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The Importance of Beaver Ponds to Coho Salmon Production in the Stillaguamish River Basin, Washington, USA

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Abstract.—The use of beaver *Castor canadensis* ponds by juvenile coho salmon *Oncorhynchus kisutch* and other fishes has been well established. However, the population-level effects on coho salmon resulting from the widespread removal of millions of beaver and their dams from Pacific Coast watersheds have not been examined. We assessed the current and historic distributions of beaver ponds and other coho salmon rearing habitat in the Stillaguamish River, a 1,771-km^2 drainage basin in Washington and found that the greatest reduction in coho salmon smolt production capacity originated from the extensive loss of beaver ponds. We estimated the current summer smolt production potential (SPP) to be 965,000 smolts, compared with a historic summer SPP of 2.5 million smolts. Overall, current summer habitat capacity was reduced by 61% compared with historic levels, most of the reduction resulting from the loss of beaver ponds. Current summer SPP from beaver ponds and sloughs was reduced by 89% and 68%, respectively, compared with historic SPP. A more dramatic reduction in winter habitat capacity was found; the current winter SPP was estimated at 971,000 smolts, compared with a historic winter SPP of 7.1 million smolts. In terms of winter habitat capacity, we estimated a 94% reduction in beaver pond SPP, a 68% loss in SPP of sloughs, a 9% loss in SPP of tributary habitat, and an overall SPP reduction of 86%. Most of the overall reduction resulted from the loss of beaver ponds. Our analysis suggests that summer habitat historically limited smolt production capacity, whereas both summer and winter habitats currently exert equal limits on production. Watershed-scale restoration activities designed to increase coho salmon production should emphasize the creation of ponds and other slow-water environments; increasing beaver populations may be a simple and effective means of creating slow-water habitat.

North American river networks contain numerous reaches dammed by beaver *Castor canadensis*, and the spatial distribution of beaver dams controls fundamental geomorphological and ecological processes (Rudemann and Schoonmaker 1938; McDowell and Naiman 1986; Johnston and Naiman 1990; Pollock et al. 2003). Of particular interest on the Pacific Coast of North America is the rearing habitat that beaver ponds provide for juvenile salmonids, most notably coho salmon *Oncorhynchus kisutch*. Coho salmon populations in parts of California, Oregon, and Washington are listed as threatened under the U.S. Endangered Species Act.

When beaver impound streams by building dams, they substantially alter stream hydraulics in ways that benefit many fish species (Murphy et al. 1989; Snodgrass and Meffe 1998). However, early research suggested that beaver dams might be detrimental to fish, such as hindering fish passage for anadromous salmonids; therefore, until recently, it was common for fish managers to remove beaver dams (Salyer 1935; Reid 1952). It has also been demonstrated that beaver dams seasonally restrict movement of fishes (Rupp 1954; Gard 1961; Murphy et al. 1989; Schlosser 1995). However, more than 80 North American fishes have been documented in beaver ponds, including 48 species that commonly use these habitats, and the beaver ponds' overall benefit to numerous fishes has been well documented (Pollock et al. 2003). Beaver ponds usually have slow current velocities and large edge-to-surface-area ratios, and therefore contain extensive cover and a highly productive environment for both vegetation and aquatic invertebrates; these conditions provide fish with foraging opportunities not found in unimpounded stream habitat (Hanson and Campbell 1963; Keast and Fox 1990). The slow water also means that energy expenditures for foraging are less than

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would be required in higher-velocity streams. Thus, sections of streams impounded by beaver dams are often more productive than unimpounded reaches in terms of both the number and size of fish (Gard 1961; Hanson and Campbell 1963; Murphy et al. 1989; Leidholt-Bruner et al. 1992; Schlosser 1995). Fishes are not the only beneficiaries of beaver dams. Relative to unimpounded reaches, areas impounded by beaver dams have been associated with biomass or diversity increases in a wide range of taxa, including birds, mammals, plants, and insects (see reviews in Naiman et al. [1988] and Pollock et al. [1994]).

Comparisons of salmonid growth and survival between reaches upstream of beaver dams and unimpounded reaches demonstrate the importance of beaver ponds. During the winter, juvenile coho salmon residing in side channels impounded by beaver dams utilize such habitats at a higher density, are consistently larger, and have a greater overwinter survival rate than juveniles that use side channels without beaver dams (Bustard and Narver 1975a; Swales et al. 1986). Beaver ponds also serve as important rearing areas during the summer. Higher densities and larger sizes of juvenile coho salmon have been found upstream of beaver dams during the summer in main-stem and off-channel habitats (Murphy et al. 1989; Leidholt-Bruner et al. 1992). In some cases, these reaches accounted for less than 1% of the total available habitat, yet over a third of all juvenile coho salmon were found there (Murphy et al. 1989). Similarly, Leidholt-Bruner et al. (1992) found that summer densities of juvenile coho salmon in beaver ponds were higher than in pools formed by wood or other obstructions. For three small, coastal island streams in southeast Alaska, Bryant (1983) found that summer populations of coho salmon juveniles were significantly higher in impounded reaches than in reaches just upstream and downstream. However, the densities in the impounded reaches were lower because the beaver dams had greatly expanded the surface area of the streams. In Carnation Creek, British Columbia, Bustard and Narver (1975a) found that the survival rate of overwintering juvenile coho salmon in old beaver ponds was about twice as high as the average for the entire stream system.

Studies of juvenile coho salmon production from beaver ponds have been limited to single or several ponds, and generally compare fish growth rates or sizes in ponds relative to those in streams (e.g., Bustard and Narver 1975a, 1975b; Peterson 1982; McDowell and Naiman 1986; Swales et al. 1986; Murphy et al. 1989; Swales and Levings 1989; Leidholt-Bruner et al. 1992; Nickelson et al. 1992). Other studies of coho salmon habitat loss were unable to estimate historic areas of beaver ponds (Beechie et al. 1994). However, we know that organized commercial trapping throughout the Pacific Northwest was initially responsible for widespread declines in beaver populations (Mackie 1997). Later, once Anglo-American settlement in the Puget Sound basin began in earnest, beaver were routinely trapped for subsistence fur trade and to eliminate what was considered an impediment to settlement. This scenario was repeated throughout much of North America such that by the early 1900s, beaver were thought to be in danger of extinction (Naiman et al. 1988). Although we know that beaver ponds were historically much more abundant, no study has examined the potential population-level effect of the widespread removal of beaver ponds on coho salmon. Here we investigate the current and historic distribution of beaver ponds in a large (1,771-km^2) Pacific Northwest drainage basin, and demonstrate how the loss of beaver ponds has greatly reduced the potential coho salmon smolt production of an entire watershed.

Methods

Study area.—We examined the historic and current distributions of beaver ponds and other stream habitats utilized by coho salmon in the Stillaguamish River, Washington (Figure 1). The Stillaguamish River originates in the North Cascade Mountains, flows westward through a glacially carved valley, and empties into the Pacific Ocean through the Puget Sound estuary. Annual rainfall in the basin ranges from 760 to 3,800 mm and increases with elevation. Forest types in the study area vary depending on elevation and physical setting. Floodplain forests were historically populated with red alder *Alnus rubra*, Sitka spruce *Picea sitchensis*, western redcedar *Thuja plicata*, black cottonwood *Populus trichocarpa*, and willows *Salix* spp. (Ayres 1899). Upland forests to an elevation of about 600 m (the western hemlock *Tsuga heterophylla* zone of Franklin and Dyrness [1973]) were dominated by Douglas-fir *Pseudotsuga menziesii*, western redcedar, western hemlock, and Sitka spruce (Ayers 1899; Gannett 1899). Silver fir *Abies amabilis* and western hemlock dominate forests from about 600 to 1,200 m (the silver fir zone), and higher elevations are in the alpine fir *Abies lasiocarpa* zone (Ayers 1899; Franklin and Dyrness 1973).

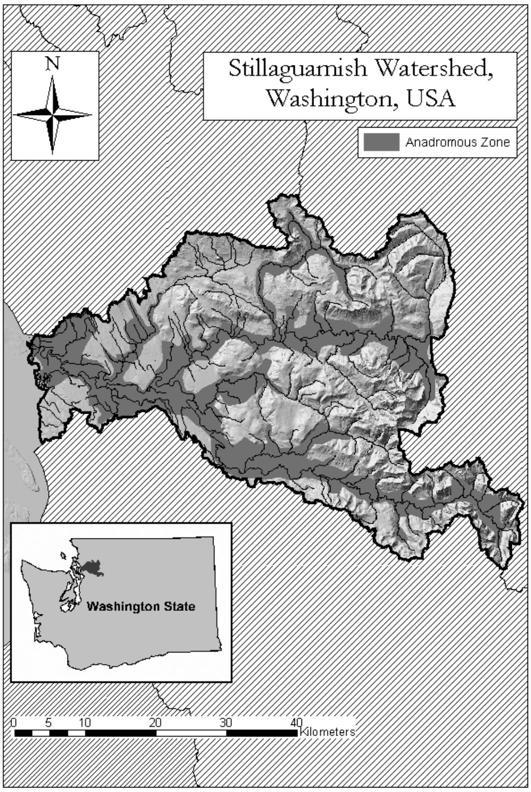

FIGURE 1.—Location of the Stillaguamish River basin, Washington. The light shading delineates the extent of the range of anadromous coho salmon in the basin.

Adult coho salmon enter the Stillaguamish River basin in late summer and early fall. Spawning is concentrated in small, low-gradient tributaries and occurs primarily between November and February. Fry emerge from the gravel in March and April and soon establish their summer rearing territories, typically remaining in their natal streams (Sandercock 1991). Coho salmon juveniles generally spend the summer in the areas of emergence (Sandercock 1991; Beechie et al. 1994); however, some juveniles are gradually displaced downstream as summer progresses (Chapman 1962). With the first fall freshets (usually in late September or October), juveniles migrate as much as 38 km downstream to winter rearing areas (Scarlett and Cederholm 1984). Preferred winter habitats include beaver ponds, off-channel ponds, and protected side channels (Peterson and Reid 1984; Scarlett and Cederholm 1984). Coho salmon smolts leave their winter rearing areas in March and April and migrate to salt water soon after. Most coho salmon in the Stillaguamish River basin spend 14–18 months in fresh water and 16–20 months in the Pacific Ocean before returning to spawn at age 3.

Historic estimates of average beaver densities across the North American continent range from 4 to 27 individuals/km^2 (Seton 1929; Pollock et al. 2003). The low-gradient habitat in the Stillaguamish River basin that exists within the range of coho salmon has physical characteristics typical of good beaver habitat. We believe that historic beaver densities in the low-gradient portions of the basin were likely within the aforementioned range. Currently, the beaver population is considerably reduced relative to historic estimates. Extensive trapping in the watershed during the first wave of Euro-American colonization decimated beaver populations, and much of the land formerly utilized by beaver has been converted to agriculture, tree farms, or residential areas (Mackie 1997). Beaver colonies today are scattered throughout the watershed, and generally are most abundant in areas where access by road is difficult. Beaver are generally absent from the prime habitat of low-gradient streams crossing the main-stem valley floor. Active beaver trapping to eliminate nuisance colonies still occurs in the watershed (WDFW 1997).

Estimation of the current abundance of beaver ponds.—Beaver ponds within the anadromous zone were identified and their surface area measured from black-and-white 1:12,000-scale aerial photographs provided by the Washington Department of Natural Resources (WDNR). We conducted field verification of approximately 10% of the sites to ensure that the ponds were correctly identified as beaver ponds. All field-verified ponds were determined to be beaver ponds; however, a number of beaver ponds not seen in the photographs were found in the field within floodplain channels away from the main stem. These ponds were narrow and long, with minimal canopy opening, and therefore were difficult to identify in aerial photographs. We were not able to systematically survey the entire watershed for these ponds, and thus they were not included in our estimates.

Estimation of the historic abundance of beaver ponds.—We developed a model to estimate the spatial distribution of beaver ponds within the anadromous zone in order to determine the historic abundance of beaver ponds. Observations suggested that the spatial distribution of beaver ponds in a drainage network is generally limited to those areas where beaver dams can withstand winter floods. The erosive capacity of a river can be characterized by stream power, which is described by:

TABLE 1.—Habitat unit usable area equivalents, parr densities, density-independent survival to smoltification, and smolt production potential estimates for five habitat types (from Reeves et al. 1989; Beechie et al. 1994).

Habitat type	Usable area equivalent (units/m^2)	Parr density (parr/unit)	Survival to smolt stage	Potential production
Side-channel and distributary sloughs				
Summer	0.75	1.7	0.25	0.319 smolts/m^2
Winter	0.50	5.0	0.31	0.775 smolts/m^2
Small and large tributaries				
Summer pool	1.00	1.7	0.25	0.425 smolts/m^2
Summer glide	0.70	1.7	0.25	0.297 smolts/m^2
Summer riffle	0.50	1.7	0.25	0.213 smolts/m^2
Winter pool	0.70	5.0	0.31	1.085 smolts/m^2
Winter riffle	0.00			0.000 smolts/m^2
Main stem				600 smolts/km
Pond				
Summer pond (all sizes)	1.00	1.5	0.25	0.375 smolts/m^2
Winter pond <500 m^2	1.00	5.0	0.31	1.550 smolts/m^2
Winter pond >500 m^2	0.50	5.0	0.31	0.775 smolts/m^2
Lake				25 smolts/ha

$$\Omega = \rho g Q S,$$

where Ω is the stream power, ρ is the density of water, g is the gravitational constant, Q is stream discharge, and S is stream slope. We hypothesized that beaver dam locations are constrained to reaches that do not exceed some critical (but unknown) stream power, above which the dams will fail (e.g., during floods). Discharge can be estimated from stream drainage area based on U.S. Geological Survey (USGS) discharge–drainage-area data.

For bankfull discharge (Q_{bf}), the general equation describing this relationship is:

$$Q_{bf} = kA^{\gamma},$$

where A is drainage area and k and γ are empirically derived constants (Dunne and Leopold 1978). By use of peak flow data from 37 USGS gauge stations located on small, low-elevation streams ($A < 1.5 \times 10^7$ m^2; elevation < 700 m) within or near our study watershed, we regressed the bankfull (2-year) flood against drainage area and determined that k was equal to 7.3×10^{-7} and γ was equal to 1.0 ($n = 37$, $r^2 = 0.56$, $P < 0.01$). By substituting for Q_{bf}, the equation for stream power at bankfull discharge may be recast as:

$$\Omega_{bf} = 7.15 \times 10^{-3} AS.$$

Thus, by measuring slope and drainage area (obtained from USGS 7.5′ topographical maps) at current locations of beaver ponds, we estimated the bankfull stream power that corresponded with the current limit of where beaver dams were maintained.

There are no direct measures of historic beaver pond frequency, but in watersheds where beaver have been allowed to recover, they maintain dam frequencies ranging from 2.5 to 16 dams/km (typically >10/km), and generally saturate all available habitat (Naiman et al. 1988; Gurnell 1998; Pollock et al. 2003). We assumed that historic beaver pond frequency was 6 ponds/km within the low-gradient portion ($S \leq 0.04$) of the stream network utilized by coho salmon. The assumption of 6 ponds/km is lower than most frequencies observed in watersheds with relatively undisturbed beaver populations, and therefore is conservative (Pollock et al. 2003).

Delineation of the anadromous zone and estimation of coho salmon production potential.—We calculated coho salmon smolt production for each of five habitat types (Table 1) as the product of total habitat area, juvenile coho salmon density, and coho salmon survival to smolt stage (Reeves et al. 1989; Beechie et al. 1994). Densities and survival rates are shown in Table 1. Each habitat type was assigned a potential smolt production estimate (smolts/m^2) based on published values or on locally collected data from Beechie et al. (1994) (Table 1). Estimates of potential winter smolt production are lower when the average winter stream temperature is less than 7°C (Reeves et al. 1989).

To estimate historic coho salmon production from small and large tributaries, we used the usable area equivalent, rearing density, and survival to smoltification values from Reeves et al. (1989) and Beechie et al. (1994) (Table 1). Estimates for present-day coho salmon production were also obtained from Reeves et al. (1989), but include more detailed data on usable area and potential smolt production in various channel units, such as different pool types (e.g., lateral-scour pool, dam pool, etc.), riffles, and glides.

It is challenging to estimate habitat and coho salmon production losses in main stems and large tributaries because their use by coho salmon is not well known (Beechie et al. 1994). There is no information on the seasonality of coho salmon use in these habitats, so we used the same habitat value for each season. We used 600 smolts/km as an estimate for coho salmon smolt production in main stems, as Beechie et al. (1994) used for the Skagit River, Washington. This estimate originated from data collected on the Bogachiel River by the Washington Department of Fish and Wildlife (WDFW, unpublished data). Annual coho salmon smolt production estimates range between 340 and 2,734 smolts/km (Beechie et al. 1994), and therefore 600 smolts/km is conservative. We calculated historic and current coho salmon smolt production for individual beaver ponds based on the usable area equivalent, rearing density, and survival to smoltification reported in Reeves et al. (1989). We applied a production estimate of 25 smolts/ha to lake habitat based on Reeves et al. (1989) and Beechie et al. (1994).

We used existing coho salmon distribution maps (Williams et al. 1975) combined with a more recent identification of physical barriers, such as falls, dams, impassible culverts, or stream gradients exceeding 20%. Summer and winter coho salmon smolt production potential (SPP) for all habitat types were estimated according to the methods of Reeves et al. (1989) and Beechie et al. (1994), except that we added substantial detail to the estimation of the historical abundance of beaver ponds and their contribution to SPP. Methods and assumptions for coho salmon smolt production estimates from all habitat types except beaver ponds are described in detail in Beechie et al. (1994).

We identified all non-beaver-pond habitat types with a combination of field measurements, USGS 7.5′ topographic maps, 1:12,000-scale orthophotos and 1:24,000-scale hydrography layers from the WDNR, and National Wetlands Inventory maps (Cowardin et al. 1979). Habitat types included the following: (1) side-channel and distributary sloughs, (2) small tributaries, (3) large tributaries and main stems, (4) lakes (surface area $>$ 5 ha), and (5) ponds (surface area $<$ 5 ha) (Beechie et al. 1994). Side-channel sloughs, sometimes called flood overflow channels, diverge and reconnect to a main stem, and usually occur on a floodplain or on the lowest terrace near a main stem. Distributary sloughs are similar to side-channel sloughs except that they do not reconnect with a main stem, instead flowing directly into an estuary. Small tributaries have a summer low-flow width of less than 6 m, whereas channels wider than 6 m are large tributaries or main stems (Beechie et al. 1994).

We also considered several aspects of physical habitat characteristics that could not be measured easily with remotely sensed data, including number of pools, pool area, and available spawning habitat. A decrease in pool spacing (increase in percent pool area) increases coho salmon SPP estimates because juveniles prefer pool habitats, such as backwater areas, sloughs, and beaver ponds (Reeves et al. 1989). Thus, a reduction in the number of pools (decrease in percent pool area) reduces winter and summer coho salmon production. A lack of available spawning habitat can limit coho salmon SPP because not enough fry are produced to seed all available rearing habitat.

We used existing physical habitat data (Beechie and Sibley 1997) and collected additional habitat data throughout the Stillaguamish River basin between the summer and winter of 1995 and 1997. Data collected in these habitat surveys included bankfull width, stream channel gradient, wood loading (e.g., number and volume), percent spawnable area, channel units (e.g., pool, riffle, glide, and rapid), and pool-forming factors (e.g., woody debris, streambank, boulders). Channel units were the same as those defined by Bisson et al. (1982) and Reeves et al. (1989). We measured bankfull width with a tape measure to the nearest 0.1 m and surveyed gradients with a hand level and stadia rod over a representative reach of each segment. We measured wood pieces and counted those that were more than 10 cm wide and 1 m long and that were at least partially situated within the bankfull width. Surface patches of gravel with a minimum area of 1 m^2 were visually identified and measured. Patches were only included if they were located in areas of potential coho salmon spawning, such as the tail-out of pools, riffles, and glides. Gravel area was expressed as percentage of the total wetted channel area. The length and width of each habitat unit was measured by use of a stadia rod or tape measure.

We compared habitat area estimates from our most recent sources to estimates from the earliest aerial photographs (taken in 1933 by Pacific Aerial Surveys), WDNR orthophotographs (1942), U.S. Army Corps of Engineers maps (1930), or unlog-

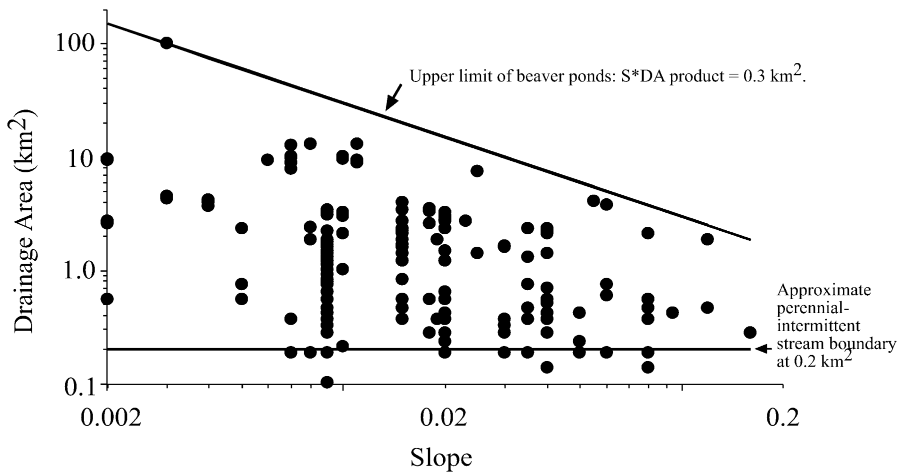

FIGURE 2.—Relationship between stream slope (*S*) and drainage area (DA) for 341 beaver ponds identified within the known distribution of coho salmon in the Stillaguamish River basin, Washington. The upper limit of beaver pond distribution is defined by a *S**DA slope of 0.3 km^2, which corresponds to a value of 2,000 $J \cdot s^{-1} \cdot m^{-1}$ for stream power at bankfull discharge. The lower limit is defined by a DA of 0.1 km^2, below which most streams are intermittent.

ged reference streams when possible. Historical areas of slough habitats (side channel and distributary) were estimated from historical maps, notes, and photographs, as well as from field evidence of their prior locations. Because the early photographic record was preceded by more than half a century of human impacts to these habitat types, our analysis provides a conservative estimate of habitat changes. Present-day slough habitat areas were measured from aerial photographs and in the field. We examined reduction of pool areas in small tributary habitats by comparing pool areas in managed streams to those in unlogged reference streams. Data for reference sites were from Beechie et al. (1994), and data for present-day conditions were derived from stream surveys in the Stillaguamish River basin. Lengths of large tributaries and main stems were also measured from historical maps, notes, and photographs, as well as determined from field evidence of their prior locations. Present-day tributary and main-stem areas were determined from aerial photographs and also measured in the field. Lake areas were measured directly from historical and current maps.

Results

Current and Historic Distribution and Abundance of Beaver Ponds

The portion of the watershed accessible to coho salmon encompassed 1,433 km of streams. Along these streams, we identified 341 beaver dams that created 0.49 km^2 of beaver pond habitat (<0.03% of the drainage basin). Our results showed that existing beaver dams were limited to sites where stream power at bankfull discharge (Ω_{bf}) was less than 2,000 $J \cdot s^{-1} \cdot m^{-1}$ (Figure 2). The lower limit of basin size where beaver build dams were built coincided approximately with the minimum drainage area of perennially flowing streams, which is defined regulatorily as approximately 0.2 km^2 in western Washington (Washington Forest Practices Board 2000). Ninety six percent of the existing beaver dams were built on streams with drainage areas of 0.2 km^2 or greater (Figure 2).

There was a significant difference in bankfull stream power between all stream reaches within the anadromous zone and those reaches where beaver chose to build dams. The average bankfull stream power for reaches where beaver constructed dams was 220 $J \cdot s^{-1} \cdot m^{-1}$, whereas the average for reaches within the anadromous zone was 3,300 $J \cdot s^{-1} \cdot m^{-1}$ (Kolmogorov–Smirnov two-sample test, $P < 0.001$, Figure 3). There were also significant differences in both slope and drainage area between all available streams and the sites where beaver chose to build dams. The mean slope was 2.1% and the mean drainage area was 2.3 km^2 for streams that hosted beaver dams, whereas these two parameters averaged 3.9% and 121 km^2, respectively, for the entire anadromous zone (Kolmogorov–Smirnov two-sample tests, $P <$ 0.001). Although these data also indicated that

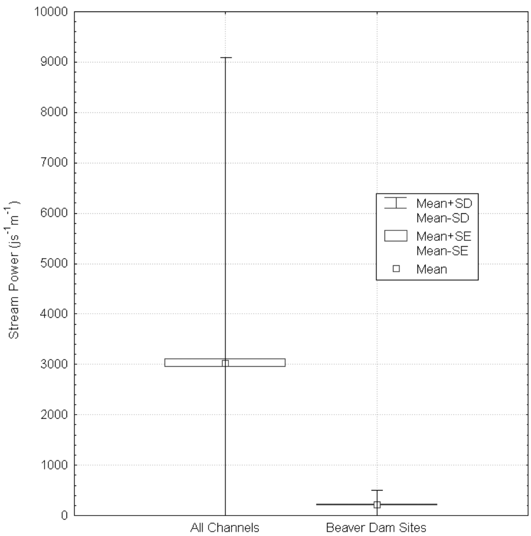

FIGURE 3.—Kolmogorov–Smirnov box plot comparing the stream power at bankfull discharge for all stream channels in the Stillaguamish River basin, Washington, versus the bankfull stream power of channels dammed by beaver.

beaver built dams on higher-gradient streams ($S >$ 0.04), our field observations suggested that the size of such ponds was usually small and that coho salmon generally did not occupy these higher-gradient streams. Therefore, we assumed that beaver ponds built on stream slopes greater than 4% did not contribute historically or currently to coho salmon production.

Based on the above data, we identified stream reaches where beaver ponds suitable for juvenile coho salmon were likely to have occurred historically by creating boundary conditions of a maximum 4% slope, a minimum drainage area of 0.1 km^2, and a maximum bankfull stream power of 2,000 $J \cdot s^{-1} \cdot m^{-1}$ (Figure 2). Of the 1,433 km of coho salmon-accessible stream in the Stillaguamish River basin, 1,091 km (76%) met these criteria. Assuming that the historic size distribution of beaver ponds is the same as the current distribution (Figure 4), we estimated that beaver dams created approximately 9.3 km^2 of pond habitat, covering just 0.5% of the entire watershed.

Current and Historic Coho Salmon Smolt Production Potential

Our analysis suggested that the current coho salmon SPP for the entire basin during summer was approximately 965,000 smolts, and that beaver ponds accounted for 18% of summer SPP (Table 2). The current winter SPP was approximately 971,000, and beaver ponds contributed 38% of winter potential (Table 2). Thus, summer and winter habitats equally limit the current quantity of coho salmon SPP. We also found that percent spawnable area averaged 4.0% and ranged between 0.1% and 20% for the 72 streams inventoried. The

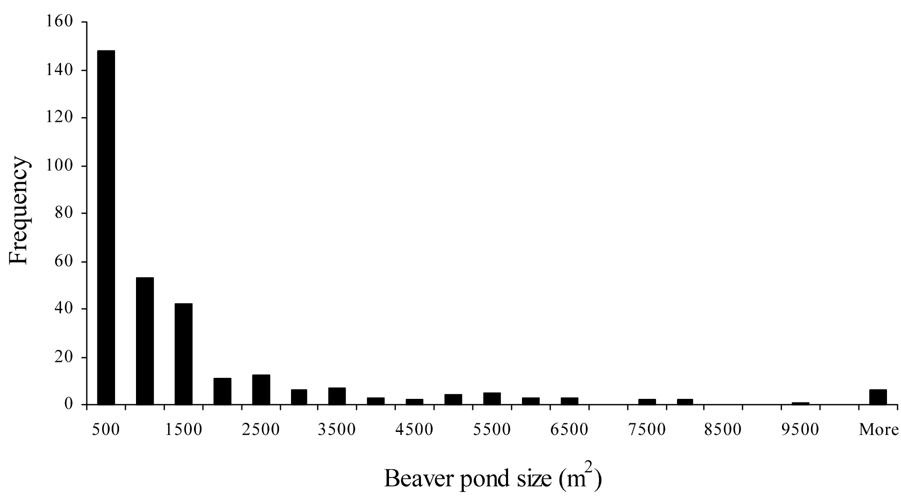

FIGURE 4.—Histogram of current beaver pond surface area on streams (n = 310) with a gradient of 4% or less within the known distribution of coho salmon in the Stillaguamish River basin, Washington. Nearly half (48%) of the ponds have a surface area of less than 500 m^2. The relationship between frequency F and pond surface area (S, in m^2) was described by the exponential decay equation $F = 3.01 + e^{(5.95\ -\ 0.00185)}$ ($n = 21$, $r^2 = 0.98$, $P <$ 0.001).

TABLE 2.—Estimates of changes in coho salmon smolt production potential (SPP) from the Stillaguamish River basin, Washington, relative to historic conditions, under an assumption that either summer habitat availability or winter habitat availability is limiting production.

Habitat type	Historic SPP	Current SPP	Numerical change in SPP	Percent change in SPP	Percent of change SPP	Percent of historic SPP
Summer-limited production						
Beaver ponds	1,521,476	169,512	−1,351,964	−89	18	61
Sloughs	292,465	92,603	−199,862	−68	10	12
Tributaries	608,850	596,206	−12,644	−2	62	24
Main stem	78,600	100,800	22,200	28	10	3
Lakes	4,875	5,925	1,050	22	1	0
Total	2,506,266	965,046	−1,541,220	−61	100	100
Winter-limited production						
Beaver ponds	6,085,904	367,750	−5,718,154	−94	38	86
Sloughs	710,535	224,974	−485,561	−68	23	10
Tributaries	285,186	260,186	−25,000	−9	27	4
Main stem	78,600	100,800	22,200	28	10	1
Lakes	4,875	5,925	1,050	22	1	0
Total	7,081,625	971,308	−6,110,317	−86	100	100

majority of spawnable area existed in channels possessing gradients of less than 2%. Based on the Reeves et al. (1989) protocol, we found that only 1 of the 72 streams was physically limited by a lack of spawning gravel.

Our data indicated that, historically, the Stillaguamish River basin was capable of sustaining about 2.5 million juveniles in the summer and 7.1 million juveniles in the winter (Table 2). We estimated that beaver ponds alone could sustain 1.5 million juveniles in the summer and 6.1 million juveniles in the winter. Thus, historically, beaver ponds accounted for 61% of the total summer SPP and 86% of the total winter SPP (Table 2). Because total historic summer SPP was about one-third of winter SPP, juvenile coho salmon production was likely physically limited by the availability of summer habitat. Comparison of current and measured maximum production estimates suggests that the historic SPP of the basin was approximately 2.5 times the current SPP, and that most of the reduction in SPP resulted from the widespread loss of slow-water habitat created by beaver dams, and to a lesser extent, sloughs (Table 2).

Discussion

Abundance of Slow-Water Habitat and Implications for Coho Salmon Smolt Production

Our analyses show the great importance, both historically and currently, of beaver pond habitat for potential juvenile coho salmon production in the Stillaguamish River watershed. Our analyses and the historical record clearly indicate the formerly tremendous abundance of off-channel or slow-water habitats in the form of beaver ponds, lakes, and sloughs, and that much of the broad Stillaguamish River floodplain was composed of wetlands or ponds (Collins et al. 2002; Collins et al. 2003). The widespread trapping of beaver in the early 1800s and the dredging and diking of floodplains in the 1850s were among the first alterations made by European settlers on the Puget Sound region (Beechie et al. 1994; Mackie 1997). Thus, most of the rearing habitat used by coho salmon was eliminated long before commercial fisheries exerted any substantive impact on coho salmon populations and well before estimates of historic coho salmon populations became available.

Although we focused on the historical role of beaver dams in creating slow-water habitat used by juvenile coho salmon, records suggest that natural features, such as floodplain levees, wood jams, oxbow lakes, and distributary sloughs, also created plentiful slow-water habitat (Collins et al. 2003). Because the aerial photographic record only extends back to the 1930s, we were unable to document habitat changes that occurred earlier, and thus we likely underestimated the amount of sloughs, lakes, and other slow-water habitats that historically contributed to coho salmon smolt production. For example, historical records in two river basins directly adjacent to the Stillaguamish River (the Skagit River basin to the north and the Snohomish River basin to the south) indicate vast floodplain wetlands that were likely formed by natural levees (Beechie et al. 1994; Collins et al. 2003). However, these wetlands were likely further

TABLE 3.—Comparison of the coho salmon smolt production potential (SPP) from pools formed by large woody debris (LWD) placement in four restored streams (gradient [S] ≤ 0.04) versus pools formed by beaver dams in streams (S ≤ 0.04) in the Stillaguamish River basin, Washington. Also included are the average SPP values for the 30 km of streams that were surveyed for both LWD abundance and pool area. Pool area estimates for LWD pools are from Pess et al. (1999); beaver pond area estimates are from this study. Estimates of SPP for both LWD pools and beaver ponds are based on data from Hankin and Reeves (1988).

Site	Restored streams		Beaver dams		Average m^2 of pool per unit	Average summer SPP per unit	Average winter SPP per unit
	Reach length (m)	LWD/m	Pond size	N			
LWD pools							
Porter Creek	900	0.1			28	12	30
Segelson Creek	98	0.14			7	3	8
Siberia Creek	390	0.29			15	6	16
Cherokee Creek	700	0.39			5	2	5
Average of restored streams					14	6	15
Average of 30 km of streams					13	6	14
Beaver ponds							
Basinwide <500 m^2				148	220	83	341
Basinwide >500 m^2				162	2,590	971	2,007
Average of beaver dams					1,405	527	1,174

modified by beaver, which is reflected in the names of some areas (e.g., the historic 10,000-acre Beaver Marsh on the Skagit River; Collins et al. 2003). Although large floodplain wetlands likely contained enough water to provide overwintering habitat for coho salmon, beaver dams would have helped to ensure flooding during summer, when production bottlenecks were greater due to limited slow-water habitat. We speculate that beaver likely built dams at breaks in the natural levees, thus raising the level of floodplain marshes and keeping them flooded throughout the summer months. However, to the extent that floodplain marshes historically existed in the Stillaguamish River basin, they were not included in our historical estimates of beaver pond habitat.

Our intent was not to precisely determine which types of coho salmon habitat are attributable to beaver activity. Rather, we sought simply to promote the recognition that beaver, through dam building, historically created abundant slow-water habitat and wetlands that were useful to juvenile coho salmon and many other species, and that most of those habitats are now gone.

At present, a primary physical limitation to coho salmon production increases in the basin is the lack of beaver ponds or similar slow-water habitats. Coho salmon SPP of the Stillaguamish River basin could be increased by a factor of 2.5 if beaver populations and the slow-water pool habitat they create are allowed to expand. Therefore, any watershed restoration plan that excludes beaver as a restoration tool will have limited success in restoring coho salmon populations. In the Stillaguamish River, reclamation of all juvenile coho salmon habitat other than beaver ponds would increase output potential by about 200,000 smolts, primarily from the reclamation of side-channel and distributary sloughs. In comparison, restoration of all former beaver pond habitat would increase smolt production by over seven times that amount. In other words, if we assume an average of 3 dams/beaver colony (Pollock et al. 2003) and an average summer SPP of 527 smolts/dam (Table 3), the establishment of just 125 new beaver colonies within the Stillaguamish River basin could increase the total watershed SPP by the same amount attained by restoring all other habitat types to their historic abundance (Table 2).

Comparison of Potential and Actual Smolt Production

Nelson et al. (1997) used a coded-wire tag study in combination with smolt traps and habitat survey data, and estimated an average production of 650,000 smolts (range 520,000–830,000) over a 4-year period (1993–1996). The higher end of their range approaches our estimate of 970,000 smolts, but is somewhat lower. There are several possible reasons why our SPP estimate was greater than the measured production. Current escapement levels in the Stillaguamish River may be insufficient to fully reach carrying capacity in all streams. This explanation could easily be tested by increasing escapement levels and observing whether there is an increase in smolt output in the following years. Alternatively, the current SPP might have been overestimated because we measured habitat quan-

TABLE 4.—Cost of Large woody debris (LWD) placement per stream kilometer for restoration projects in British Columbia (BC), Washington (WA), and Oregon (OR). Costs are in U.S. dollars. Estimates are based on data from Cederholm et al. (1997).

Site	Description	Distance (km)	Cost ($/km)
Fish Creek, OR	Attached LWD	14.0	50,000
Swamp Creek, WA	Interconnected pools with LWD	0.2	23,000
Porter Creek, WA	Free-fall and cabled LWD	0.5	18,000
Porter Creek, WA	Cabled LWD; extensive engineering	0.5	224,000
East and Lobster creeks, OR	LWD and alcoves	3.4	29,000
Shop Creek, BC	LWD, V-weirs, and boulders	1.0	60,000

tity and then assumed an average smolt production output per unit area of habitat based on the work of Hankin and Reeves (1988), who determined potential production for streams in a relatively natural condition. We did not take into account that some habitats might be highly degraded and therefore unproductive. For example, many floodplain tributaries in the Stillaguamish River basin flow through agricultural lands, and could have water quality problems due to the fertilizers, pesticides, and herbicides present in agricultural runoff. Such streams might have greatly diminished smolt output capacity.

Implications for Habitat Restoration

Much of the recent restoration efforts to create slow-water juvenile coho salmon rearing habitat have focused on instream placement of large woody debris (LWD) rather than encouraging the expansion of beaver populations. However, the SPP per beaver dam ranges from 527 to 1,174 fish, whereas the SPP from a pool formed by instream LWD is about 6–15 individuals, indicating that beaver dams may be the better option (Table 3). Further, the cost of LWD restoration activities can be quite expensive, ranging from US$18,000 to $224,000 per stream kilometer (Table 4). In contrast, allowing beaver to dam streams involves only the cost of translocating the animals and adopting a no-trapping policy to encourage expansion of existing populations. Although LWD placement is often a worthwhile activity, promotion of beaver dam building in suitable areas is often the most cost-effective and appropriate restoration technique for watersheds where coho salmon production is limited by the lack of pool habitat.

Impacts of Beaver Pond Losses on Other Species

Although we focused on coho salmon populations, numerous other species have likely been affected by loss of beaver ponds as well. Beaver ponds have been identified as important habitat for numerous fish, mammalian, avian, and amphibian species (Collen and Gibson 2000; see also reviews by Naiman et al. [1988] and Pollock et al. [1994, 2003]). Published studies indicate that fishes and waterfowl have been the most severely impacted by reduced beaver pond habitat. Within the Pacific coastal ecoregion, fishes identified as making substantial use of beaver ponds include cutthroat trout *Oncorhynchus clarki*, sockeye salmon *O. nerka*, steelhead *O. mykiss*, Dolly Varden *Salvelinus malma*, and chinook salmon *O. tshawytscha* (Gard 1961; Bryant 1983; Swales et al. 1986; Swales et al. 1988; Murphy et al. 1989). For example, Murphy et al. (1989) found that juvenile sockeye salmon heavily used reaches upstream of beaver dams, averaging 0.48 fish/m^2; similar to observations of coho salmon, juvenile sockeye salmon that used these reaches were larger and grew faster than conspecifics that used other instream habitats. Studies to determine how the loss of beaver ponds has affected populations of these and other species would be worthwhile.

Beaver dams create slow-water habitat that is favorable to rearing juvenile coho salmon, and such habitat existed in greater abundance historically than it does today. Decimation of beaver populations in the Stillaguamish River basin has resulted in a drastic loss of pond habitat and a subsequent reduction in the coho salmon SPP. Loss of beaver habitat is the single most important factor currently limiting coho salmon production in the Stillaguamish River basin. As such, there is great potential for increasing coho salmon populations through an increase in the abundance of slow-water habitats, such as those created by beaver dams.

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