to be balanced against the costs of lower abundance. If smaller individuals reared at higher densities in streams are capable of surviving when ocean conditions are favorable, and if territorial behavior of stream-rearing fish ensures a constant number of larger individuals even at high densities, then the lower average size of fish from stream-type side channels may be less relevant.

Design Considerations

The most important design consideration from our review is that smaller side channels are likely to be more productive (in terms of smolts/m^2) than larger ones. This conclusion needs to be tempered by that fact that total smolt output increases with increasing side channel area, but the incremental benefits are a decreasing function of channel area. The benefits of building larger side channels therefore depend on the incremental increase in cost associated with constructing larger habitats relative to the decreasing return in additional smolt production. For instance, four 5,000-m^2 ponds will produce more fish than one 20,000-m^2 pond and therefore constitute a more-optimal restoration design if they can be produced at the same cost.

While our observation of higher habitat quality (as reflected by fish density [smolts/m^2] or biomass [g/m^2]) in stream-type side channels is an important design consideration, total production remains the product of habitat quality (fish density) and quantity (area). A 200-m-long, stream-type side channel may support higher fish densities than a pond of similar length, but if the pond has 10 times the surface area it may produce more smolts despite potentially lower habitat quality (in terms of fish density; Blackwell et al. 1999).

Although the moderate velocities in side channels (relative to main-stem velocities; Collins and Montgomery 2002) contribute to their quality as juvenile rearing habitat, natural side channels are subject to periodic scour at high flow that sorts substrate and prevents excessive sedimentation of riffle substrate (Amoros 2001; Saldi-Caromile et al. 2004). In contrast, intakes of constructed side channels can draw in large quantities of sediment, but volume-restricted intake pipes usually prevent sufficient flow to scour and export fines deposited in side channels. This is particularly problematic for bottom-draw intakes, which can draw in large quantities of sediment when the main-stem river is at high stage and fine particles are in suspension (Lister and Finnigan 1997). Intake designs that are raised off the bottom, allow discharge to be adjusted to periodically flush accumulated sediments, or allow discharge to increase significantly with river stage may help prevent siltation; alternatively, placement of a large pond at the head of a side channel will act as a settling pond to delay movement of silt into downstream channel habitat (Lister and Finnigan 1997). Large numbers of spawning fish (e.g., chum salmon) that mobilize fine sediment during redd construction are also a key factor in the maintenance of high-quality spawning and rearing habitat in natural and artificial side channels (Kondolf et al. 1993; Saldi-Caromile et al. 2004).

In general, side channels that combine stream- and pond-type habitats are likely to be most productive insofar as they provide spawning, summer rearing, and overwintering habitats for a range of year-classes and species (Lister and Finnigan 1997; Morley et al. 2005). Design recommendations to date have generally focused on construction and engineering techniques like those described above, rather than on decision criteria, to select the most appropriate designs for different species under different habitat limitation scenarios. A better understanding of the function of different side channel habitats relative to main-stem environments (e.g., Pollock et al. 2004; Morley et al. 2005) during juvenile ontogeny would help inform the appropriate design and application of alternative side channel types, which should be based on the habitat factors limiting the population of interest (e.g., summer rearing versus overwintering; Reeves et al. 1989; Solazzi et al. 2000). Further research to understand design effects on spring and summer growth versus overwinter survival will require (1) monitoring of growth and abundance in contrasting side channel types and (2) operation of fish fences to differentiate in situ production from main-stem immigrants as sources of smolt production (e.g., Brown and Hartman 1988). Design effects on species other than coho salmon also remain poorly understood, as are species interactions (i.e., habitat effects on competition and predation between species and age-classes).

Stream ecologists rarely have the opportunity for the large-scale habitat manipulations that are sometimes possible in lake or terrestrial systems (Carpenter et al. 1995). However, stream habitat restoration is now widespread (Bernhardt et al. 2005) and represents a unique opportunity to better understand the underlying processes that drive habitat limitation and productivity of flowing waters, while providing useful information to adaptively manage habitat restoration efforts (Bradford et al. 2005; Jansson et al. 2005). Greater collaboration among fundamental stream ecologists and restoration practitioners is needed (Palmer and Bernhardt 2006), including the design of selected resoration projects as experiments to understand the fundamental drivers of stream productivity. Key issues that need to be resolved to optimize the design of side channel habitats are the factors that influence (maximize) prey abundance for juvenile salmonids, the role of side channels as summer rearing versus overwintering habitats, and the population significance of side channel habitat design to species other than coho salmon and spawning chum salmon.

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