

CHANGES IN FISH COMMUNITIES FOLLOWING RECOLONIZATION OF THE CEDAR RIVER, WA, USA BY PACIFIC SALMON AFTER 103 YEARS OF LOCAL EXTIRPATION[†]

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ABSTRACT

Migration barriers are a major reason for species loss and population decline of freshwater organisms. Significant efforts have been made to remove or provide passage around these barriers; however, our understanding of the ecological effects of these efforts is minimal. Installation of a fish passage facility at the Landsburg Dam, WA, USA provided migratory fish access to habitat from which they had been excluded for over 100 years. Relying on voluntary recruitment, we examined the effectiveness of this facility in restoring coho (*Oncorhynchus kisutch*) salmon populations above the diversion, and whether reintroduction of native anadromous species affected the distribution and abundance of resident trout (*O. mykiss* and *O. clarki*). Before the ladder, late summer total salmonid (trout only) density increased with distance from the dam. This pattern was reversed after the ladder was opened, as total salmonid density (salmon + trout) approximately doubled in the three reaches closest to the dam. These changes were primarily due to the addition of coho, but small trout density also increased in lower reaches and decreased in upper reaches. A nearby source population, dispersal by adults and juveniles, low density of resident trout and high quality habitat above the barrier likely promoted rapid colonization of targeted species. Our results suggest that barrier removal creates an opportunity for migratory species to re-establish populations leading to range expansion and potentially to increased population size. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: barriers; habitat fragmentation; migration corridors; fish; river landscapes; salmon; trout

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INTRODUCTION

Habitat fragmentation is a major cause of biodiversity loss, population decline, changes in species composition and alteration in the flux of essential elements (Pringle, 2001; Tallmon *et al.*, 2003; Jansson *et al.*, 2007). As a result, the study of habitat fragmentation is a major focus in conservation biology (Meffe and Carroll, 1997). Fragmentation of river landscapes, however, is typically not considered in the habitat fragmentation literature (Pringle, 2001), which is surprising given that barriers are a major cause of habitat isolation (Giller, 2005; Moyle and Williams, 1990; Richter *et al.*, 1997). Our study attempts to address this knowledge gap by examining the temporal and spatial dynamics of fish recolonization following removal of a migration barrier and the effects of recolonizing fish on resident communities.

Habitat isolation is particularly detrimental to migratory species, such as fish in the subfamily salmoninae (salmon, trout and char) that require access to large portions of river networks to complete their life cycle (Beechie *et al.*, 1994; Holmquist *et al.*, 1998; Eikaas and McIntosh, 2006). Movement between and among habitat patches is

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critical to the restoration and conservation of these migratory taxa (Riemann and Dunham, 2000; Morita and Yamamoto, 2002), as well as other species that must move between habitat patches seeking resources for growth, reproduction and survival (Fraser *et al.*, 1999; Jansson *et al.*, 2007), and species that operate as metapopulations (Hanski and Gilpin, 1991; Riemann and Dunham, 2000).

About 70% of the large rivers in Europe, North America and the former Soviet Union are regulated, and there are more than 800 000 dams worldwide that divert water (Giller, 2005). Many of these barriers fragment rivers by obstructing migration of freshwater organisms leading to local population decline and species extinction. For example, migration barriers are a major reason for listing a number of salmon stocks as either threatened or endangered under the U. S. Endangered Species Act (1973) (NRC, 1992). In Washington State, over 7700 km of historical habitat are inaccessible to migratory fishes because of impassable culverts or road crossings, despite state regulations requiring fish passage (Roni *et al.*, 2002). Lack of fish passage is a global problem that has been documented throughout North America (USGAO, 2001; Langill and Zamora, 2002; Gibson *et al.*, 2005), Europe (Yanes *et al.*, 1995) and New Zealand (Eikaas and McIntosh, 2006). As a result of worldwide decline and extinction of some migratory animals, removal of passage around barriers is considered a key restoration action to recover and conserve these species.

Although much effort has been made to remove blockages to anadromous fish, surprisingly little is known about the functionality of these migration corridors, the dynamics of fish recolonization after passage, or how resident organisms respond to reintroduction of species after a barrier is removed (Bernhardt *et al.*, 2005). Research on fish invasions and use of corridors by terrestrial species might help us predict how colonists interact with resident fishes and ecosystems and the spatial patterns of recolonization (Baxter *et al.*, 2004; Becker *et al.*, 2007). For example, colonizers might displace organisms previously occupying a particular habitat, especially if the colonizer has a size advantage (Sabo and Pauley, 1997; Dunham *et al.*, 2002). Mobile species, such as fish, birds or mammals might shift their distribution to take advantage of the food resources provided by species reintroduction: spawning salmon (eggs and flesh) and emerging fry provide energy and nutrients for a variety of aquatic and terrestrial organisms (e.g., Schindler *et al.*, 2003).

The installation of a fish ladder at the Landsburg Dam on the Cedar River, WA, USA in September 2003 provided a unique opportunity to increase our understanding of some of the ecological and management issues related to species reintroduction following circumvention of a barrier. This diversion dam blocked upstream migration of numerous species including two threatened anadromous species (chinook salmon, *O. tshawytscha*) and steelhead trout, *O. mykiss*), two species of concern (coho salmon and anadromous cutthroat trout), as well as resident fish for over 100 years.

We established baseline conditions (distribution, abundance and composition) for resident fish populations during 2000 and 2001 before installation of the ladder. Similar data were collected after the ladder was installed. To the best of our knowledge, this is one of the first studies to document the recolonization of Pacific salmon into native habitat from the first generation of population expansion by relying on voluntary recruitment (Bryant *et al.*, 1999; Milner *et al.*, 2000; Quinn *et al.*, 2001; Ciancio *et al.*, 2005). We argue that the monitoring approach used in our study plus the patterns of recolonization we observed can be applied to other projects that aim to restore migratory species by circumventing barriers.

In this paper, we test the hypotheses that circumvention of a migration barrier leads to the recolonization of the Cedar River by anadromous salmon and that this recolonization leads to broad-scale changes in the distribution, abundance and composition of fish populations due to the addition of two species. Because we have two years of baseline data, this study also allows us to address potential mechanisms of change.

MATERIALS AND METHODS

Study site

The 36 644 ha Cedar River Municipal Watershed is protected from all recreational activities, managed as a wildlife conservation area located on the west slope of the Cascade Mountains, and the source of approximately two-thirds of the water supply for the greater Seattle metropolitan area (Figure 1). Climate of the watershed is typical of the Pacific Northwest with mild temperatures (annual temperature range = 4–15°C), wet falls and winters

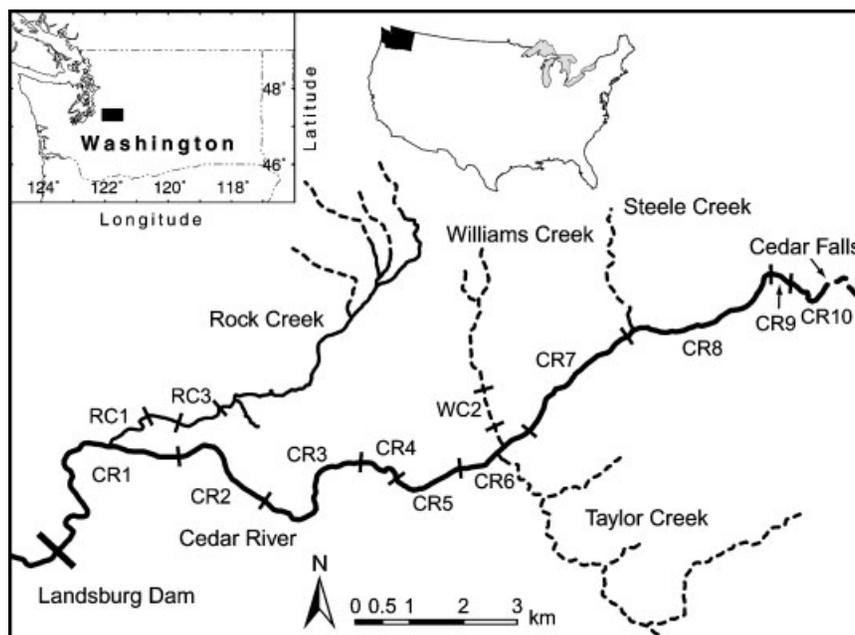


Figure 1. Map of Cedar River main stem and tributaries above Landsburg Diversion Dam including reach breaks and natural upstream barriers to anadromous fish. Solid lines represent habitat available to anadromous fish and dashed lines inaccessible habitat above natural barriers

and dry summers (NOAA, 2005). The watershed consists of a mixture of forest ages, but is primarily second-growth (~60 years old), dominated by conifers. In 1900, the City of Seattle constructed Landsburg Diversion Dam, a low head, run-of-the river facility at river kilometer 35.1. This dam blocked upstream fish migration to 33 km of habitat until passage facilities were completed by the City in 2003.

The Cedar River between Landsburg Dam and Cedar Falls (a natural barrier) is a low gradient (less than 1%), relatively wide (20–30 m wetted width), clear water, alluvial stream characteristic of the Pacific coastal ecoregion (Naiman and Bilby, 1998). Mean (± 1 sd) annual discharge at Landsburg Dam ($47^{\circ}23'28''\text{N}$, $121^{\circ}57'12''\text{W}$) between 1895–2006 was $19.1 (\pm 4.2) \text{ m}^3 \text{ s}^{-1}$; discharge was generally lowest in September ($9.1 \text{ m}^3 \text{ s}^{-1}$) and peaks in January ($27.7 \text{ m}^3 \text{ s}^{-1}$) (USGS, 2007). Four main tributaries flow into the main stem: Rock, Taylor, Williams and Steele creeks. Most of Rock Creek (approximately 10 km), which is about 4–6 m wide (wetted width), is accessible to anadromous fish, while only short reaches (< 0.5 km) of the other creeks are accessible to salmon (Figure 1). In total, about 20 km of main stem and 13 km of tributary habitat is available to anadromous fish.

Before the passage facility, the fish community of the main stem comprised rainbow and cutthroat trout, mountain whitefish (*Prosopium williamsoni*) and several species of sculpin (*Cottus* spp.). Fish communities in tributaries were comprised of trout and sculpin with speckled dace (*Rhinichthys osculus*) common in Rock Creek. Numerically, rainbow trout made up about 95% of the trout population of the main stem with cutthroat dominant in tributaries (Riley *et al.*, 2001).

Habitat and fish surveys

The main stem and tributaries were divided into geomorphic reaches based on channel confinement and gradient (Figure 1, Table I). We categorized summer, low-flow habitat types within each reach based on a modification of methods described in Bisson *et al.* (1982) and Hawkins *et al.* (1993). In 2000, all of the habitat accessible to salmon in Rock Creek and the main stem were quantified; approximately 600–800 m sections per reach were assessed during the summers of 2001, 2004–2006. A hand-help GPS (Garmin, Inc.) was used to define the start and end point of each survey.

Within each habitat type, we measured habitat length, width and depth, and counted the number of pieces of wood that were in the active channel and put them in three size categories (small wood, 10–20 cm in diameter

Table I. Mean (\pm upper and lower 95% CI) wetted width, water depth, channel slope and total wood abundance (summed across size classes) in main stem reaches, and Rock and Williams creeks

Stream	Reach	Wetted width (m)	Water depth (m)	Channel slope	Wood abundance (pieces km ⁻¹)
Cedar River	1	21 (18, 24)	0.53 (0.43, 0.65)	0.53 (0.37, 0.68)	65 (42, 89)
	2	23 (22, 25)	0.61 (0.53, 0.70)	0.63 (0.43, 0.85)	112 (31, 194)
	3	24 (22, 26)	1.2 (1.0, 1.3)	1.1 (0.9, 1.4)	33 (13, 52)
	4	24 (20, 26)	0.80 (0.55, 1.0)	0.50 (0.13, 0.88)	57 (14, 100)
	5	23 (20, 24)	0.70 (0.50, 0.90)	0.90 (0.52, 1.3)	91 (35, 146)
	6	22 (19, 24)	0.47 (0.38, 0.56)	0.86 (0.57, 1.2)	176 (19, 332)
	7	21 (19.0, 23)	0.61 (0.49, 0.72)	1.1 (0.67, 1.5)	63 (32, 93)
	8	21 (19, 23)	0.74 (0.45, 1.0)	0.75 (0.55, 0.96)	24 (13, 35)
	9	11 (9, 13)	0.73 (0.59, 0.86)	3.3 (1.8, 4.7)	33 (2, 64)
	10	13 (11, 15)	0.49 (0.36, 0.60)	1.5 (1.0, 2.0)	48 (22, 74)
Rock Creek	1	4.9 (3.7, 6.2)	0.40 (0.19, 0.63)	1.8 (0.90, 2.7)	381 (232, 531)
	3	4.2 (3.8, 4.6)	0.32 (0.21, 0.45)	0.81 (0.41, 1.2)	272 (211, 333)
Williams Creek	2	3.0 (2.3, 3.7)	0.16 (0.10, 0.23)	1.2 (0.50, 1.96)	188 (21, 356)

and ≥ 1 m and ≤ 2 m long; medium wood, 20–50 cm in diameter and ≥ 2 m and ≤ 3 m long; large wood, ≥ 50 cm in diameter and ≥ 3 m long). Channel gradient was quantified over a representative section (~ 300 – 800 m long) of each reach using a laser range finder and stadia rod.

To enumerate fish communities, snorkel counts were conducted in the main stem during August–September before (2000–2001) and after (2004–2006) the ladder was installed. Snorkel surveys were used to quantify fish populations because (i) some habitat units were fast and deep, which made electrofishing logistically difficult, (ii) water clarity was excellent (~ 5 m), (iii) there were relatively few species and they were easily discriminated visually and (iv) it was necessary to use a consistent method to quantify fish populations across habitat types, reaches, channel sizes and years. Previous research in the Cedar River demonstrated this variation was most effectively captured by snorkeling. A comparison of sampling efficiency between electrofishing and snorkeling in the main stem revealed that electrofishing underestimated total trout density by four-fold compared to snorkeling (Riley *et al.*, 2001).

Observers were first trained in classifying fish to species and size class. Trout < 90 mm could not be assigned to species so were categorized as trout. In 2000 and 2001, all 10 main stem reaches were snorkeled, while in 2004 reaches 1–6 were surveyed; in 2005 and 2006, nine and seven reaches were snorkeled, respectively. We attempted to snorkel at least three replicates of each habitat type per reach each year.

To quantify coho salmon colonization patterns in tributaries, we snorkeled pools during August–September in two reaches ($n = 3$ – 5 pools per reach) of Rock Creek and one in Williams Creek before (2000–2001) and after (2004–2006) the installation of ladder. Pools in Williams Creek were above a natural barrier that excluded upstream migration of adult or juvenile salmon; therefore, this tributary provided a reference site with which to track patterns of fish density without salmon.

One to five observers (depending on stream width) entered the habitat unit at the downstream end and moved upstream through each site, counting and recording species and size classes of all fish encountered (Dolloff *et al.*, 1996). Resident salmonids and juvenile coho in the main stem were divided into two size classes (small fish < 90 mm and medium to large fish > 90 mm). Stable isotope and diet data suggest that these size classes represent distinct functional feeding groups (Kiffney, unpublished data). We only present data on salmonid populations because snorkel counts underestimated sculpin density relative to electrofishing and whitefish were rare ($< 0.1\%$ relative abundance).

Salmon nests (also known as redds) in the main stem above Landsburg Dam were visually located from inflatable rafts annually in 2003–2006. Observed redds were marked with flagging to prevent double counting. A hand-held GPS unit was used to identify the spatial location of each redd. In some cases, redds were attended by salmon whose species could be identified. Unattended redds found after mid-November were assumed to be made by coho since chinook spawning is typically complete by early November (Burton *et al.*, 2005). Our assessment of coho salmon

spawning in the tributaries was primarily limited to 2003 and 2004, when a large portion of colonists were radio tracked (Anderson and Quinn, 2007).

Statistical analysis

We focused our analysis of salmon recolonization on adult chinook, adult and juvenile coho and resident trout. Juvenile chinook salmon in this population seldom over winter in freshwater (Myers *et al.*, 1998) and most in the Cedar River migrate downstream in the Spring (Kiyohara and Volkhardt, 2007). Reach-scale densities were obtained by averaging the densities of individual habitat units (as opposed to dividing total fish counted within a reach by area sampled). Reach was used as a covariate in an analysis of covariance (ANCOVA) to test whether fish density differed by time (before vs. after ladder), reach (covariate) or the interaction of time and reach. Reach-scale density averaged across years before (2000 and 2001) and after (2004–2006) the ladder was installed was our sample unit. A two-way ANOVA was used to determine whether patterns of trout and total salmonid density in Rock and Williams creeks differed by stream, time and the interaction between stream and time.

To examine whether juvenile coho were competing with small trout, we used *t*-tests to compare the density of small trout in main stem and Rock Creek pools before and after ladder installation. If small trout density was lower, one might infer competition for resources (e.g., space or food) with larger juvenile coho as a potential mechanism for this change. Pool densities were used because this was the habitat where both species were most abundant. We also examined bivariate plots of small trout versus juvenile coho in Rock Creek pools within years. If the density of small trout declined as juvenile coho density increased, competition may partially explain this pattern. We tested for normality using Shapiro–Wilkes test: if variables exhibited non-normal distributions, a $\log_{10}(x + 1)$ transformation was used. All analyses were conducted using JMP (Sall *et al.*, 2005). An $\alpha < 0.1$ was used to determine statistical significance.

RESULTS

Fish recolonization

The fish ladder successfully provided a dispersal corridor for adult salmon: combined adult salmon (coho + chinook) passing Landsburg Diversion Dam increased by approximately 79 fish per year (Figure 2). The distribution of coho redds was primarily explained by distance from the dam: averaged across years reach location explained 60% of the variation in coho redd density (Figure 3a). All identified spawning sites were located in the Cedar River with little or no spawning occurring in tributaries. Coho appeared to select spawning sites further upriver each year. Distribution of juvenile coho largely reflected adult spawning locations (Figure 3b, $r^2 = 0.84$,

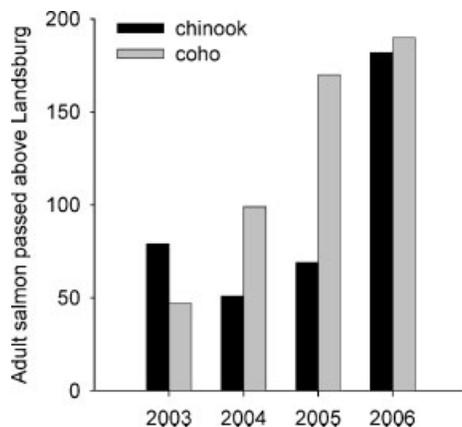


Figure 2. Annual adult coho and chinook salmon passed above Landsburg Diversion Dam since 2003

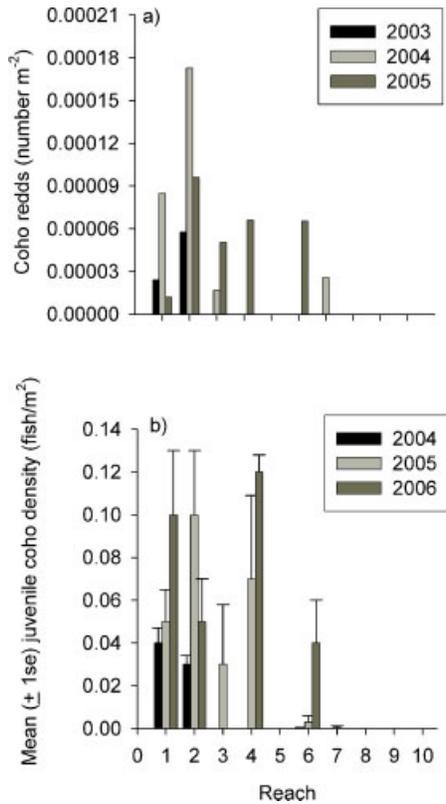


Figure 3. (a) Adult coho redd density (number m⁻²) and (b) mean (± 1 se) juvenile coho density versus main stem reach

$p = 0.0002$ for reach-scale juvenile coho density versus coho redd density) and densities (range = 0.00009–0.10 fish/m²) increased in most reaches each year.

Fish distribution changed markedly following salmon recolonization. Before the ladder was installed, total salmonid density (trout only) increased with distance from the diversion dam (Figure 4). We hypothesize this distribution was a result of higher ambient productivity in upstream reaches; total salmonid density before ladder installation was positively correlated with summer maximum water temperature ($r = 0.71$, $p = 0.01$, $n = 10$). This

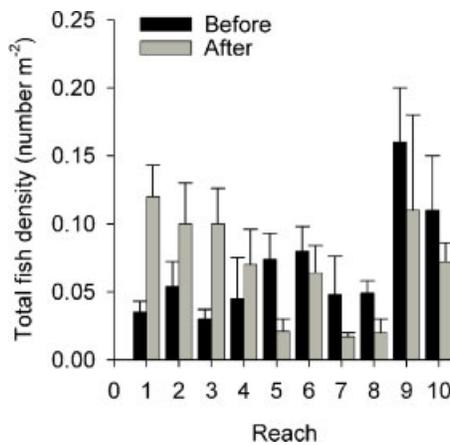


Figure 4. Mean (± 1 se) reach-scale total salmonid density (number m⁻²) during late summer before (black bars, trout only) and after (grey bars, salmon + trout) the fish passage facility was installed

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Table II. *F*-values from ANCOVA model (*df*=3, 16) testing the effects of time (before vs. after ladder), reach and the time × reach interaction on small and large trout, total trout and total salmonid density (number m⁻²)

Response	Model	Time	Reach	Time × reach	<i>r</i> ²
Small trout (< 90 mm)	2.6*	1.2	3.5*	3.1*	0.33
Large trout (> 90 mm)	5.0**	3.5*	8.0**	0.8	0.48
Total trout	3.5**	2.1	6.3**	2.2	0.40
Total salmonids	2.7*	0.01	0.6	7.3**	0.33

p* < 0.1.; *p* < 0.01.

pattern was reversed after ladder installation, as total salmonid density increased in reaches closest to the dam, while declining in upper reaches (Figure 4). Redistribution of small trout and addition of juvenile coho were primarily responsible for this pattern; these changes were reflected in the significant reach × time interaction term for small trout (*p* = 0.07) and total salmonid density (*p* < 0.01, Table II).

To further explore these patterns, mean reach-scale fish density during the period after installation of the ladder was subtracted from the density before the ladder, with this difference plotted as a function of reach. These plots show how small trout and total trout density has changed over time, as differences in both measures declined with distance from the dam (Figure 5a and b). Specifically, trout density in the upper reaches declined or remained the same after the ladder was installed, while increasing in lower reaches. The re-distribution of trout was primarily a result of changes in the distribution of small trout.

Some of this temporal variation in total salmonid density can be attributed to the distribution of coho redds. The distribution of redds across reaches was positively associated with changes in trout and total salmonid density: redd distribution explained 55 and 84% of the variation in small and total salmonid density differences, respectively (Figure 6a and b). A quadratic term significantly improved model fit for both response variables.

We also observed significant changes in the distribution and abundance of fish populations in Rock and Williams creeks after the ladder was constructed. Averaged across years, small and large trout density was about three-fold higher at Williams Creek compared to Rock Creek (Table III, Figure 7a and b). Trout density also varied over time, with this effect conditional upon stream (stream × time, *p* < 0.01). Small and large trout density in Rock Creek was either stable over time (reach 1) or increased (reach 3), whereas both size classes of trout declined in Williams Creek. Similar to the main stem, changes in salmonid density in Rock Creek were primarily a result of colonization by juvenile coho.

There was little evidence for competition between small trout and coho in the Cedar River or Rock Creek. Firstly, there was no significant difference in small trout densities in pools in either the Cedar River or Rock Creek between time periods (*t*-test, *p* > 0.1). Secondly, in 2004 and 2005 juvenile coho density in Rock Creek was positively correlated with small trout (e. g., 2005, *r* = 0.22, *p* = 0.06), a pattern not expected if competition for resources was occurring. In 2006, however, this relationship exhibited a hump-shaped pattern: small trout and coho densities were positively correlated up to certain point, then declined at high coho density (> 0.3 coho m⁻²) (Figure 8).

We used linear regression to quantify the rate of change in fish density in the main stem and Rock Creek. Total salmonid population growth rate has increased linearly since the ladder was installed. Juvenile coho density in the main stem has increased at a rate of 0.007 fish m⁻² yr⁻¹ (*r*² = 0.22, *p* < 0.001), while total salmonid density has increased by 0.009 fish m⁻² yr⁻¹ (*r*² = 0.01, *p* = 0.01). The rate of population increase in Rock Creek was about three times greater than the main stem: juvenile coho density increased by 0.023 fish m⁻² yr⁻¹ (*r*² = 0.22, *p* < 0.001) and total salmonid density by 0.03 fish m⁻² yr⁻¹ (*r*² = 0.19, *p* < 0.001).

DISCUSSION

Fish recolonization

Recolonization of the Cedar River above Landsburg by adult salmon was rapid and supports previous research demonstrating that fish can recover from habitat fragmentation or disturbance relatively rapidly (Leider, 1989;

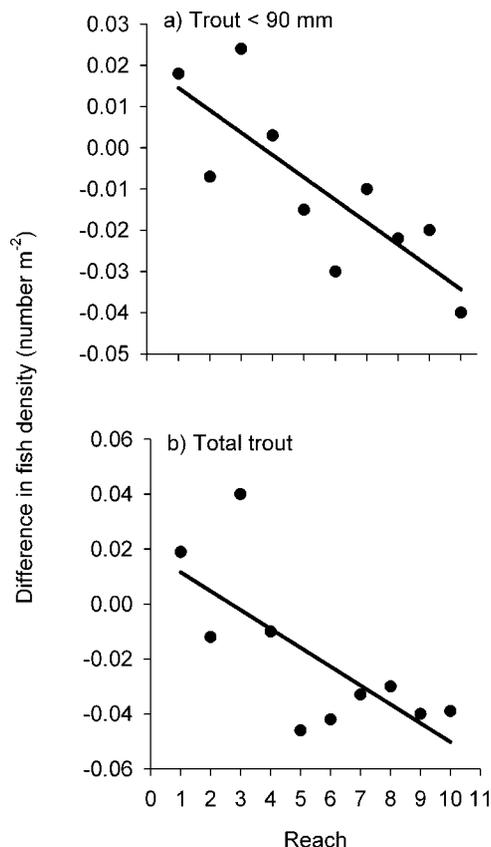


Figure 5. Relationship between reach-scale differences in fish density (i.e., after ladder mean—before ladder mean = fish difference [number m⁻²]) and reach for (a) small trout ($r^2=0.64$, $p=0.006$, $n=10$) and (b) total trout ($r^2=0.53$, $p=0.02$)

Syms and Jones, 2000). A number of factors may promote recolonization following removal of a migration barrier such as a nearby source of colonists, dispersal by both adults and juveniles, relatively high quality habitat in the recolonized ecosystem and low density of resident organisms that compete with colonists for resources.

Because there was little competition for nests sites and spawning habitat quality in reaches immediately above the dam was relatively high, the distribution of salmon nests for these straying adults was mainly a result of distance from the source population (assuming that the majority of spawning salmon were originally from the Cedar River below Landsburg). Specifically, reach 1 and 2 possessed relatively high quality spawning habitats for coho and chinook including coarse substrate (gravel and cobble) with low levels of sedimentation, cool incubation temperatures, and groundwater upwelling (Sandercock, 1992; Healey, 1992).

The pattern of spawning sites in the Cedar River has been shown with other anadromous fish species post dam-removal (Burdick and Hightower, 2006) and is similar to recolonization of newly connected habitat by terrestrial species. For example, dispersal corridors allowed the recolonization of Bachman's Sparrows (*Aimophila aestivalis*) in a fragmented landscape, and density within these newly connected habitats declined with distance from source populations (Dunning *et al.*, 1995). The distribution of redds was also qualitatively similar to theoretical and empirical dispersal curves to describe colonization of islands by insects (Simberloff and Wilson, 1969) and grey seals (Gaggiotti *et al.*, 2002). As population size increases, we might expect an increase in intraspecific interactions for spawning sites near Landsburg resulting in upstream expansion of spawning locations, as well as into tributaries.

High juvenile coho densities in reaches with high redd densities (i.e., reaches 1 and 2) suggest minimal upstream movement of juveniles in the Cedar River. As with spawning habitat, these reaches exhibited characteristics suitable for juvenile rearing: they were relatively low-gradient sections that possessed medium to high wood

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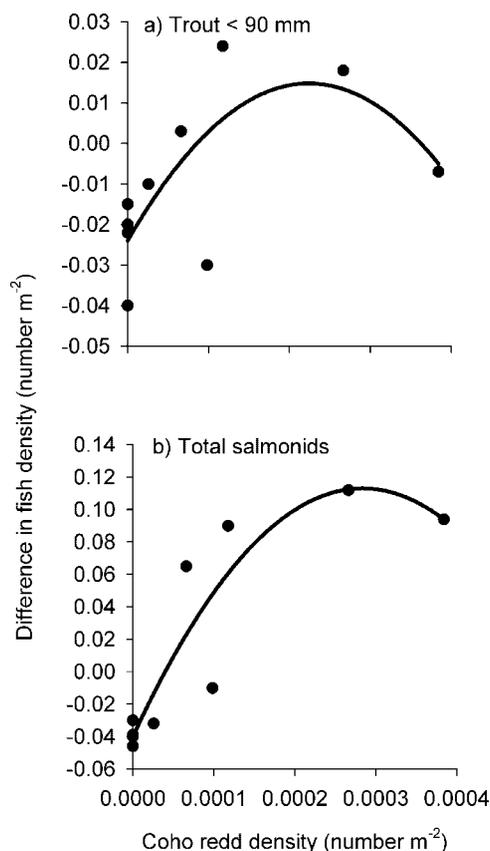


Figure 6. Relationships between reach-scale differences in fish density and adult coho redd density (number m⁻²) by reach for (a) small trout ($r^2 = 0.53$, $p = 0.03$; linear term, $p = 0.03$; quadratic term, $p = 0.07$), and (b) total salmonids ($r^2 = 0.84$, $p = 0.004$; linear term, $p = 0.001$; quadratic term, $p = 0.03$)

abundance compared to other reaches in the main stem. A number of studies have shown that juvenile coho prefer low-gradient channels with abundant wood for cover (e.g., Rosenfeld *et al.*, 2000). Furthermore, resident trout density in downstream reaches of the main stem was relatively low compared to other Pacific Northwest rivers (Platts and McHenry, 1988) potentially minimizing interspecific interactions thereby limiting coho dispersal within the main river channel and promoting successful recolonization by salmon.

Despite relatively low levels of inter-reach movement in the Cedar River, two lines of evidence suggest exploration by some juvenile coho contributed to population expansion. First, the distribution of juvenile coho in the main stem shifted upstream each year after recolonization, and these shifts were not always associated with identified spawning sites (Figure 3). Second, little or no spawning occurred in Rock Creek; therefore, we

Table III. *F*-values from two-way ANOVA model ($df = 7, 61$) testing the effects of time (before vs. after ladder), stream and the time \times stream interaction on small and large trout and total salmonid density (number m⁻²) in Rock and Williams creeks

Response	Model	Stream	Time	Stream \times Time	r^2
Small trout	7.0**	25.2**	2.4*	6.2**	0.45
Large trout	2.4*	11.2**	0.3	3.3**	0.22
Total salmonid	5.3**	4.5*	0.9	6.8**	0.38

* $p < 0.1$; ** $p < 0.01$.

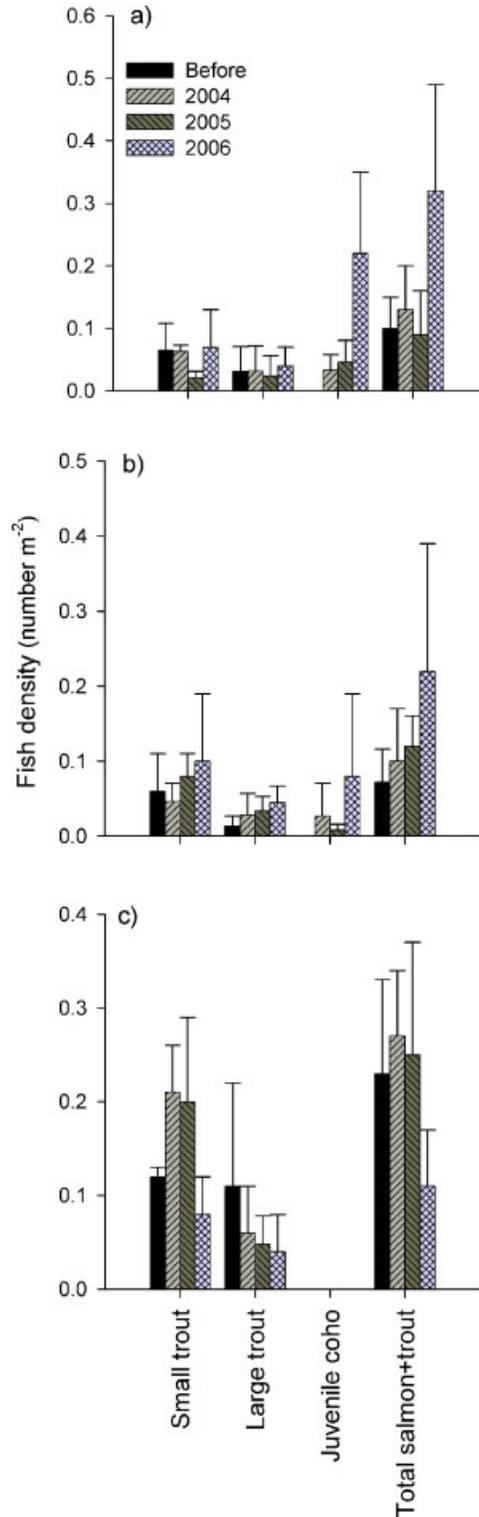


Figure 7. Mean (± 1 se) summer densities for small and large trout, juvenile coho salmon and total salmonids in pools before (2000–2001) and after the ladder was installed in reach (a) 1 and (b) 3 of Rock Creek, and (c) 2 of Williams Creek

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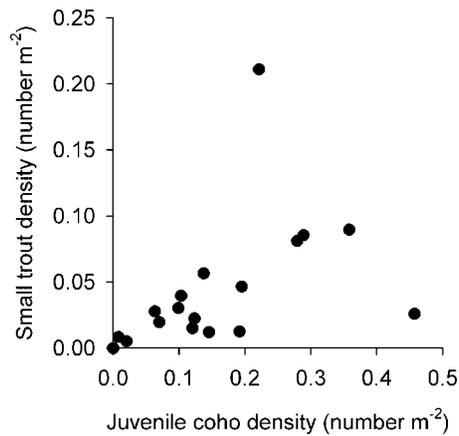


Figure 8. A plot of juvenile coho density versus small trout density in Rock Creek pools during summer 2006 ($r^2 = 0.40$, $p = 0.01$; linear term, $p = 0.004$; quadratic term, $p = 0.06$)

hypothesize that some segment of the main stem juvenile coho population dispersed into Rock Creek (Anderson *et al.*, 2008).

Why these individuals decided to disperse from their natal habitat is unknown, but may be a result of juvenile coho seeking rearing habitat that confers high growth rates, protection from predators or minimizes competitive interactions. Kahler *et al.* (2001) observed that most juvenile coho exhibited upstream movement and it was suggested that this movement was partly a search for high quality rearing habitat. Wood density in Rock Creek was higher and water temperature warmer than reach 1 and 2 of the main stem providing juvenile coho increased protection from predators, low velocity foraging habitat and more optimal growing conditions. Ambient productivity in the main stem, as defined by water temperature and algal biomass, increased with distance from Landsburg Dam (Kiffney, unpublished data). Increased ambient productivity may explain upstream movement of juvenile coho in the main stem because increased prey resources and warmer water temperatures can increase fish growth rates (Metcalf *et al.*, 1999; Giannico, 2000). Movement of juvenile coho in the Cedar River watershed accessible to salmon may also draw adult fish to these areas to spawn in subsequent years. Several studies have shown that juvenile and adult salmon can distinguish odours of their own population from other populations (Quinn, 2005).

Therefore, range expansion of reintroduced salmonids within the Cedar River may be a result of adult straying, juvenile habitat selection, adults following chemical cues from conspecifics and distribution of resident fish populations. Juvenile dispersal may be important in range expansion, gene flow and population persistence for a variety of mobile species such as birds, fishes and mammals. Post-juvenile dispersal of Hazel grouse (*Bonasa bonasia*) contributed to population expansion in the southeastern French Alps (Montadert and Léonard, 2006) and marine dispersal of juvenile *Galaxias maculatus*, one of the world's most widespread freshwater fish species, facilitates considerable gene flow at the inter-continental scale (Waters *et al.*, 2000).

Fish communities

There have been few studies quantifying the impacts of species reintroduction on resident communities (except see Mittlebach *et al.*, 2006) or interactions between resident and reintroduced species (except see Ward *et al.*, 2008). The potential ecological consequences resulting from reconnecting this fragmented river landscape and species reintroduction include changes in fish diversity, density, distribution and composition; spawning patterns of resident fishes; aggregation of terrestrial and aquatic predators to exploit increased prey resources (e.g., emerging salmon fry); changes in invertebrate prey abundance and composition; and habitat partitioning.

We observed some of these effects in that species reintroduction led to broad-scale changes in the distribution, abundance, diversity (addition of two species, coho and chinook) and species composition of fish in the main stem and Rock Creek during summer. Increases in density were primarily a result of colonization by coho; however, we

also observed that trout distributions changed after the ladder was installed. This result was unexpected but may reflect movement of trout to take advantage of new access to spawning habitat provided by the fish ladder or additional food resources resulting from salmon carcasses. For example, between February 20 and June 30, 2005, 180 trout ranging in size from 20 to 49 cm in total length migrated above Landsburg Dam (Faulds, 2006). This upstream migration coincides with the spring spawning season for resident trout: increased density of small trout in reaches near the dam may be a result of this increased spawning activity.

We observed that juvenile coho and trout largely selected similar rearing habitat setting the stage for potential competitive interactions. Sabo and Pauly (1997) observed in controlled experiments that larger coho had a competitive advantage over smaller trout. Coho have such a size advantage in the Cedar River as they emerge from the gravel much earlier than trout (~30–60 days). We found evidence to both reject and support the occurrence of density-dependent interactions. Trout density in Rock Creek was either stable or increased slightly over time despite an expanding coho population, while declining in Williams Creek which is inaccessible to coho. Evidence supporting density-dependent effects was provided by quadratic models that increased the statistical fit to the relationship between coho redd density and changes in fish density over time in the main stem and between juvenile trout and coho in Rock Creek during summer 2006. These relationships imply that density-dependent interactions, such as competition for preferred rearing habitat, limited increases in reach-scale fish density. More data may allow us to determine whether these statistical relationships hold or were simply spurious (e.g. driven by one data point, see Figure 6a). Moreover, we relied on changes in density to quantify competition; however, density-dependent effects could be manifested in changes in survival, growth or movement.

SUMMARY

Our understanding of the ecological consequences of circumvention of barriers or environmental factors that promote recolonization of native species is rudimentary. This study addressed some of these knowledge gaps and has implications for barrier circumvention as a strategy for conservation of threatened migratory fish and other migratory animals. We found that adult salmon rapidly dispersed into the Cedar River after provision of fish passage and primarily spawned in reaches closest to the dam. The distribution of juvenile coho largely reflected distribution of redds, but a segment of the juvenile population dispersed and colonized portions of Rock Creek and the main stem where there was no evidence of adult spawning. Overall, salmonid populations have increased in the main stem and Rock Creek, mostly due to the addition of juvenile coho, but trout populations may have also contributed to these increases.

We suggest that three factors contributed to the rapid and successful natural recolonization of the Cedar River by salmon: (1) a source population below the dam, (2) relatively high quality habitat above the dam and (3) relatively low densities of resident salmonids. The first factor promoted immediate dispersal into the new habitat without artificial supplementation, while the second and third factors likely increase the probability of successful recolonization. Therefore, we recommend an assessment of habitat quality and distribution of resident fishes before barrier removal because this assessment will identify potential constraints on recolonization success. For example, removal of other blockages above a dam will allow colonists access to additional rearing and spawning habitat. Knowing the distribution and composition of resident species may also aid in restoration planning. If resident densities are particularly high in portions of the recolonized habitat, additional restoration measures such as increasing habitat complexity may minimize potential density-dependent interactions. Also, if exotic species are below or above the barrier, management measures should be implemented to limit their dispersal and interactions with targeted species. Our study also showed that access to small streams was particularly important for juvenile rearing, and tributaries of larger rivers can provide important growth and survival benefits to juvenile salmon (Ebersole *et al.* 2006).

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