

## Summer Distribution and Growth of Juvenile Coho Salmon during Colonization of Newly Accessible Habitat

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**Abstract.**—Pacific salmon *Oncorhynchus* spp. are capable of exploiting vacant habitat, but most research has focused on straying and colonization by adults. However, dispersal of juveniles of stream-rearing species, such as coho salmon *O. kisutch*, may also be an important component of colonization. Installation of fish passage structures on the Cedar River, Washington, and subsequent adult migration into the newly accessible habitat provided a rare opportunity to investigate colonization as coho salmon regained access to 33 km of habitat from which they had been excluded for more than a century. In this study, we describe the spatial distribution and growth patterns of the first two generations of juvenile coho salmon produced in the new habitat. Snorkel surveys in the Cedar River revealed patchy distributions of juvenile coho salmon that largely matched the distribution of adults spawning the previous fall, and higher densities occurred in lower reaches (i.e., those not far upstream from the dam). However, sequential surveys indicated that juveniles entered and moved upstream within a Cedar River tributary, Rock Creek, where few, if any, adults spawned. Juveniles captured in the Cedar River were similar in size to those in Rock Creek, but sizes differed between years and larger fish tended to occur farther upriver. We found no evidence for density-dependent growth; there was no relationship between fish size and local density in either main-stem or tributary habitat. Abundance estimates suggest that relatively few juvenile coho salmon dispersed long distances into reaches neglected by spawning adults. We were unable to find any clear evidence that juvenile dispersal would increase the number of adults returning in the next generation, but such movements could accelerate the spatial expansion of the colonizing population in philopatric species like coho salmon.

Notwithstanding their justifiable reputation for homing accuracy (Quinn 1993; Hendry et al. 2004), Pacific salmon *Oncorhynchus* spp. have repeatedly colonized areas made available by glacial retreat (Milner et al. 2000) and by introductions outside their native ranges (Quinn et al. 2001; Ciancio et al. 2005). Processes of successful colonization are critical to understanding patterns of distribution and abundance within each species' past, present, and probable future geographic ranges. Research has tended to emphasize the expansion of adults and their capacity for upstream migration as a factor in colonization, but juvenile salmonids can also move substantial distances both downstream and upstream (Kahler et al. 2001; Gowan and Fausch 2002).

To the extent that spawning and rearing areas are spatially segregated, juvenile salmon must disperse to find suitable habitat. In some cases, spawning and rearing areas are naturally disconnected, although the magnitude of such separation probably varies between watersheds. Even if the distances between potential spawning and rearing areas are not great, low abundances of spawning adults during the initial stages of colonization may preclude saturation of juvenile rearing habitats in the whole system. Fry emerging in the proximity of siblings (i.e., from the same nest) could decrease local density or locate better rearing habitat by dispersing into unoccupied areas, perhaps boosting growth potential. Density dependence is a primary mechanism regulating growth in stream salmonids (Spalding et al. 1995; Jenkins et al. 1999; Keeley 2000; Imre et al. 2005); by reducing competition, dispersers may enjoy faster growth. In addition, differences in physical habitat and prey availability within a watershed often lead to spatial variation in

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growth (Quinn and Peterson 1996; Arnekleiv et al. 2006; Ebersole et al. 2006), so fish might also achieve larger sizes by searching for higher-quality rearing areas.

Juvenile redistribution could accelerate the numerical and spatial expansion of a colonizing population. Higher growth rates achieved through dispersal could increase freshwater survival, marine survival, and the rate of population abundance increase. Size is often correlated with survival rates at a variety of life stages, as larger fry may enjoy increased overwinter survival (Quinn and Peterson 1996; Biro et al. 2004; Ebersole et al. 2006) and larger smolts may experience higher marine survival rates than smaller individuals of the same cohort (Holby et al. 1990). Dispersal by juveniles may also catalyze spatial expansion of the new population, particularly if as adults they return to juvenile rearing sites instead of nest incubation sites.

Juvenile salmon can and often do move significant distances. Summer dispersal distances measuring hundreds of meters both upstream and downstream were recorded for Atlantic salmon *Salmo salar* (Einum and Nislow 2005) and coho salmon *O. kisutch* (Kahler et al. 2001). Movements are often interpreted as resulting from competition (Chapman 1962; Webb et al. 2001; Einum and Nislow 2005), although Kahler et al. (2001) concluded that habitat was the primary factor affecting dispersal. Coho salmon often redistribute during the fall–winter period of increased streamflows into off-channel alcoves and ponds (Peterson 1982; Nickelson et al. 1992) and tributaries of larger rivers (Bustard and Narver 1975; Tschaplinski and Hartman 1983; Scarlett and Cederholm 1984; Hartman and Brown 1987). In some cases, coho salmon moved long distances down the main river in search of overwinter tributary habitat (maximum reported distance = 38 km: Scarlett and Cederholm 1984; 8.1 km: Ebersole et al. 2006).

Modification of the Landsburg Diversion Dam on the Cedar River, Washington, provided a rare opportunity to investigate the process of salmon colonization. Beginning in fall 2003, fish passage facilities permitted adult coho salmon and Chinook salmon *O. tshawytscha* to naturally recolonize relatively high-quality habitat from which they had been excluded since the dam was erected in 1900 (Burton et al. 2006; Anderson and Quinn 2007). Juvenile Chinook salmon in this population seldom overwinter in freshwater (Myers et al. 1998), but the coho salmon in Puget Sound streams typically spend a full year in freshwater before migrating to sea (Weitkamp et al. 1995), allowing us to investigate their movements as part of the colonization process. Our first objective was to determine the extent to which juvenile coho salmon

dispersed from spawning sites and the significance of dispersal to the spatial and numerical expansion of the population. We surveyed (1) Rock Creek, a small tributary (3.4 km upriver from the dam) that contained apparently suitable habitat for coho salmon but where very little or no spawning occurred in the first 2 years of colonization and (2) the Cedar River, which contained the vast majority of spawning sites (Anderson and Quinn 2007). Our second objective was to evaluate the effects of habitat features and competition on juvenile coho salmon redistribution and size at the end of the summer. The analysis compared fish size between main-stem and tributary habitats, between downriver and upriver reaches, and between sites varying in local density. We reasoned that evidence of movement into previously unoccupied habitats and growth advantages for mobile individuals would suggest that dispersal increases population productivity.

### Methods

*Study site.*—The Cedar River is a 487-km<sup>2</sup> watershed in western Washington, draining westward from the crest of the Cascade Mountains into Lake Washington (Figure 1). Landsburg Diversion Dam is a low-head, run-of-the-river dam that blocked migration of anadromous fish for over 100 years until construction of fish passage facilities in fall 2003 made 33 km of habitat available in the Cedar River and its tributaries. Approximately 20 km of new habitat are now accessible to salmon in the Cedar River (wetted width mean  $\pm$  SD = 20.3  $\pm$  4.5 m) between the dam and Cedar Falls, a natural barrier to migration. The remaining 13 km of accessible length consist of tributary habitat in four creeks. Williams, Steele, and Taylor creeks have only very short (i.e., <0.5 km) sections that are accessible to salmon before natural barriers prevent upstream movement. The majority of tributary habitat available to salmon is in Rock Creek (wetted width = 5.5  $\pm$  1.3 m), the first tributary (3.4 km) upriver from the dam. The City of Seattle now manages the area above the dam for municipal water supply and as a de facto reserve without development, recreation, or commercial logging. In addition to the new salmon populations, the Cedar River watershed below Cedar Falls contains resident salmonids, primarily rainbow trout *O. mykiss* and mountain whitefish *Prosopium williamsoni* in the Cedar River and cutthroat trout *O. clarkii* in the tributaries (Kiffney et al. 2002). Nonsalmonid fishes in the system include speckled dace *Rhinichthys osculus*, brook lampreys *Lampetra richardsoni*, and several sculpins *Cottus* spp. that are numerically dominant. Further details on the

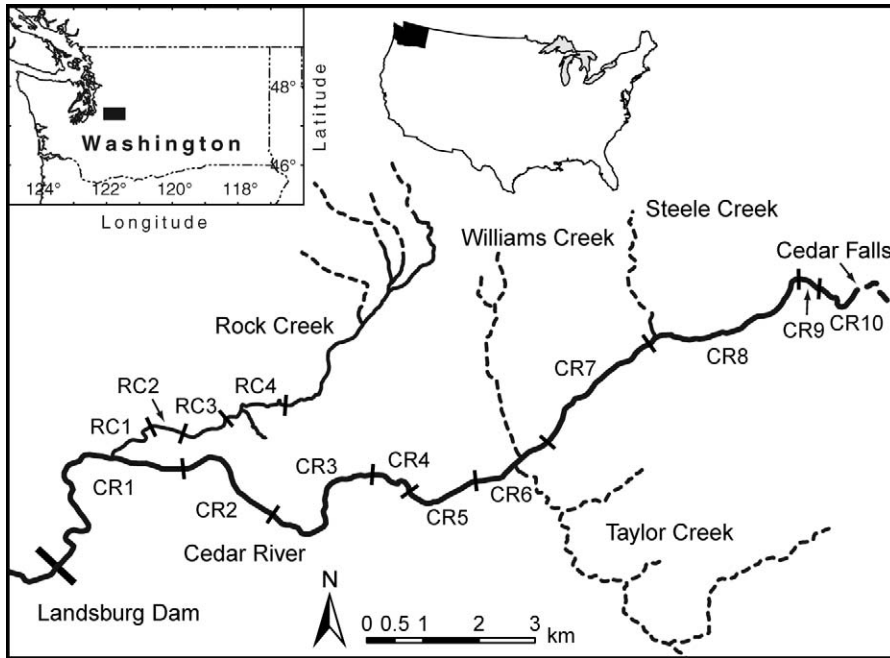


FIGURE 1.—Map of the Cedar River watershed, Washington, above Landsburg Diversion Dam, where fish passage modifications allowed for coho salmon recolonization of habitat and where juvenile coho salmon spatial distribution and growth were studied. Study reaches were in Rock Creek (RC1–RC4) and the Cedar River (CR1–CR10); habitat that was still inaccessible to coho salmon is indicated by dashed lines.

newly accessible habitat and biota are discussed by Seattle Public Utilities (2000) and Kiffney et al. (2002).

*Field techniques: distribution and abundance.*—The accessible Cedar River watershed above Landsburg Diversion Dam was divided into reaches (CR1–CR10; RC1–RC4) based on gradient, confinement, and tributary junctions (Kiffney et al. 2002; Figure 1). Adult spawning sites ( $n = 14$  in 2003,  $n = 18$  in 2004) were identified based on the best available information using a combination of inference from the movements of radio-tagged female salmon and direct visual observation of nests (also known as redds) during raft surveys of the Cedar River (Anderson and Quinn 2007). For 2003, when many female salmon were radio-tagged ( $n = 14$ ) but few redds were observed ( $n = 5$ ), we report spawning sites based upon inference from female movements. For 2004, when few female salmon were tagged ( $n = 4$ ) but many redds ( $n = 18$ ) were found, the observation data were used. Both approaches support the conclusion that in both years, the vast majority of spawning sites were in CR1 and CR2. We were unable to find all spawning sites, as the number of female salmon accessing the new habitat in these years ( $n = 21$  in 2003,  $n = 34$  in 2004) exceeded the number of known breeding sites, although some of the adult

female colonists probably spawned below the dam (Anderson and Quinn 2007). Thus, the spawning data are numerically incomplete due to the difficulty of finding all redds (e.g., because of high discharge, turbid water, or cryptic coloration of coho salmon) but are representative of the spatial distribution of spawning sites.

Within each Cedar River reach, habitat units were classified based on criteria modified from Bisson et al. (1988) and measured for length and width. We used snorkel counts for all analyses of distribution and abundance. In 2004, the entirety of CR1–CR6 was classified and measured, and a subset of the habitat units was snorkeled. Habitat units were selected for snorkeling based on access and the overall proportions of the different habitat types within that reach. In 2005, an 800-m section of each main-stem reach was classified, measured, and snorkeled in its entirety, and all main-stem reaches except CR5 were surveyed. Our surveys identified habitat units at a finer spatial scale in 2005, as evidenced by a smaller mean area surveyed per unit ( $1,122 \text{ m}^2/\text{unit}$  in 2004,  $621 \text{ m}^2/\text{unit}$  in 2005). Classification, measurement, and snorkeling in the Cedar River main stem occurred during summer base flow periods (July–September). Reach-scale

densities of juvenile coho salmon were calculated by dividing the total number of fish counted in each reach by the total area surveyed (as opposed to averaging densities from individual habitat units within a reach).

In the tributaries, our goal was to evaluate coho salmon abundance at various locations rather than to reveal habitat preference, so snorkeling was only conducted in pools, their preferred habitat (Bisson et al. 1988). Furthermore, we aimed to evaluate seasonal changes in coho salmon abundance, and so we selected a small number of pools to survey multiple times throughout the growing season. Among the four Rock Creek reaches (RC1–RC4), RC1 and RC3 were selected for snorkeling; five pools within each of the two reaches were surveyed. These 10 pools were snorkeled once in the spring (30 April 2004 and 8 March 2005), once in early summer (6 July 2004 and 30 June 2005), and once in late summer (27–29 September 2004 and 16 August 2005) in both study seasons. Age-1 and older coho salmon, easily identified by their larger size, were rarely observed and were excluded from the analysis of distribution and abundance.

*Field techniques: fish collections.*—To assess patterns of size among years and habitats, coho salmon were collected, measured for fork length, and weighed. In the main-stem Cedar River, fish were collected via a small ( $1.0 \times 0.6 \times 0.2$  m) seine net. Coho salmon aggregations were first located by snorkeling, allowing us to estimate the number of juveniles present in each group (e.g., 20 fish present, 15 captured). Coho salmon in the Cedar River were collected between 18 August and 15 September 2004 for brood year (BY) 2003 and between 25 July and 9 August 2005 for BY 2004.

All other fish were captured in Rock Creek via three-pass depletion with a backpack electrofishing unit. A visual survey of habitat units within Rock Creek was conducted, and only pools were sampled. For BY 2004, we also measured the length and width of each pool during the same week of fish sampling for estimates of coho salmon and total salmonid (coho salmon plus sympatric trout) density. Sampling of Rock Creek occurred between 13 August 2004 and 11 March 2005 for BY 2003 and between 9 August 2005 and 21 February 2006 for BY 2004. The majority of Rock Creek juvenile coho salmon were measured in summer and fall ( $n = 34$  for BY 2003,  $n = 163$  for BY 2004), and smaller sample sizes were collected during the subsequent winter or spring ( $n = 24$  for BY 2003,  $n = 20$  for BY 2004). Densities obtained from seining (Cedar River) and electrofishing (Rock Creek) were only used to predict fish size in a regression analysis of competition and were never compared with densities obtained from snorkeling.

*Data analysis.*—To evaluate the significance of juvenile dispersal to the rate of population increase during colonization, we used densities to extrapolate abundance estimates for each snorkeled reach. Survey methods differed between Rock Creek (only pools snorkeled) and the Cedar River (all habitat units snorkeled). To facilitate comparison of reach-scale densities between the two habitats, raw Rock Creek densities from the late-summer group were multiplied by the reach-specific proportion contributed by pools to the total surface area reported by Riley et al. (2001). We considered this a conservative adjustment because it assumed that coho salmon were absent from riffles, glides, and any nonpool habitat types in Rock Creek. Within each reach, density was multiplied by the total surface area (Riley et al. 2001) to obtain an abundance estimate.

We used the relationship between coho salmon size and date as a surrogate for direct measurement of growth rates. Size data were modeled using the von Bertalanffy growth equation (Wootton 1990) and adjusted to yield size on a common date. The equations for size were:

$$L_t = L_\infty \left\{ 1 - e^{-K(t-t_0)} \right\} \quad (1)$$

and

$$W_t = W_\infty \left\{ 1 - e^{-K(t-t_0)} \right\}^3, \quad (2)$$

where  $L_t$  and  $W_t$  are predicted length and weight,  $L_\infty$  and  $W_\infty$  are asymptotic length and weight,  $K$  defines the rate at which the curve approaches the asymptote, and  $t_0$  is the hypothetical time at which size is zero. For each equation, the  $L_\infty$  or  $W_\infty$ ,  $K$ , and  $t_0$  values were estimated using ordinary least-squares. Separate model fits were done for each BY. Collection date explained 19% of the variation in length and 17% of the variation in weight for BY 2003 and 18% of the variation in both length and weight for BY 2004.

The fitted von Bertalanffy growth models were then used to adjust the size of each fish to an expected size on 15 September, which was chosen because little growth occurred after this date and because it also minimized the number of days of growth requiring extrapolation across the dataset. For each individual, the equation used to calculate adjusted size (length and weight) was:

$$S_A = S_O + (P_C - P_O), \quad (3)$$

where  $S_A$  is adjusted size,  $S_O$  is observed or raw size,  $P_C$  is size predicted by the growth model on the common date, and  $P_O$  is size predicted by the growth model on the date of size data collection.

TABLE 1.—Estimated number of coho salmon spawning sites, juvenile density, and juvenile abundance in the Cedar River (CR) and Rock Creek (RC), Washington, after fish passage modification of Landsburg Diversion Dam in 2003 allowed for recolonization of habitat. Spawning sites were identified based on inference from the movements of radio-tagged females (2003) and direct observation (2004; see text). Juvenile density and abundance were estimated in 2004 and 2005. Reach-scale densities for RC (pools only) were adjusted by multiplying raw density by the pool proportion of total surface area to facilitate comparisons with CR reaches.

Brood year	Reach	Spawning sites	Juvenile	
			Density (fish/m <sup>2</sup> )	Abundance
2003	CR1	7	0.021	1,709
	CR2	6	0.033	1,707
	CR3	0	0	0
	CR4	0	0	0
	CR5	0	0	0
	CR6	0	0.00046	14
	RC1	0	0.020	77
	RC3	0	0.023	166
	RC4	1	—	—
	2004	CR1	7	0.027
CR2		9	0.040	2,104
CR3		1	0.0041	243
CR4		0	0.022	330
CR6		0	0.0021	64
CR7		1	0.00049	19
CR8		0	0	0
CR9		0	0	0
CR10		0	0	0
RC1		0	0.028	106
RC3		0	0.0075	55

## Results

### *Distribution and Abundance*

In both years, the vast majority of spawning adult and rearing juvenile coho salmon was found in the lower reaches of the Cedar River. We estimated that 93% of all BY 2003 juveniles and 84% of BY 2004 juveniles in the newly accessible habitat were located in CR1 and CR2 (Table 1). Juveniles from BY 2003 were absent from CR3–CR5 and were observed at extremely low densities in CR6, which is consistent with the failure to detect spawning in these reaches (Table 1). Juvenile coho salmon from BY 2004 were observed in four Cedar River reaches besides CR1 and CR2. Densities were low in CR3 and CR6–CR7, consistent with the low levels of spawning observed in these areas (Table 1). Densities were much higher in CR4 (comparable with those in CR1) despite the lack of observed spawning sites (Table 1). Finally, at the scale of the entire Cedar River, densities were higher for BY 2004 juveniles than for BY 2003 fish in every reach that was snorkeled in both years (CR1–CR4 and CR6; Table 1), consistent with the higher number of female colonists observed in 2004 (34 in 2004 versus 21 in 2003).

Juvenile coho salmon in the Cedar River were observed in dense, distinct aggregations associated with woody debris along river margins. For BY 2003, 9 of 22 habitat units within CR1, CR2, and CR6 contained no juveniles; among all 22 units, there was a high variance in density (SD = 0.031 fish/m<sup>2</sup>, overall density = 0.019 fish/m<sup>2</sup>). For BY 2004, 112 of 172 habitat units within CR1–CR4, CR6, and CR7 contained no coho salmon, and a high variation in density was evident among all units (SD = 0.13 fish/m<sup>2</sup>, overall density = 0.015 fish/m<sup>2</sup>). Thus, areas of the Cedar River containing coho salmon were interspersed between long sections of potential habitat (roughly hundreds of meters) where the species was absent.

As time progressed within each growing season, successive snorkel surveys of Rock Creek revealed that age-0 coho salmon occurred at higher densities and greater distances upriver (Figure 2). During the first spring survey, BY 2003 juveniles were observed only at the pool closest to the confluence with the Cedar River (10 m from the main stem), but no BY 2004 fish were observed at any pool. In both years, the early summer survey yielded age-0 coho salmon throughout much of the lower reach, but none were found in the upper reach (2.4 km upriver from the confluence) until the end of the summer. Mean densities in the 10 pools snorkeled in Rock Creek differed between seasons but not between years (two-way analysis of variance [ANOVA], season:  $P = 0.003$ , year:  $P > 0.10$ ). Maximum local densities in Rock Creek were lower than those of the Cedar River; the dense aggregations exceeding 50 individuals often seen in the Cedar River were never observed in Rock Creek. Nevertheless, late-summer densities in Rock Creek were comparable with those of CR1, though abundances in Rock Creek were a fraction of those estimated for the Cedar River (Table 1).

### *Size and Growth*

Juveniles from BY 2003 were larger than BY 2004 fish in both adjusted length and weight (Welch's  $t$ -test:  $P < 0.0001$ ; Table 2), but neither length nor weight differed between the Cedar River and Rock Creek samples in either year (Welch's  $t$ -test:  $P > 0.10$ ; Table 2). Within both the Cedar River and Rock Creek, larger fish were found upriver; the only exception was BY 2004 fish in CR4 (Table 2). In the Cedar River, differences between reaches were significant for BY 2004 juveniles (Kruskal–Wallis test:  $P < 0.0001$  for both adjusted length and weight) but not for BY 2003 fish (Welch's  $t$ -test:  $P > 0.10$ ). In Rock Creek for BY 2004, the pattern of larger fish upstream was significant

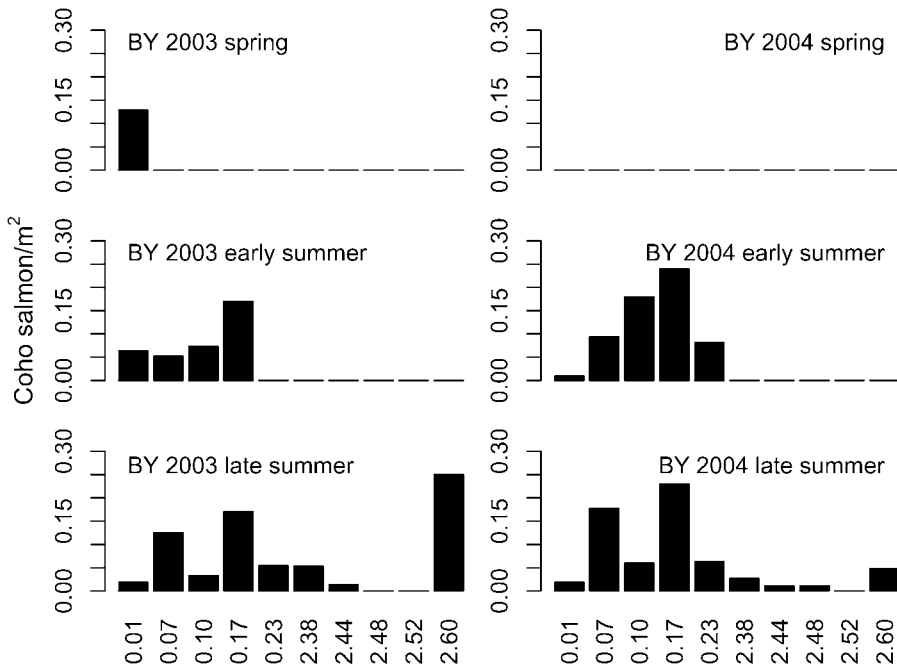


FIGURE 2.—Age-0 coho salmon density (fish/m<sup>2</sup>; raw, unadjusted data) in individual pools, presented in relation to pool distance (km; x-axis) from the mouth of Rock Creek (RC), Washington. The large discontinuity in distance (i.e., between 0.23 and 2.38 km) is due to the distance between reaches RC1 and RC3, where densities were estimated.

(Welch’s *t*-test:  $P < 0.001$ ; Table 2) for both length and weight.

We also used ordinary least-squares regression to test the hypothesis that coho salmon captured at high-density sites would be smaller than those captured at low-density sites due to competition. Local density for each sampling site was used to predict average coho salmon size within the site. In the Cedar River, there was no relationship in either year between length or weight and coho salmon group size ( $P > 0.10$ ). In Rock Creek, we collected habitat data for BY 2004

fish, but neither coho salmon density nor total salmonid density was related to coho salmon length or weight ( $P > 0.10$ ).

**Discussion**

The distribution of juvenile coho salmon largely matched that of the spawning adults, as both were consistently highest in the lower two reaches of the Cedar River. However, two lines of evidence suggested that juvenile coho salmon dispersed during the colonization of the Cedar River above Landsburg

TABLE 2.—Raw and adjusted average sizes ( $\pm$ SD) fork length and weight of juvenile coho salmon in the Cedar River (CR) and Rock Creek (RC), Washington, collected after fish passage modification of Landsburg Diversion Dam in 2003 allowed for recolonization of habitat. Sizes were measured in 2004 and 2005 and were adjusted to a common date at the end of the growing season (see Methods) because collection dates differed.

Brood year	Reach	Sites (n)	Fish (n)	Raw		Adjusted	
				Length (mm)	Weight (g)	Length (mm)	Weight (g)
2003	CR1	13	168	81.0 $\pm$ 6.9	5.99 $\pm$ 1.69	87.0 $\pm$ 6.7	7.27 $\pm$ 1.65
	CR2	13	227	86.5 $\pm$ 7.2	7.22 $\pm$ 1.93	87.7 $\pm$ 7.2	7.51 $\pm$ 1.95
	RC1	8	58	87.3 $\pm$ 9.1	7.74 $\pm$ 2.07	88.0 $\pm$ 7.6	7.61 $\pm$ 1.58
2004	CR1	18	387	70.2 $\pm$ 8.3	3.94 $\pm$ 1.43	79.3 $\pm$ 8.3	5.60 $\pm$ 1.43
	CR2	7	134	75.7 $\pm$ 6.4	4.95 $\pm$ 1.28	82.1 $\pm$ 6.4	6.20 $\pm$ 1.28
	CR3	1	18	80.2 $\pm$ 4.8	5.81 $\pm$ 1.04	86.1 $\pm$ 4.8	6.99 $\pm$ 1.04
	CR4	5	82	74.3 $\pm$ 5.0	4.55 $\pm$ 1.01	78.4 $\pm$ 5.0	5.42 $\pm$ 1.01
	RC1	19	139	77.5 $\pm$ 7.9	5.31 $\pm$ 1.54	78.0 $\pm$ 7.1	5.37 $\pm$ 1.40
	RC3	13	44	83.0 $\pm$ 7.3	6.42 $\pm$ 1.70	83.3 $\pm$ 6.9	6.45 $\pm$ 1.60

Diversion Dam. First, over both years, fry were present in three of the nine snorkeled Cedar River reaches where no adult spawning sites were found the previous fall (Table 1). In one of these reaches (CR4 for BY 2004), density was comparable with that in the lower reaches despite the absence of known spawning sites. Second, spawning in Rock Creek was nonexistent or extremely rare for both BYs (Anderson and Quinn 2007), but in both years juvenile coho salmon were detected at progressively higher densities and greater distances upriver from spring to late summer (Figure 2). These fish probably entered from the Cedar River and dispersed as much as 2.6 km up Rock Creek. The summer movement into Rock Creek was unusual; previous studies have reported that tributary immigration by juvenile coho salmon primarily occurs during late fall and winter as fish avoid high discharges in main rivers (Bustard and Narver 1975; Tschaplinski and Hartman 1983; Scarlett and Cederholm 1984; Bramblett et al. 2002).

Our analysis assessed the importance of juvenile dispersal for the spatial and numerical expansion of the colonizing population. Spatially, juvenile coho salmon were found in twice as many (BY 2004) or over twice as many (BY 2003) reaches as were adult spawning sites (Table 1). Movements by juveniles could accelerate colonization of reaches with few spawners if they return as adults to their rearing sites rather than the sites of emergence from the gravel. There is abundant evidence that salmon imprint to odors during the parr-smolt transformation (Dittman and Quinn 1996), so immigrants to Rock Creek may return there as adults. However, seaward-migrating Chinook salmon have been observed in tributaries of the Fraser River, British Columbia, during summer, despite a continued absence of spawning in these small creeks (Murray and Rosenau 1989; Scrivener et al. 1994), so the use of nonnatal habitat for rearing does not necessarily mean that adults will return there.

Although juvenile dispersal clearly expanded the spatial range of occupied rearing habitats, its significance to the rate of population abundance increase was less apparent. Our results provided no clear support of the hypothesis that lowering rearing densities via dispersal would increase freshwater growth and, hence, survival and population productivity. The abundance estimates suggested that relatively few juvenile coho salmon dispersed into nonspawning reaches; the vast majority of juveniles were found in the primary spawning reaches, CR1 and CR2. Therefore, any survival advantage conferred by inter-reach dispersal was limited to a small portion of the population. Furthermore, we found no difference in size in the end of the summer between the dispersers in Rock Creek

and fish remaining within spawning reaches in the Cedar River.

Unfortunately, data limitations constrained our ability to directly quantify long-distance movements by juvenile coho salmon. Undetected spawning could also explain the presence of juvenile coho salmon in some reaches without known spawning sites. However, it seems unlikely that all juveniles observed in presumed nonspawning reaches emerged from undetected redds. This is particularly true for Rock Creek, where the search for radio-tagged adults was thorough (Anderson and Quinn 2007) and where the sequential snorkel surveys indicated upstream movement by juveniles. The single radio-tagged female from BY 2003 that settled in RC4 could not have produced all of the juveniles present in Rock Creek because her offspring would have been observed first in RC3 and later in RC1 and this was clearly not the case (Figure 2). Furthermore, this lone Rock Creek female probably did not spawn successfully because she was never approached by any radio-tagged male, and only two potential mates without radio tags ascended the fish ladder within 1 month of her passage of the dam.

Regardless, we could not identify the incubation sites for individual juvenile coho salmon, and this prevented us from quantifying the distances moved. We have now begun new work to measure dispersal distance more directly using mark-recapture techniques (Kiffney et al. 2007) and genetic analysis similar to that conducted by Webb et al. (2001). Initial results from both of these approaches corroborate the conclusion that juvenile coho salmon immigrated into Rock Creek from the Cedar River during the summer.

To evaluate the role of habitat in coho salmon redistribution and growth, we compared the end-of-summer size between main-stem and tributary habitats and between downriver and upriver reaches. There was no clear difference in size between fish in the Cedar River and Rock Creek; thus, no obvious summer growth benefits were afforded by the tributary. Larger fish tended to be found farther upriver (Table 2); this pattern could result from spatial differences in growth or size-selective movement. Reach-scale differences in environmental conditions (e.g., Arnekleiv et al. 2006) or density (see later discussion of density dependence) could have led to spatial differences in growth. Alternatively, downstream movement by smaller coho salmon (Chapman 1962) could have resulted in the same pattern, although such movement may only occur at high densities (Bilby and Bisson 1987) or not at all (Kahler et al. 2001). Finally, upstream movement by large fish may have caused the longitudinal size trend (Hughes 1999). The ability to disperse long distances upriver may have been size dependent, a hypothesis

that seems particularly plausible in Rock Creek, where coho salmon moved upstream. Size- or condition-dependent dispersal has been hypothesized for coho salmon in streams (Scarlett and Cederholm 1984) and for a broad array of taxa (Stamps 2006).

We found no direct evidence of density-dependent growth, although competition still may have played a role in dispersal. Local densities in both the Cedar River (number of coho salmon in an aggregation) and Rock Creek (pool density of coho salmon and all salmonids combined) were unrelated to size. However, density dependence may have operated over larger spatial scales; for BY 2004, the largest fish were found in reaches with the lowest densities (RC3 and CR3). Jenkins et al. (1999) and Imre et al. (2005) both reported the strongest patterns of density-dependent growth at larger spatial scales ( $\sim 1,000 \text{ m}^2$  in creeks similar in size to Rock Creek), and much weaker relationships at scales similar to those of the habitat units we analyzed ( $\sim 10\text{--}100 \text{ m}$ ). Unfortunately, we did not measure coho salmon from enough reaches to permit robust statistical tests. Furthermore, the ability to disperse into unoccupied habitats after emergence may have decreased the effects of competition on growth (Keeley 2000). Movement may have confounded the effects of density on growth, as local densities were probably changing throughout the growing season (see Figure 2). Finally, fish often adjust densities to match habitat quality according to the ideal free distribution, such that lower fish densities are offset by lower food availability, thereby equilibrating growth across habitats of varying local density (Power 1983).

We postulate that an interaction between competition and habitat prompts the dispersal of juvenile coho salmon during colonization. Despite low reach-scale coho salmon densities in the Cedar River, fish were aggregated and locally dense along river margins. Aggression within main-stem river groups may have encouraged movement by juveniles (Chapman 1962) in the Cedar River. Densities were lower than those in most similar habitats with established populations (Rosenfeld et al. 2000; Ebersole et al. 2006), and the effects of competition on growth are often most pronounced at low densities (Jenkins et al. 1999; Imre et al. 2005). Despite our inability to detect density-dependent growth, competition may have promoted dispersal of juvenile coho salmon that were unable to secure feeding resources or quality habitats. In addition to competition, habitat quality probably influenced the redistribution of fish, particularly in Rock Creek. Rock Creek is quite similar to the small tributary habitat type (channel width  $< 10 \text{ m}$ ) in which juvenile coho salmon density is typically the highest (Rosenfeld et al. 2000;

Scarnecchia and Roper 2000). Fish may have sought the discrete pool-riffle sequences and abundant riparian cover that were characteristic of a small creek in preference to the large, open habitats along the margins of the Cedar River.

The results of this study contribute to our knowledge of the colonization process in salmon. Most juvenile coho salmon remained in reaches where their parents spawned, but some dispersed by as much as several kilometers into previously unoccupied habitats, notably a tributary of the main river. Although difficult to quantify with our field approaches, juvenile dispersal clearly expanded the range of habitats used for rearing. We speculate that juvenile dispersal accelerates the spatial expansion by adults in the next generation if they home to rearing rather than incubation sites. The importance of juvenile dispersal to the numerical expansion of the population was not evident in this analysis; fish dispersing into Rock Creek did not grow detectably faster during the summer than those remaining in spawning reaches. However, tributaries may provide survival benefits unrelated to end-of-summer size, such as increased overwinter growth (Ebersole et al. 2006) or refuge from high winter discharge (Brown and Hartman 1988). The results presented here did not demonstrate a clear benefit to dispersal in terms of population productivity, but continuing research will address the movement, growth, and survival of juvenile coho salmon more directly.

Our observations also highlight the importance of maintaining access to stream habitats for juveniles as well as adult salmon. Road crossings and culverts that are impassable to juvenile fish plague many streams of North America (USGAO 2001; Gibson et al. 2005), and resource managers should prioritize reconnection of isolated stream habitats (Roni et al. 2002). Providing access to small streams would benefit juvenile salmon that are seeking rearing habitat, even if these areas are not preferred by adults for spawning.

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