

**Recolonization of Anadromous Fish in the Cedar River above
Landsburg Diversion Dam: A Ten-Year Evaluation**

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Report of research by

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EXECUTIVE SUMMARY

As part of the City of Seattle Habitat Conservation Plan, a fish ladder was constructed at the Landsburg Diversion Dam to provide passage of Pacific salmon *Oncorhynchus* spp. to ~33 km of available habitat. In September 2003, adult salmon passed above Landsburg Dam for the first time since 1900. This report describes changes in fish populations, communities, and ecosystem attributes in the Cedar River above the dam before (2000 and 2001) and after (2004-2009) installation of the Landsburg Fish Passage Facility. The objectives of these collective studies were as follows:

- 1) Determine the efficacy of the fish passage facility in restoring anadromous salmon above Landsburg Dam
- 2) Document the colonization dynamics of salmon following habitat reconnection,
- 3) Determine whether salmon had measurable ecological effects on water chemistry, trophic relationships, or resident fish species
- 4) Evaluate the movement, growth, and survival of coho *O. kisutch* and rainbow trout *O. mykiss* and identify environmental covariates associated with variation in these individual traits;
- 5) Evaluate habitat-fish associations to identify specific habitat or reach types that support high fish density, growth, and survival

In each August from 2005 to 2009, we surveyed sections (ca. 200-800 m long) of main stem Cedar River habitat within 10 reaches established in 2000. Sections surveyed started above the diversion pool upstream from Landsburg Dam (reach 1 or CR1) and extended to Cedar Falls (CR10), a natural barrier to Pacific salmon. In 2004, reaches CR1-CR6 were surveyed. During these surveys, physical habitat was quantified and fish were identified and counted using snorkeling. Similar habitat and fish surveys were conducted in the main stem during winters 2007-2009. We also conducted seasonal (spring, summer, fall) snorkel surveys of multiple pools to monitor colonization of Rock Creek by juvenile coho. Beginning in 2005 we tagged and recaptured coho and trout in Rock Creek and the main stem Cedar above Landsburg to monitor fish movement, growth, and survival.

To quantify the effects of salmon recolonization on ecosystem processes, tissue samples were collected from riparian vegetation and the stream food web (periphyton, invertebrates, sculpin *Cottus* spp. rainbow trout, and coho salmon) in September 2000-2001, 2004, and 2007-2009 (only fish were sampled in 2008) to measure concentrations of carbon and nitrogen isotopes. Fish collected below Landsburg Dam by

King County were also analyzed, and provided a useful benchmark to examine whether ecosystem processes (nutrient flux from the ocean to freshwater) affected by salmon had changed with recolonization. Stomach contents were also analyzed from many of the fish sampled for isotopes. These samples allowed us to determine the importance of fish in the diets of resident trout and provided additional insight into trophic relationships in the Cedar River and its tributaries.

Juvenile salmon, especially coho, have rapidly dispersed and colonized multiple habitats within the main stem and Rock Creek. Juvenile coho are now the most abundant salmonid in lower 5 km of Rock Creek and the lower 15 km of the main stem. Coho densities appear to have stabilized in reaches closest to the dam, but this pattern can certainly change, as it is still early in the recolonization process.

Upstream expansion in Rock Creek appeared to be limited by the culvert at the 41 road; however, beginning in spring 2009, coho salmon young-of-the-year were observed in the first reach above this culvert, indicating spawning by coho the previous fall/winter. The reconnection of Walsh Creek with Rock Creek during winter 2009 provided an additional opportunity for spatial expansion of salmon into the Walsh Lake subbasin. Young-of-year coho were observed in sections immediately above the diversion gate in spring 2010, with adult coho spawning in Walsh and Webster Creeks during fall/winter 2009-2010.

Low-velocity habitat with abundant cover was the preferred habitat for juvenile coho in both summer and winter. The lower 2 km of Rock Creek provides an abundance of these habitat types, which may be limited in the relatively confined main stem Cedar River. Beaver ponds, and similar wetland and lacustrine habitats with abundant edge habitat, are typically more productive overwintering habitats for coho than tributaries and mainstem areas of confined rivers. For this reason, it is expected that further improving access to the upper portions of the Rock and Walsh Creek basins through planned restoration actions will increase the productivity of coho populations above Landsburg Dam.

The reconnection of this junction has also provided an opportunity for invasive species to move out of Walsh Lake into habitat that was previously free of non-native fish. Two largemouth bass *Micropterus salmoides* were captured in summer 2009 during electrofishing surveys of Rock Creek, while one bass was observed during a snorkel survey of Rock Creek in 2010. Juvenile Chinook has also increased in abundance and distribution; we found juvenile Chinook up to reach CR9 in the main stem Cedar River, which is about 17 km upstream from the dam. However, Chinook summer abundance was orders of magnitude lower than that of coho, and Chinook were found primarily in the main stem. Lower summer abundance of Chinook relative to coho was not surprising

given that Chinook primarily exhibits an ocean-type life history. During summer surveys in 2009 and 2010, two fish taxa (Pacific lamprey *Lampetra tridentata* and steelhead trout *O. mykiss*) were observed for the first time since our study began, and a third species (bull trout) observed for only the second time.

Analyses of habitat-fish associations showed that juvenile and larger size classes of salmonids were positively associated with cover, including undercut banks, overhanging riparian vegetation, and especially cover provided by wood. We also observed that food resources were positively associated with total salmonid density and growth of juvenile coho. Thus, both cover and prey availability were positively related to fish populations. The experimental study clearly demonstrated that increased prey availability causes increased growth and body size of juvenile salmonids.

There was contradictory evidence to suggest that the return of Pacific salmon has affected ecosystem processes (i.e., energy flow). For example, in reach CR1 of the main stem Cedar River, C^{13} levels in resident fish were higher after than before the ladder was installed; this reach received the highest inputs of salmon-derived nutrients as determined by abundance of salmon nests. Although some patterns in isotope levels above the dam were suggestive of positive salmon-nutrient feedback, levels of N^{15} in fish collected below the dam in 2008 were twice as high as those in fish above the dam. These data corroborated samples collected from periphyton and invertebrates from Rock Creek below Landsburg Dam in previous years, which showed N^{15} levels higher in tissue from this tributary below compared above the dam. In terms of trophic relationships, diet analysis ($n = 1,263$ diet samples analyzed) revealed that piscivory was relatively low, ranging from 0 to 4%. We found that fish became piscivorous when they exceed 100 mm in fork length. The proportion of fish exhibiting piscivory was similar before vs. after the ladder was installed.

Our results show a significant shift in fish populations and communities in the Cedar River and Rock Creek as a result of Pacific salmon recolonization. The rapid colonization by salmon of the Cedar River above Landsburg Dam emphasized their innate ability to colonize newly available habitat. We observed, however, that expansion can be limited by small, artificial barriers (e.g., culverts, diversion gates) and species. Specifically, the coho population has generally increased over time, whereas Chinook population dynamics were more variable, with no clear time trend. This difference may reflect life history differences, with coho populations increasing because of their shorter life span and longer freshwater residence.

Despite these differences, salmon now occur in most of the accessible habitat except for reach CR10 of the main stem, which lies above numerous cascades and a bedrock canyon, and Rock Creek above the major wetland complex. In contrast to the

expanding Pacific salmon populations, especially coho, trout populations have remained relatively stable over time. In 2009 juvenile coho density surpassed that of trout in Rock Creek for the first time; yet consistent with previous years, there has been no observable negative association between coho density and trout population dynamics or individual performance.

Although salmon populations are generally increasing above the Landsburg Diversion Dam, we found limited evidence to support the hypothesis that salmon recolonization has affected nutrient dynamics as determined by carbon and nitrogen isotopes. Isotope values from sites below the dam, which have experienced continual exposure to anadromy, were almost twofold higher than those from sites above the dam. This comparison indicated little or no evidence that a positive feedback effect of adult salmon nourishing future generations has returned to Cedar River above Landsburg Dam. Our experimental study showed that such a feedback would occur at a biomass loading of 0.6 kg/m^2 . By comparison, cumulative biomass loading in CR1, which has experienced the highest numbers of salmon redds, was ca. 0.014 kg/m^2 . This biomass load remains an order of magnitude lower than streams in Alaska that have robust salmon populations, or in Griffin Creek, a productive coho tributary to the Snoqualmie River.

In summary, the Landsburg fish passage facility has been successful in reconnecting the Cedar River above and below the dam for Pacific salmon. Pacific salmon rapidly colonized and established populations above Landsburg Dam. They now occur from above Landsburg Dam to CR9, which is about 20 km upstream. Salmon have also colonized Rock Creek, and are now observed in the lower portions of the wetland complex about 3 km upstream from the confluence with the main stem. Coho appear to be more successful in establishing a self-sustaining population relative to Chinook, but given the longer life cycle of Chinook, positive population growth trends may take longer to manifest.

As mentioned in previous reports, increasing the complexity of edge habitat in the main stem Cedar River may accelerate population growth of Chinook. Both winter and summer surveys have demonstrated that this edge habitat supports some of the highest densities of juvenile trout, coho and Chinook, especially when associated with wood cover. Our surveys indicated that wood additions would most benefit juvenile salmon populations in CR1, CR2, CR4, CR6 and CR8, all relatively low-gradient reaches that support relatively high densities of juvenile salmon.

The partial reconnection of Walsh Creek to Rock Creek allowed adult coho salmon to spawn in Walsh and Webster creeks in winter 2009-2010, and coho fry were observed rearing there in spring 2010. Juvenile coho densities in Rock Creek are now similar to those of other streams in the Pacific Northwest that have had uninterrupted

anadromy, while juvenile Chinook densities are lower than those found in similar-sized Puget Sound Rivers (K. Bartz, unpublished data). We anticipate coho populations will continue to increase, given the recent colonization of Walsh Lake subbasin and the anticipated reconnection of Walsh and Rock Creek subbasins.

Diet and isotope analysis showed little evidence that resident fishes are directly or indirectly benefiting from salmon-derived nutrients or energy. Energy and nutrients (N and P) provided by adult salmon have increased over time, but they are extremely low relative to those found in healthy salmon streams, with little evidence that these amounts have affected nutrient flux. Thus, salmon have re-established populations, but they remain orders of magnitude lower than necessary to achieve a positive feedback effect of adult salmon on future generations.

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INTRODUCTION

Fishing, habitat loss and degradation, poor hatchery practices, climate change, and non-native species are the main causes of decline for Atlantic *Salmo salar* and Pacific *Oncorhynchus* spp. salmon populations (NRC 1996; Montgomery 2003). Some of the primary culprits in habitat loss are barriers to fish migration, such as road crossings, levees, and dams, which block access to upstream and floodplain habitats. Obstruction to fish passage is a problem that has been documented throughout North America (USGAO 2001; Langill and Zomora 2002) and Europe (Yanes et al. 1995; Glen 2002). In Washington State, over 7,700 km of historical salmon habitat are inaccessible to migratory fishes because of impassable culverts or road crossings, despite state regulations requiring fish passage (Roni et al. 2002).

In the United States, many salmon occupying truncated river systems have precipitously low population levels, and several have recently been listed as either threatened or endangered under the United States Endangered Species Act (NRC 1996; Montgomery 2003). Removal of a blockage, whether it is a small culvert or a series of dams in a large watershed, is considered a key restoration action to aid in the recovery of listed salmon. These actions are currently being implemented across North America and will likely become more prevalent in the next 5-10 years (Roni et al. 2002). Although much effort has been made to remove blockages to salmon passage, surprisingly little is known about why salmon colonize new habitats and what occurs after a barrier is removed. For example, What are the key environmental factors that determine salmon colonization success? What restoration actions might promote colonization success?

As part of the City of Seattle Habitat Conservation Plan (HCP) for the Cedar River Watershed, a fish ladder was opened at the Landsburg Diversion Dam located on the Cedar River main stem in September 2003. For over 100 years, this diversion had blocked access to approximately 33 km of main stem and tributary habitat, potentially contributing to population declines of a number of anadromous fish species and resulting in the loss of important food resources for a variety of other species. An additional 10 km of lake and river habitat was made accessible with reconnection of the Walsh Lake subbasin to Rock Creek during winter 2009.

It has been shown in other studies that salmon carcasses provide important nutrient subsidies to their natal streams and the surrounding terrestrial ecosystem (Bilby et al. 1996; Willson et al. 1998; Chaloner and Wipfli 2002). In addition, resident fishes above Landsburg Dam have been isolated from anadromous salmon for a number of generations; thus there are likely to be ecological effects (e.g., competition, predation) on these resident fishes resulting from the return of anadromous species.

We initiated a long-term monitoring study to evaluate recolonization success of anadromous fish above Landsburg Dam, to describe the ecological effects of recolonizing salmon, and to determine potential restoration actions to promote recolonization success. As far as we know, this is one of the first studies to document the natural recolonization process of Pacific salmon into native habitat. Other studies have reported on stocking fish (Bryant 1999) or on salmon colonization of fishless streams in Alaska after glacial recession (Milner et al. 2000). This project presents a unique opportunity to understand the colonization process of Pacific salmon under natural conditions when a barrier is removed or altered to allow fish passage. Study objectives were:

- 1) Determine the efficacy of the fish passage facility in restoring anadromous salmon above Landsburg Dam
- 2) Document the colonization dynamics of salmon following habitat reconnection,
- 3) Determine whether salmon had measurable ecological effects on water chemistry, trophic relationships, or resident fish species
- 4) Evaluate the movement, growth, and survival of coho *O. kisutch* and rainbow trout *O. mykiss* and identify environmental covariates associated with variation in these individual traits;
- 5) Evaluate habitat-fish associations to identify specific habitat or reach types that support high fish density, growth, and survival

Results from this study will inform managers and policy makers on the effectiveness of the Landsburg passage facility in restoring populations of anadromous fish above Landsburg Dam, and will provide insights into the ecological effects of salmon on the Cedar River ecosystem, as well as potential restoration or conservation measures that will benefit resident and anadromous fish.

1.0. HABITAT CHARACTERIZATION

Methods

We categorized low-flow habitat types in the main stem Cedar River over 10 reaches established in 2000 (Figure 1). Reaches were distinguished based on distinct differences in channel gradient and confinement and substrate composition. Habitat types were based on a modification of the methods established and described in detail by Riley et al. (2001). We modified this method in 2005 to allow for classification of habitat types within the six main-channel units used in previous years (pool, riffle, run, cascade, step pool, side channel). Our present habitat and survey protocols are similar to those used by Dr. Roger Peters (USFWS) in the Cedar River below Landsburg Diversion.

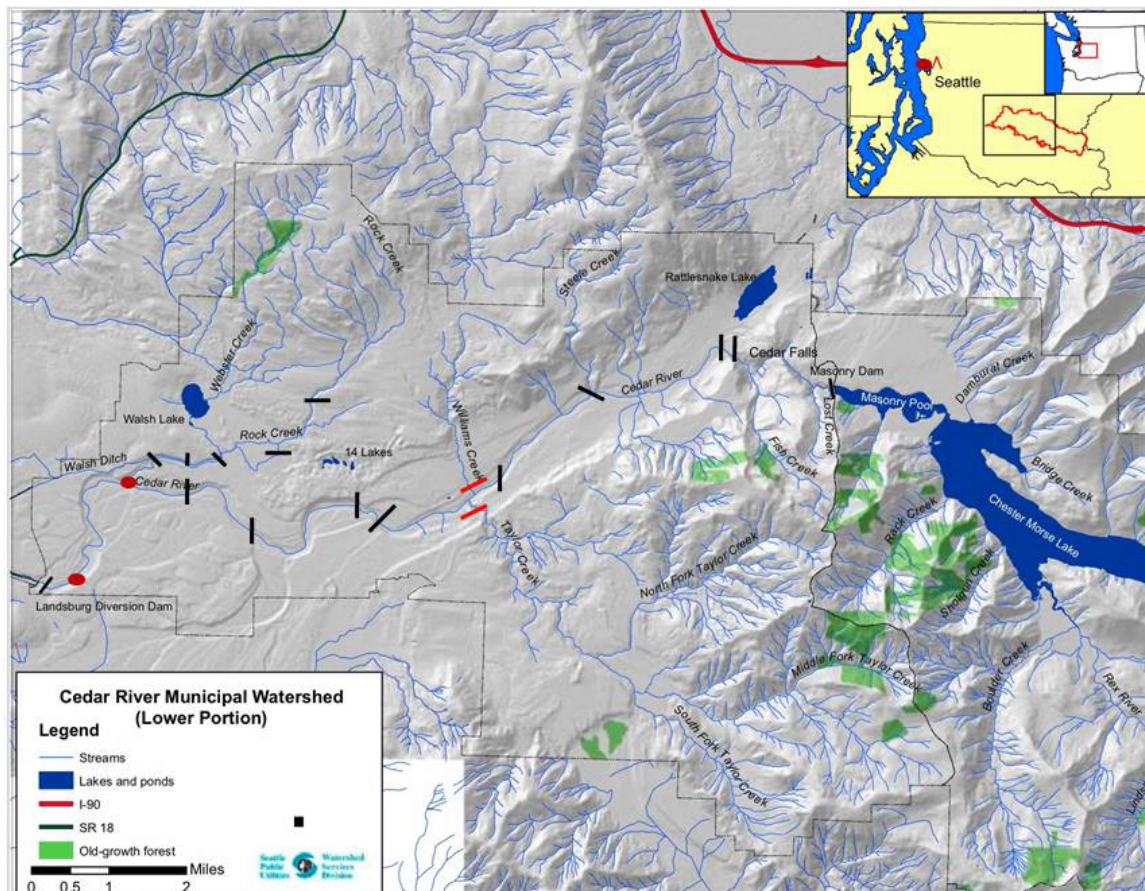


Figure 1. Map of the Cedar River watershed above Landsburg Dam. Reach breaks are represented by solid black lines, solid red lines indicate natural migration, and red ovals represent location of instream PIT-tag readers.

Specifically, we described habitats within each reach using a hierarchical classification scheme (Hawkins et al. 1993). The first level classified channel type as main or side channel. The second classified main geomorphic units as fast (riffle) or slow (pool). The third level classified fast water as cascades, riffles, step pools, or runs and slow water as scour or lateral pools. These two pool types were combined for the purpose of this report. The fourth level described secondary habitat types within level-3 units using the same terminology, where the level-4 units comprised at least 20% of the wetted area within a level-3 unit.

We measured habitat length, width, current velocity, maximum and average depth, percent riparian cover, vegetation overhang, depositional areas (areas of low or zero flow along river margins), undercut banks, and length and width of available cover for each level-4 habitat class. Flow was measured with a Swoffer¹ model 2000 current meter at 60% of total depth. Depth was measured using a stadia rod and recorded to the nearest 0.1 m. Percent overhead riparian and vegetation overhang were estimated and included only vegetation within 30 cm (1 ft) of the water surface. Each cover component (Table 1) was measured for length and width using a stadia rod to the nearest 0.5 m. We also estimated dominant and subdominant substrate composition (Riley et al. 2001). Bankfull width and a GPS coordinate were taken every fifth unit. Habitat surveys were also conducted as part of our mark-recapture and tributary snorkel studies, and are described below.

Table 1. Relative proportion of habitat types by reach as categorized during summer 2005-2010, and change in the rank of each reach in relation to wood abundance between 2000 and 2009. For example, reach 1 was ranked 4th of 10 in 2000 but 2nd of 10 in 2009, thereby increasing its relative rank by 2.

Reach	Depositional	Pool	Riffle	Run	Side-channel	Step-pool	Cascade	Rank Δ
1	0.23	0.32	0.22	0.20	0.04	0.00	0.00	2
2	0.29	0.29	0.14	0.24	0.02	0.02	0.00	-2
3	0.11	0.26	0.10	0.20	0.01	0.30	0.01	0
4	0.14	0.45	0.14	0.18	0.05	0.03	0.00	3
5	0.08	0.50	0.10	0.10	0.02	0.19	0.00	-6
6	0.13	0.46	0.21	0.16	0.01	0.03	0.00	0
7	0.19	0.30	0.22	0.15	0.03	0.11	0.00	0
8	0.08	0.34	0.19	0.30	0.00	0.05	0.03	-1
9	0.03	0.21	0.00	0.06	0.00	0.62	0.08	3
10	0.09	0.42	0.29	0.17	0.01	0.01	0.00	1

¹ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Channel geomorphology of the Cedar River alternated between low- and high-gradient confined reaches. Habitat types in high-gradient, confined reaches (CR3, CR7 and CR9) were primarily riffles, cascades, or step-pool habitat, while depositional habitats, pools, and side channels were more abundant in low-gradient reaches (CR1, CR2, CR4, and CR6; Table 1). The confined nature of the main stem river above Landsburg Dam limited large-scale changes in habitat type. However, we did observe some changes in the relative distribution of wood from 2000 to 2009.

Reaches were ranked in terms of wood abundance or cover, and we determined changes in rank within a reach by subtracting its rank in 2000 from its rank in 2009. CR1 appeared to have gained and CR2 to have lost wood in 2009 relative to 2000 (Table 1). Similar patterns were observed in CR4 and CR5, as CR5 lost wood while the downstream reach, CR4, gained wood. CR9 and CR10 also gained wood in 2009 relative to 2000.

Long-term median monthly water temperature at Landsburg Dam was about 9°C; median water temperatures in 2002, 2003, 2004 and 2006 were warmer than the long-term median, while median temperature in 2007 was slightly cooler (Figure 2a). Long-term median monthly flow at the dam was around 18 m³/s, with flows higher than the median in 2006 and 2008, and lower in 2005 and 2007 (Figure 2b).

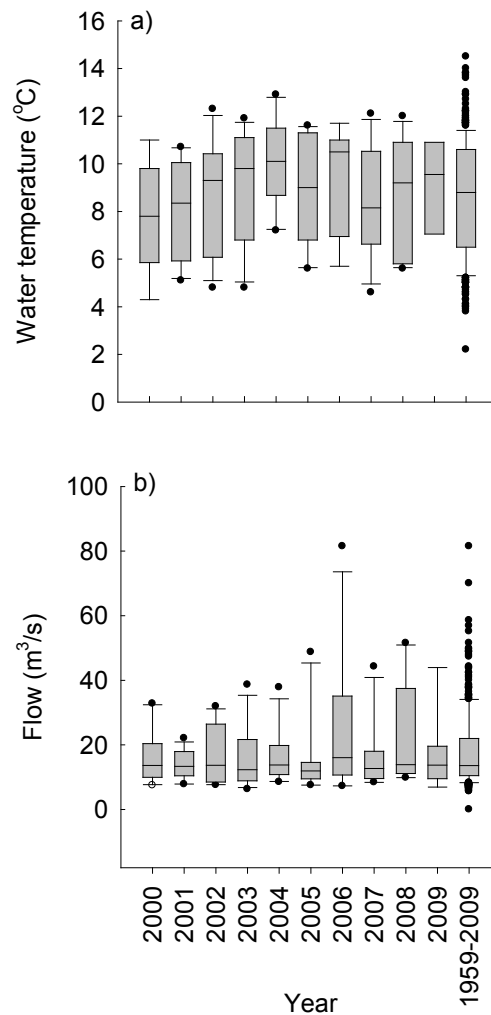


Figure 2. Box plots of monthly a) flow and b) water temperature measured at Landsburg Dam during the study. Also presented are flow and temperature measured since 1959.

2.0. JUVENILE SALMONID RECOLONIZATION

2.1. Mark-Recapture Study

Methods

To examine juvenile salmon performance (defined as growth, movement, and survival) in recolonizing the Cedar River, we initiated a mark-recapture study in fall 2005. For this study, we completed the following:

- Tagged over 4,800 fish in upper Rock Creek through fall 2009
- Monitored seasonal movement and growth using mark-recapture techniques
- Monitored juvenile migration and estimated survival using data from instream PIT-tag monitors
- Compared differences in growth, movement, and survival among species and life stages within Rock Creek

To determine species composition and estimate fish abundance and biomass, we used three-pass electrofishing during summer, fall, winter, and spring in 30-50 pools in upper Rock Creek (Carle and Strub 1978). All vertebrates captured were identified to species, anesthetized, weighed, and measured. All coho or trout greater than 55 mm were tagged using a passive integrated transponder (PIT) tag. The PIT tag provides a unique identifier for each fish that can be detected in recapture events when pools are sampled again or at stationary instream monitor locations. Tagged fish were released into the same habitat unit they were captured.

Habitat surveys were conducted to quantify habitat characteristics at the same time or prior to electrofishing. During habitat surveys, we measured wetted stream length and width, maximum depth, tail out depth, and wood abundance, and we estimated dominant and subdominant substrate size (e.g., sand/silt, gravel, cobble, or boulder) of each pool. A GPS coordinate was also recorded at each pool sampled.

To continually monitor the movement of PIT-tagged fish, we used six instream detection antennas, multiplex transceiver units (MUX) and six antennas at the mouth of upper Rock Creek, which has been operational since October 2005. An additional reader was installed in the main stem in February 2007 (Figure 1). With a PIT tag reader at the Ballard Locks, we can recapture fish at three locations as they move through the Lake Washington system. This infrastructure has been invaluable in documenting life history, growth, movement, and survival of multiple species.

Movement data were downloaded on a weekly basis. Additional data on downstream migration of marked fish were collected at the Ballard Locks. In addition, a mobile PIT tag reader was used at the screw trap near the mouth of the Cedar River. The screw trap was typically deployed during the spring/early summer juvenile migration period (April to July). Trap efficiency was low (2%, personal communication, Greg Volkhardt, Washington Department of Fish and Wildlife, Olympia, WA), so it is not known if these data will be used in forthcoming analysis.

Results

Fish Capture and Tagging—From June 2008 through September 2009 growth, movement, and survival of fish populations in Rock Creek and the Cedar River were assessed using mark-recapture methods including both physical recapture and remote PIT-tag detection. During this period, 11 discrete fish-capture events occurred, defined as single or consecutive days on which fish were captured. The timing of events was consistent with years prior to 2008, with spring, summer, and fall recapture events occurring on the lower 2.5 km of Rock Creek, and summer (two in 2008) and fall events occurring on the Cedar River from Landsburg Dam to the Cedar Falls Powerhouse. On Rock Creek, fish were captured using three-pass backpack electrofishing, whereas in the Cedar River, fish were captured using a combination of electrofishing and barbless hook and line angling. Each year, PIT tagging was also conducted at Landsburg Dam during the late spring annual dewatering event.

Over 5,000 fish were captured during these events, the largest proportion of which was coho salmon, followed by sculpin *Cottus* spp, cutthroat trout *O. clarkii*, and rainbow trout (Table 2). The frequency of occurrence of each species varied between Rock Creek and the Cedar River, with coho salmon, sculpin, cutthroat trout, speckled dace *Rhinichthys osculus*, and Pacific lamprey *Lampetra tridentata* comprising, in declining order, the majority of fish captured in Rock Creek. Rainbow trout comprised the majority of fish captured in the Cedar River (Table 3).

Catches of most species were similar in 2008 and 2009 with two exceptions; 19 Chinook salmon were captured in Rock Creek in 2008, but none were captured there in 2009. Two largemouth bass *Micropterus salmoides* were captured in Rock Creek during summer 2009, and this was the first documented occurrence of the species in Rock Creek during this study.

During these capture events, unlike previous years, mortality was not recorded separately for electrofishing, tagging, and angling; however, mortality rates remained very low (~ 1%) and comparable to those reported previously (see 2008 report). Incidental mortalities were collected as specimens and used to augment sample size for stable isotope analysis.

Table 2. Numbers of aquatic species captured in Rock Creek and the Cedar River from summer 2008 (June 2008) to fall 2009 (October 2009).

Species	2008		2009		Total	
	Summer	Fall	Spring	Summer		Fall
Chinook salmon	8	11	0	0	0	19
Coho salmon	158	747	58	291	428	1,682
<i>Pacifastacus leniusculus</i>	0	0	5	3	9	17
Cutthroat trout	140	217	58	194	309	918
Speckled dace	29	23	14	134	118	318
Pacific lamprey	8	16	2	20	18	64
Largemouth bass	0	0	0	2	0	2
Rainbow trout	198	112	90	204	101	705
Sculpin	129	380	113	284	294	1,200
Trout fry	137	64	2	92	83	378
Mountain whitefish <i>Prosopium williamsoni</i>	0	0	0	0	2	2
Total	807	1,570	342	1,224	1,362	5,305

Table 3. Numbers of species captured in Rock Creek, the Cedar River, and Landsburg Diversion Dam from Spring (June) 2008 through Fall (September) 2009 by location.

Species	Rock Creek	Cedar River	Landsburg Dam	Total
Chinook salmon	18	1	0	19
Coho salmon	1463	1	218	1682
Crayfish	16	1	0	17
Cutthroat trout	873	35	10	918
Speckled dace	318	0	0	318
Pacific lamprey	64	0	0	64
Largemouth bass	2	0	0	2
Rainbow trout	43	574	88	705
Sculpin	1,178	20	2	1,200
Trout fry	368	10	0	378
Mountain whitefish	0	2	0	2
Total	4,343	644	318	5,305

The trends observed since 2005 of increasing coho salmon density and stable trout density in Rock Creek continued in 2008 and 2009 (Figure 3). In 2005 and 2006, the total number of unique trout captured in Rock Creek was greater than the total number of unique coho captured; however, in 2007 the total number of unique coho captured was greater than the total number of unique trout captured (e.g. Kiffney et al. 2007, Figure 17; 2008 report).

Although the number of unique coho captured surpassed that of trout in 2007, coho density, which is a more relevant ecological measure, did not exceed that of trout until 2009 in Rock Creek. This disparity was likely due to greater movement of coho between summer and fall sampling periods, leading to more new coho than trout being tagged each year in the fall; this was further evidenced by the lower recapture rate for coho relative to trout (Table 4). The greater density (as opposed to number) of coho than trout in 2009 suggests that the fish community in Rock Creek has switched from a trout-dominated to a coho-dominated system for the first time since this study began.

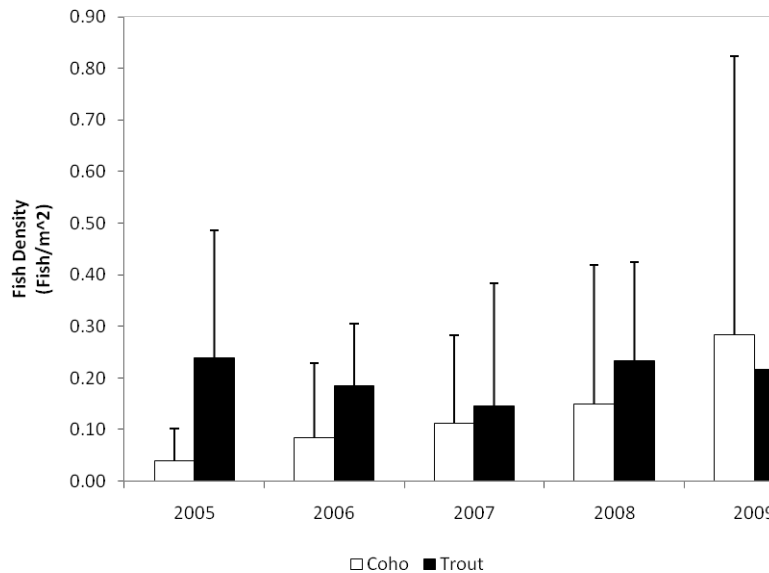


Figure 3. Mean end-of-summer pool densities of coho salmon and trout in Rock Creek from 2005 to 2009. Error bars show standard deviation.

Recapture Rates—We defined recaptures as salmonids that were either physically captured in a tagging event following initial tagging, or were detected by the PIT-tag monitoring systems located at the mouth of Rock Creek, at Landsburg Dam on the Cedar River, or at Ballard Locks. We recaptured 328 (11.5%) of the 2,848 salmonids tagged during the capture events, a rate similar to that reported previously (10%; Kiffney et al. 2008; Table 4). The recapture rate was greatest for cutthroat trout (28%), but much lower for other species (7, 6, and 5% for coho, trout fry, and rainbow trout, respectively). This was likely due to both biological differences between species and variable capture efficiencies: capture efficiency with electrofishing in Rock Creek, where most cutthroat trout, trout fry, and coho were tagged, was likely much higher than capture efficiency using hook and line angling in the Cedar River, where most rainbow trout were tagged.

Table 4. The number of fish tagged, recaptured, and not tagged in the Cedar River and Rock Creek from June 2008 to October 2009.

Species	Tagged	Recaptured		Not Tagged
		N	(%)	
Chinook salmon	1	0	0	18
Coho salmon	1477	99	7	106
Crayfish	0	0		17
Cutthroat trout	683	194	28	41
Speckled dace	0	0		318
Lamprey	0	0		64
largemouth bass	0	0		2
Rainbow trout	651	33	5	21
Sculpin	0	0		1200
Trout fry	34	2	6	342
Whitefish	2	0	0	0
Total	2,848	328	12	2,129

Rates of detection on PIT-tag monitors for fish tagged in Rock Creek, which were also one measure of movement, were similar in 2008 to recapture rates reported for previous years. Coho was the most frequently recaptured species (mean 64%), both by number and proportion, followed by rainbow trout (mean 60%), cutthroat trout (mean 41%), and trout fry (mean 27 %; Table 5). A longitudinal pattern of recaptures similar to past years was also observed in Rock Creek; the proportion of each species detected was generally greater for fish tagged in reach RC1 (mouth-400 m upstream) than in than in reach 3 (2,300-2,500 m upstream from mouth). Antenna recapture rates for 2009 were generally lower through September relative to previous years, but may increase with inclusion of the remaining 2009 detections (October-December).

Table 5. Number of coho, cutthroat trout, rainbow trout, and trout fry PIT tagged in reaches RC1-RC3 of Rock Creek, and the percent subsequently detected at the mouth from 2006 through September 2009.

Year	Reach 1		Reach 2		Reach 3		Total	
	Detected (%)	Total tags (n)	Detected (%)	Total tags (n)	Detected (%)	Total tags (n)	Detected (%)	Total tags (n)
Coho salmon								
2006	53	193	37	63	45	60	48	316
2007	71	464	67	158	54	243	65	865
2008	73	288			57	382	64	670
2009	43	522			15	123	38	645
Cutthroat trout								
2006	52	104	23	104	27	120	34	328
2007	53	85	31	125	26	53	37	263
2008	54	177			11	75	41	252
2009	16	194			1	218	8	412
Rainbow trout								
2006	53	36	17	12			44	48
2007	75	28			33	3	71	31
2008	67	9			0	1	60	10
2009	46	26			20	5	42	31
Trout fry								
2006	29	14	30	20	15	33	22	67
2007	49	35	41	17	18	50	32	102
2008	33	27			0	6	27	33
2009	100	1			0	1	50	2

Patterns of Fish Movement—Seasonal patterns of movement based on detections at the mouth of Rock Creek were similar among years, but varied by species. In order to determine the pattern of seasonal movements by fish in and out of Rock Creek, PIT-tag detections were summarized by the net directional movement of an individual on a given date (first and last detections) based on the pattern of detection on upstream, middle, and downstream antennas. Individuals were assigned as moving upstream, downstream, or remaining within the antenna reach for each day they were detected. Coho downstream movements were generally most frequent in fall and spring, with ~20% of downstream movements detected in both October and November, and over 30% of downstream movements detected in May, presumably as smolts migrated out of Rock Creek (Figure 4).

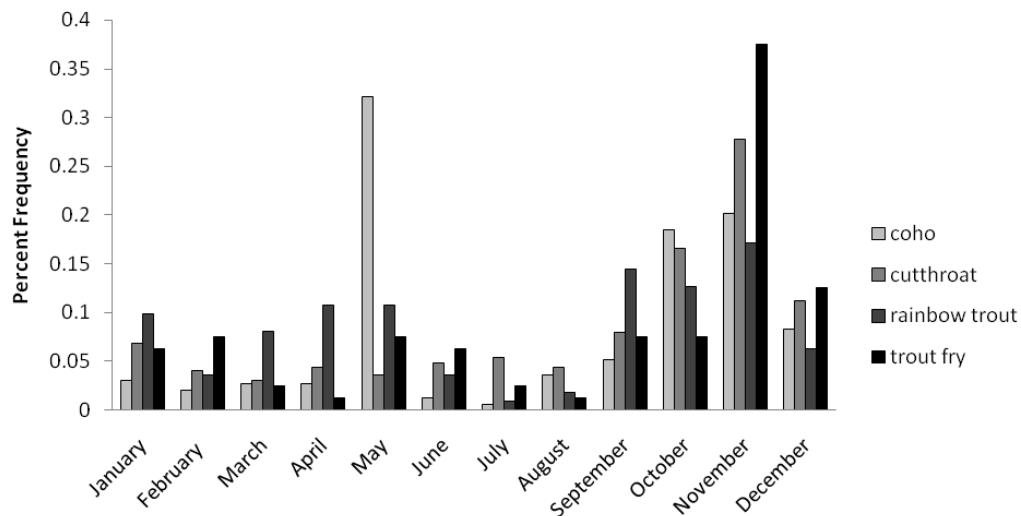


Figure 4. The monthly percent frequency of downstream movements for coho salmon, cutthroat trout, rainbow trout, and trout fry detected at the mouth of Rock Creek from 2004-2009.

Coho upstream movement was greatest in the late summer and fall, with almost no upstream movement in spring and early summer by age-1+ fish (Figure 5). Cutthroat and rainbow trout had seasonal patterns of downstream movement similar to coho. One notable exception was spring, when rainbow trout downstream movement slowly increased starting in February and then decreased by June, without a spike in May, and cutthroat showed little downstream movement. Cutthroat and rainbow trout seasonal upstream movement was similar, and was lowest in April, generally increasing to a peak in November and December. The exception to this pattern occurred in May and June, when a greater frequency of upstream movement was observed for rainbow trout than cutthroat trout.

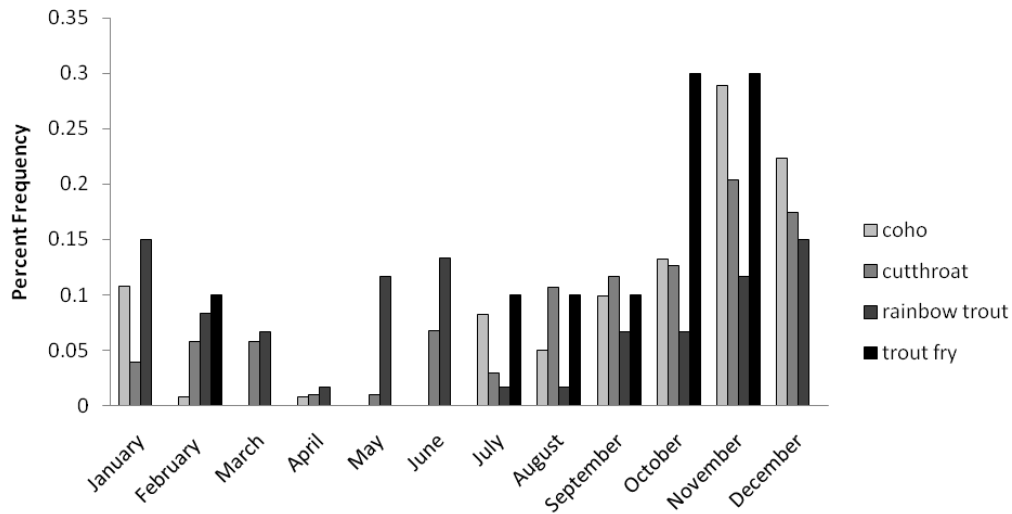


Figure 5. The monthly percent frequency of upstream movements for coho salmon, cutthroat trout, rainbow trout, and trout fry detected at the mouth of Rock Creek from 2004-2009.

Movement of individuals in Rock Creek was also measured by the distance between the habitat units in which a fish was tagged and physically recaptured. Movers were defined as fish recaptured in a habitat unit other than the one in which they were originally captured and tagged, whereas non-movers were recaptured in the same habitat unit. Movement patterns from 2005 to 2009 revealed that a similar proportion of each species moved (range 29-43%). Rainbow trout had the greatest proportion of movers followed by trout fry, with coho salmon and cutthroat trout having the same proportions (Table 6). The average distance moved for each species differed more substantially, with coho moving the greatest distance (mean 245 m), followed by trout fry (mean 114 m), cutthroat trout (mean 109 m), and rainbow trout (mean 25 m).

Table 6. Numbers of non-movers vs. movers in Rock Creek (movers were recaptured in a habitat unit different from the one in which they were tagged), distance moved.

Species	Non-movers (n)	Movers		Mean distance moved (m)
		(n)	(%)	
Coho salmon	151	63	29	245
Cutthroat trout	270	112	29	109
Rainbow trout	8	6	43	25
Trout fry	51	27	35	114

Growth—Instantaneous specific growth rates of fish recaptured in the Cedar River and Rock Creek were calculated to determine seasonal, annual, and interspecific patterns of variability. Growth rates in the Cedar River were calculated only for rainbow trout because sample sizes were insufficient for other species. Summer and annual growth rates of rainbow trout in the Cedar River ranged from 0.0010 to 0.0026 $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ in 2007 and from 0.0008 to 0.0037 $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ in 2009. These rates were not significantly different between years (one-way ANOVA, $P > 0.05$); however, summer and annual growth rates appeared to follow the same temporal trend, with slightly lower growth rates in 2007 and 2009 than in 2008 (Figures 6 and 7). Due to the small number of recaptures in the Cedar River, our scope of inference was limited.

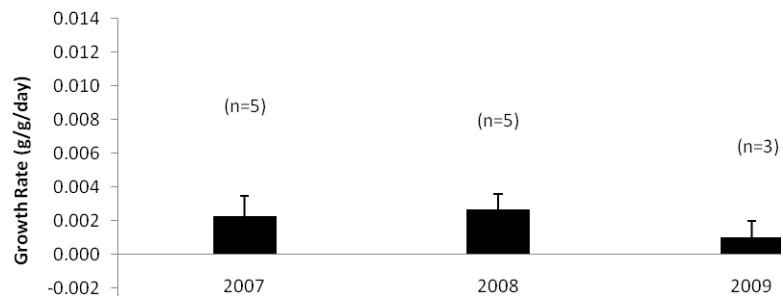


Figure 6. Mean summer growth rate (± 1 se) of rainbow trout in the main stem Cedar River.

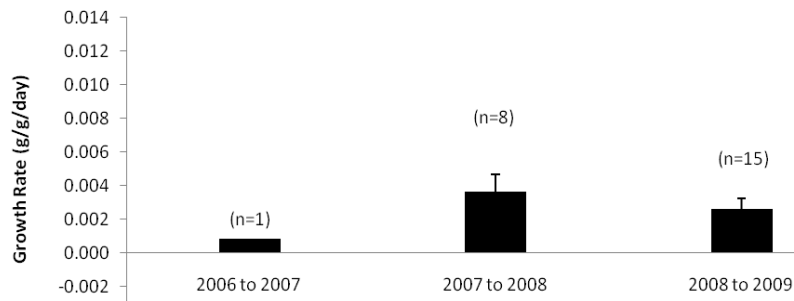


Figure 7. Mean annual growth rate (± 1 se) of rainbow trout in the main stem Cedar River.

Seasonal growth rates of fish in Rock Creek revealed differences between seasons, years, and species (Figures 8 and 9). Sample sizes were generally greatest for the summer growth period for all species in all years. Sample sizes to calculate growth rates during fall-to-spring and spring-to-summer periods were limited by the low numbers of fish tagged and recaptured in spring sampling events.

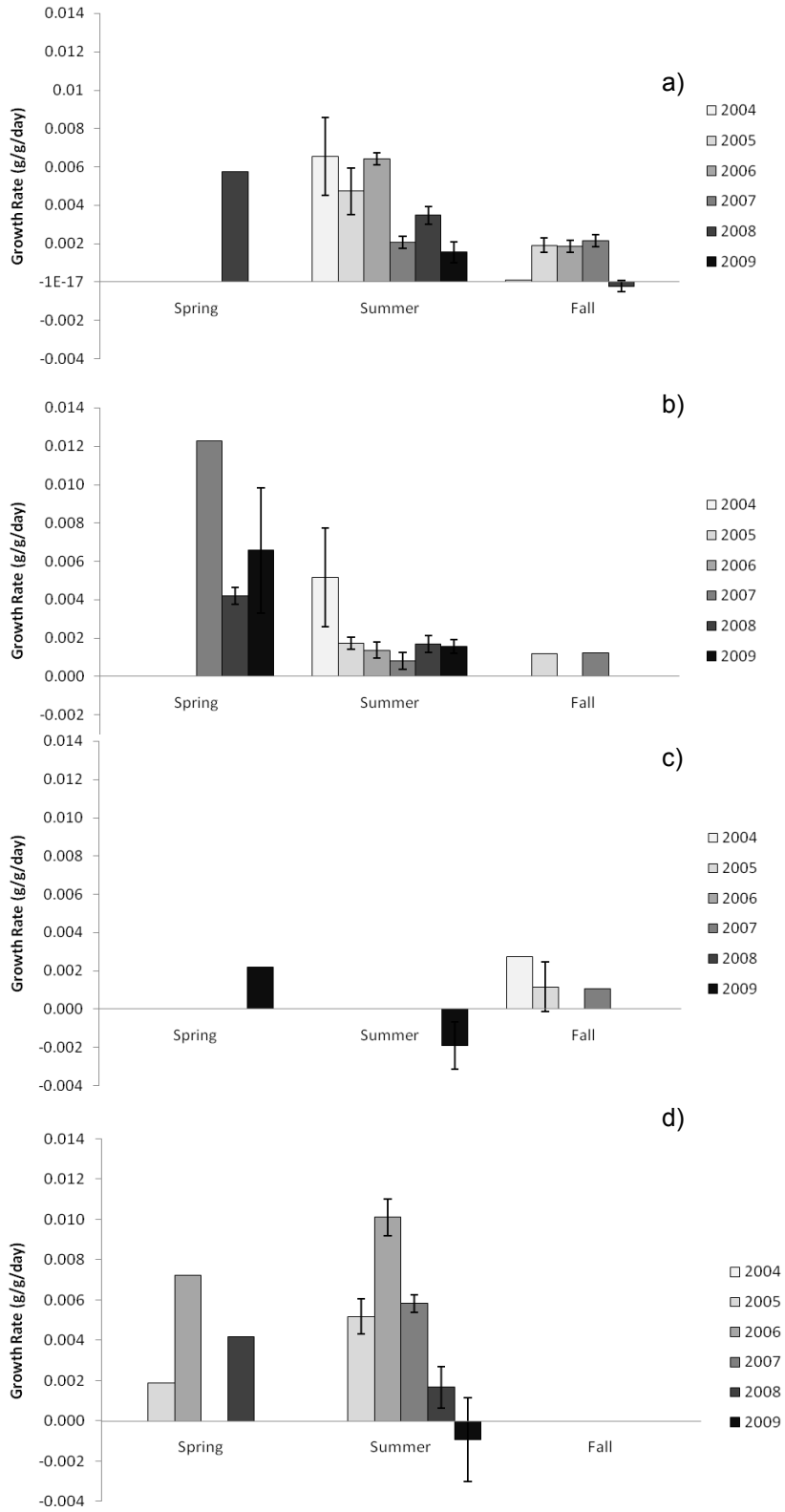


Figure 8. Mean seasonal growth rates (± 1 se) of Rock Creek a) coho, b) cutthroat trout, c) rainbow trout, and d) trout fry from 2004-2009.

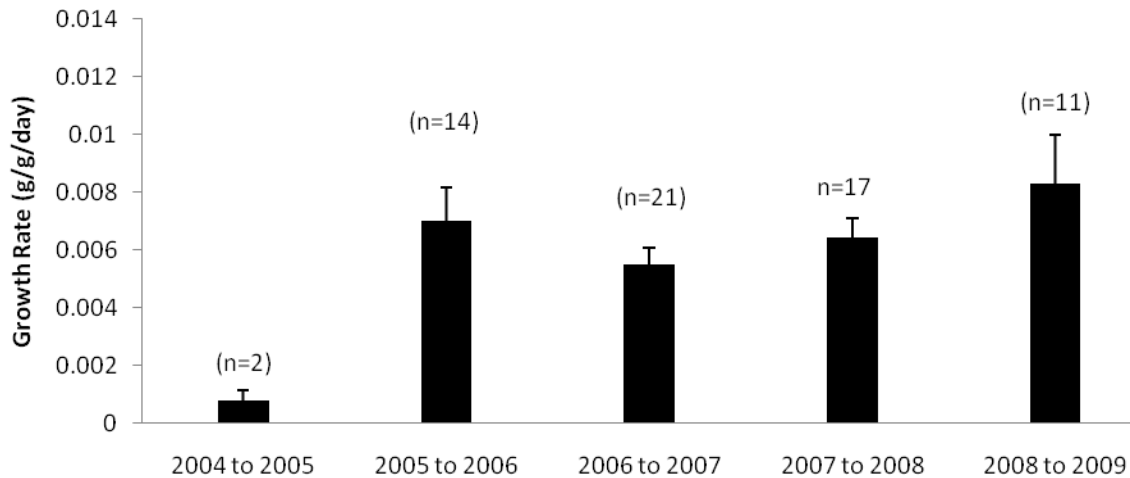


Figure 9. Mean annual (four consecutive seasons) growth rates (± 1 se) of Rock Creek cutthroat trout from 2004 to 2009.

In general, cutthroat trout growth rates were highest from spring to summer, followed by summer to fall, and fall to spring. Summer-to-fall growth rates were generally greater than fall-to-spring rates for coho as well; few tagged coho remain in Rock Creek from spring to summer, limiting inferences into spring growth. An interesting interannual pattern was evident in summer growth of coho, cutthroat trout, and trout fry, with growth rates of coho and trout fry generally decreasing from 2004 to 2009, while cutthroat growth remained relatively constant except in 2004 (when sample sizes were very limited). In Rock Creek, annual (four consecutive seasons) growth rates of cutthroat trout from 2004-2009 did not vary significantly among years (one-way ANOVA, $P > 0.05$, Figure 9).

Trout Genetic Markers—A subsample of Rock Creek trout tagged in summer 2008 were genotyped using four bi-parentally inherited, species-specific nuclear DNA markers and one mitochondrial DNA marker that distinguish between cutthroat trout and rainbow trout. The vast majority (78%) of trout genotyped were pure cutthroat trout, but first generation (F1) as well as later generation (FN) or backcross (BCN) cutthroat/rainbow hybrids were also identified in Rock Creek. These latter three groups together comprised approximately 20% of the trout (Table 7). The frequency of various combinations of cutthroat and rainbow trout markers present in individual fish revealed that most fish, including hybrids, had a majority of cutthroat alleles, suggesting most post-F1 hybridization in Rock Creek occurred between hybrids and cutthroat trout (Figure 10).

Table 7. The number and percent of cutthroat trout, rainbow trout and cutthroat/rainbow hybrids from Rock Creek from genetic assignment. The percentage of fish with cutthroat and rainbow trout mitochondrial DNA (mtDNA) is also listed

Genotype	Trout sampled		Cutthroat mtDNA (%)	Rainbow mtDNA (%)
	(n)	(%)		
Cutthroat	145	78	100	0
Rainbow	4	2	0	100
F1 hybrid	6	3	100	0
Post-F1 hybrid	31	17	94	6
All hybrids	37	20	94	6

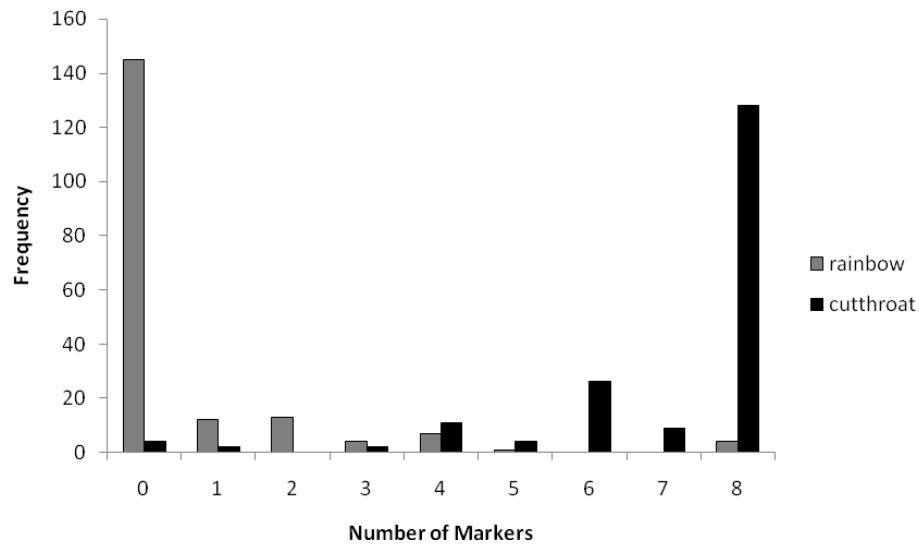


Figure 10. Frequency distribution of the number of Rock Creek individuals with rainbow and cutthroat nuclear DNA markers.

Mitochondrial DNA, which is maternally inherited, allows for determination of the maternal species lineage of individuals. Mitochondrial DNA marker genotype results for Rock Creek trout revealed that 100% of cutthroat and hybrids had cutthroat maternal lineage, and only pure rainbow trout had rainbow trout maternal DNA, suggesting unidirectional hybridization occurred in Rock Creek, and further supporting the nuclear DNA marker results (Table 7). These data suggest that the rainbow trout present in Rock Creek were likely produced elsewhere, such as in the Cedar River itself.

2.2. Snorkel Surveys

Methods

Using the snorkeling techniques of Thurow and Schill (1996), we counted and identified fish in the main stem Cedar River during each August before (2000-2001) and after the ladder was installed (2004-2010). In 2000 and 2001, all 10 reaches were snorkeled, while in 2004 reaches CR1-CR6 were surveyed; in 2005-2010 seven to 10 reaches were snorkeled, including a reach below Landsburg Dam. The section snorkeled in each reach was the same section where habitat was quantified, and the area surveyed was proportional to the total length of the reach: about 20% of each reach was surveyed.

We counted and identified all fish in each habitat type (pool, riffle, run, cascade, depositional, and side channel) in proportion to their abundance within that reach. At a minimum, we attempted to snorkel at least three replicates of each habitat type. Snorkel surveys were efficient for counting trout, bull trout, salmon, and whitefish, which are found in the water column, but not for sculpin (Riley et al. 2001), which is a benthic species. Therefore, density estimates for sculpin from the main stem were not reported.

To determine seasonal variation in fish distribution and abundance in the main stem Cedar River, snorkel surveys were also conducted in late spring/early winter 2007-2009 at select reaches of the main stem and tributaries. Reaches were snorkeled during daylight hours except when water temperature was below 8°C; night snorkels were conducted below this temperature, because juveniles exhibit nocturnal behavior. We measured habitat surface area, maximum and residual depth, wood abundance and wood volume. A GPS coordinate was also recorded. In addition to main stem surveys, fish counts have been conducted seasonally since 2005 in replicate pools of Rock Creek above and below Landsburg Dam and in Taylor and Williams Creeks. The length, width, and maximum and residual depth of each pool were quantified.

One to five observers (depending on stream width) entered the habitat unit at the downstream end and proceeded upstream through each site, counting and recording species and size classes of all fish encountered. Resident fish (rainbow and cutthroat trout and whitefish) and juvenile salmon were divided into five size classes. However, for the sake of brevity in reporting, we grouped fish into two size classes: small (≤ 90 mm) and large (>90 mm total length).

To determine trends in fish density over time within each reach, simple linear regression was used. Pearson's correlation coefficient was used to determine the direction and strength of relationships between fish abundance and habitat cover variables (undercut banks, wood cover) within each season (summer and winter/spring) and year (2005-2009), as well as drift biomass and total salmonid abundance in (summer 2007).

We also used correlation (Pearson's correlation coefficient) to examine patterns in mean summer trout density by size class (≤ 90 mm and > 90 mm) in relation to the previous year's maximum, mean and minimum annual flow and water temperature. These data have been collected on a monthly basis at Landsburg Dam (WSDE 2010).

Simple linear regression was used to determine associations between juvenile coho abundance and wood cover within each year (summer 2005-2009). Multiple linear regression was used to examine the relationship between reach-scale juvenile coho growth rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) during summer 2007 and reach-scale invertebrate drift biomass (mg/m^3) and total salmonid density.

Results

Density and Species Composition in the Main Stem Cedar River—Average densities of trout populations exhibited little variation across our study reaches in the main stem Cedar River. Densities of small trout (≤ 90 mm) ranged from ca. 0.03 to 0.05 fish/ m^2 , while those of large trout (> 90 mm) ranged from 0.02 to about 0.03 fish/ m^2 (Figure 11a and 11b). In contrast, juvenile coho densities increased over time, from about 0.01 fish/ m^2 in 2004 to 0.35 fish/ m^2 in summer 2008, a thirty-fivefold increase (Figure 11c). Juvenile Chinook displayed more year-to-year variability than coho, with no clear trends (Figure 11d); Chinook density ranged from 0.0002 fish/ m^2 in 2009 to 0.008 fish/ m^2 in 2005. No whitefish were detected in the main stem until 2004, and densities appear to be increasing at about 0.0003 fish/ m^2 per year ($R^2 = 0.56$, $P = 0.06$; Figure 11f). Total salmonid density was about five times higher in 2010 (0.22 fish/ m^2) than during 2000-2001 (0.05 fish/ m^2 ; Figure 11f), with highest densities in 2008 at 0.43 fish/ m^2 .

At the reach-scale, changes in fish density occurred primarily in reaches CR1-CR6, which cover about 10 km of main stem habitat, and largely reflected colonization by coho salmon. Increases in other fish species and size classes also affected total fish density, but these patterns varied by reach. In CR1, there was some evidence that average densities of small (≤ 90 mm) and large trout (> 90 mm) were slightly higher after the ladder was installed than before (Figure 12a and 12b), but the relationship between time and trout density was not statistically significant from zero.

Both juvenile coho and total salmonid density have increased over time, with juvenile coho density increasing at a rate of 0.1 fish/m² (Table 8).

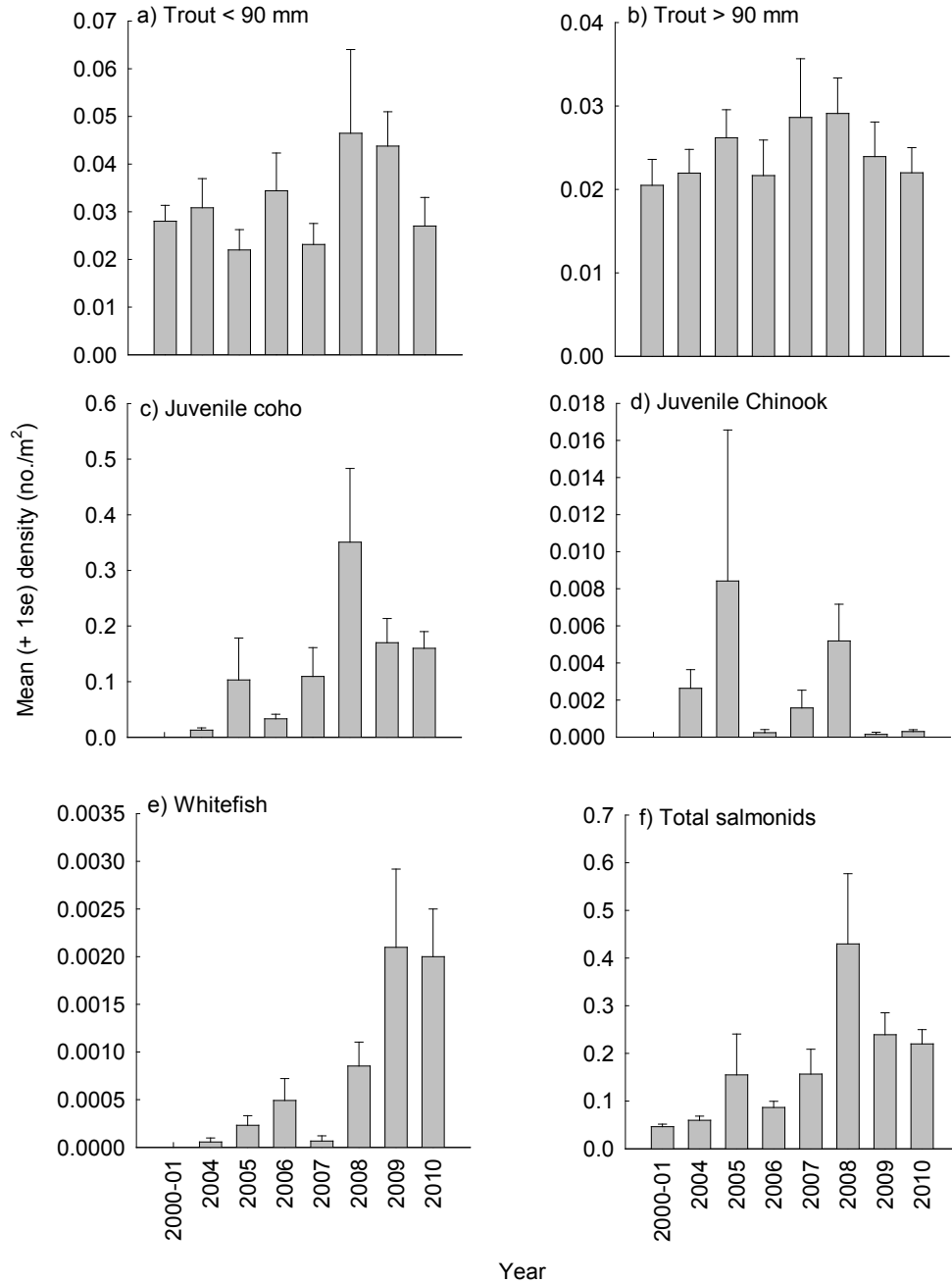


Figure 11. Mean density (± 1 se) of a) small trout (≤ 90 mm), b) large trout (> 90 mm), c) juvenile coho, d) juvenile Chinook, e) whitefish, and f) total salmonids averaged across reaches CR1-CR10 in the main stem Cedar River, WA. In 2004, only reaches CR1-CR6 were surveyed.

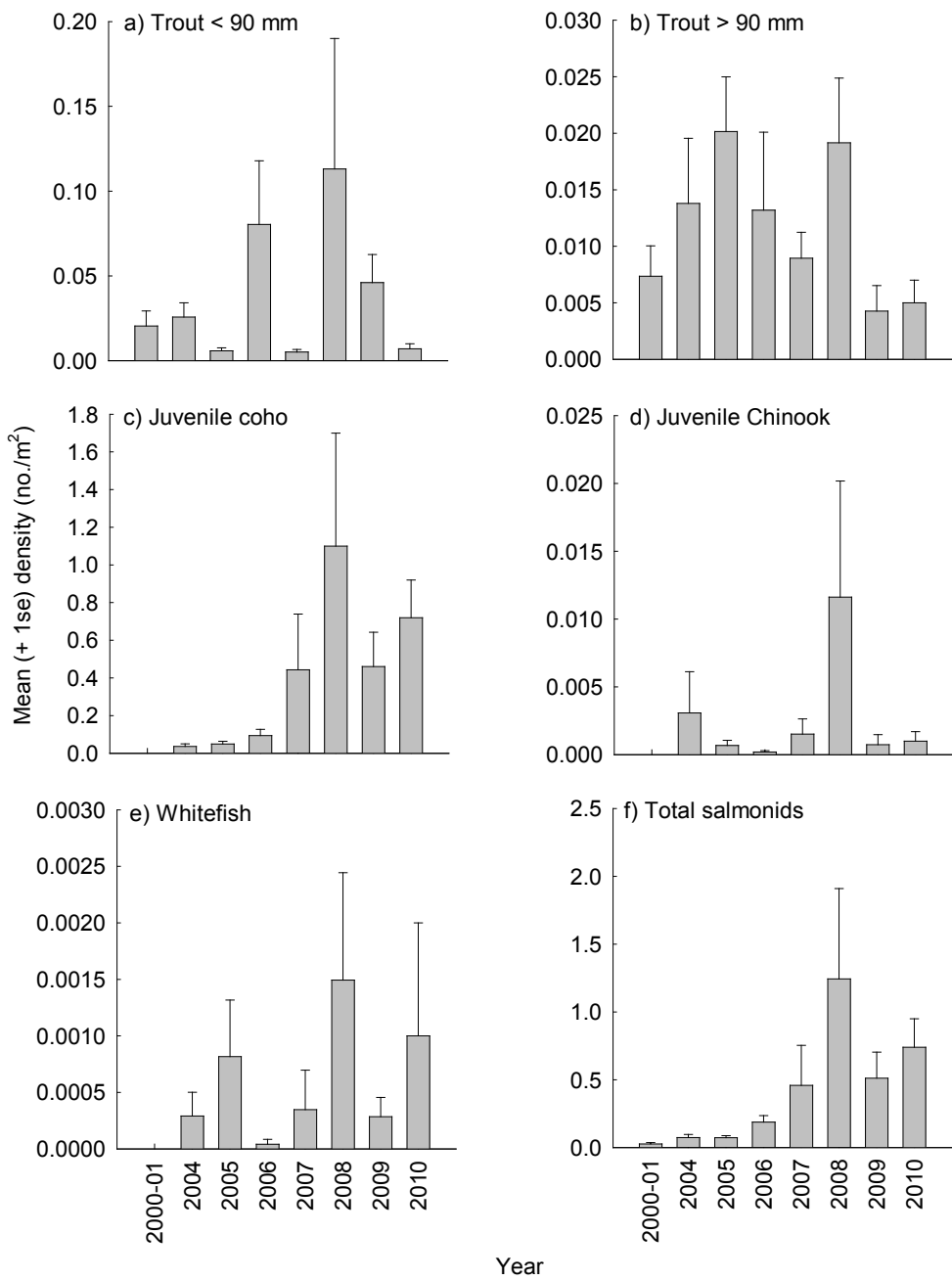


Figure 12. Mean density (± 1 se) of a) small trout (≤ 90 mm), b) large trout (> 90 mm), c) juvenile coho, d) juvenile Chinook, e) whitefish, and f) total salmonids in reach CR1 of the main stem Cedar River, WA.

Similar, but less pronounced patterns were observed in CR2 (Figure 13a-13f; Table 8). In reach CR6, which is about 10 km from Landsburg Dam, total salmonid density increased in 2009 relative to 2008 (Figure 14a-14f), while in CR1 and CR2, the opposite pattern emerged. Coho density in CR6 has increased at a rate of about 0.05 fish/m², while total salmonid density increased threefold in 2009 relative to 2008.

Total salmonid densities in CR9, which is about 18 km upstream of the dam, have been relatively stable over time; nevertheless, there were some differences between trout size classes, with small trout exhibiting a greater range in density than large trout (Figure 15a-15d). Small trout (≤ 90 mm) ranged in density from 0.02 fish/m² in 2008 to 0.14 fish/m² in 2006, about a sevenfold difference. In contrast, density estimates for large trout (> 90 mm) were 0.06-0.08 fish/m² for 4 out of 6 survey periods, peaking in 2007 at 0.12 fish/m². In CR9, juvenile coho and Chinook were observed during summer 2008, but no Chinook was observed in 2009 or 2010 and no coho in 2010. Furthermore, whitefish have yet to be observed in CR9 or CR10 during any survey.

Table 8. Simple linear regression models describing the relationship between summer fish density (number/m²) and time within each reach of the main stem Cedar River above Landsburg Dam. Density estimates were based on averaging across multiple habitat types within each reach. Year 1 for trout responses represented data averaged across 2000 and 2001 and collected before the ladder was installed. 2004 represented year 1 for salmon responses. The last year of this time series included 2009.

Reach	Response	Intercept (1 se)	β (1 se)	R^2	P -value
CR1	Juvenile coho	-205 (82)	0.10 (0.04)	0.04	0.01
CR2	Juvenile coho	-69 (12.2)	0.04 (0.01)	0.06	<0.01
CR4	Juvenile coho	-33 (12)	0.02 (0.005)	0.06	<0.01
CR5	Juvenile coho	-3 (1.5)	0.001 (0.0007)	0.10	0.02
CR6	Juvenile coho	-90 (28)	0.05 (0.01)	0.07	<0.001
CR7	Trout ≤ 90 mm	-10 (0.005)	0.006 (0.002)	0.06	<0.01
	Juvenile coho	-30 (11)	0.01 (0.005)	0.07	<0.01
CR8	Trout ≤ 90 mm	7 (3)	-0.003 (0.001)	0.09	0.01
	Juvenile coho	-0.5 (0.2)	0.0002 (0.0009)	0.10	<0.01

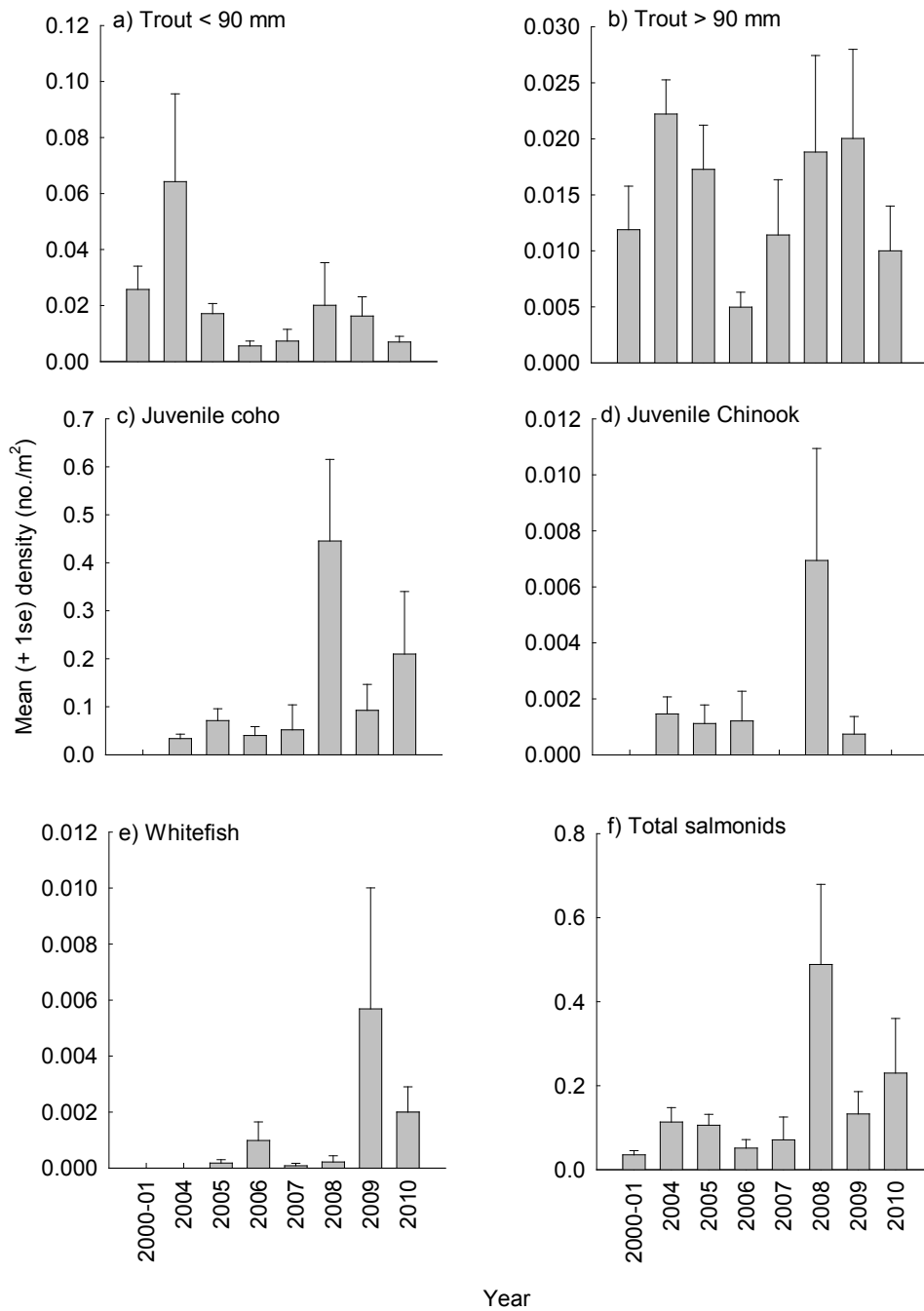


Figure 13. Mean density (± 1 se) of a) small trout (≤ 90 mm), b) large trout (> 90 mm), c) juvenile coho, d) juvenile Chinook, e) whitefish, and f) total salmonids in reach CR2 of the main stem Cedar River, WA.

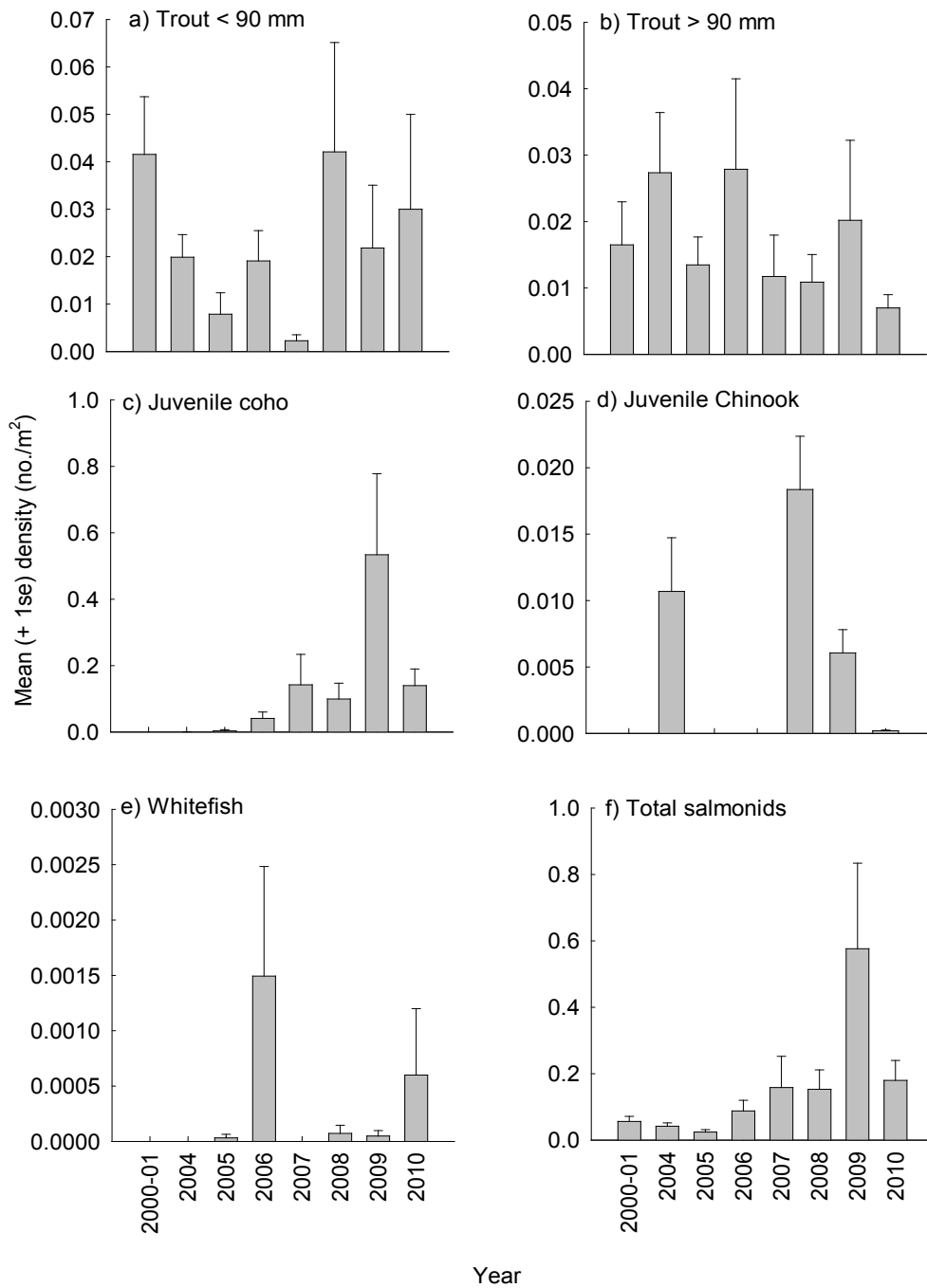


Figure 14. Mean density (± 1 se) of a) small trout (≤ 90 mm), b) large trout (> 90 mm), c) juvenile coho, d) juvenile Chinook, e) whitefish, and f) total salmonids in reach CR6 of the main stem Cedar River, WA.

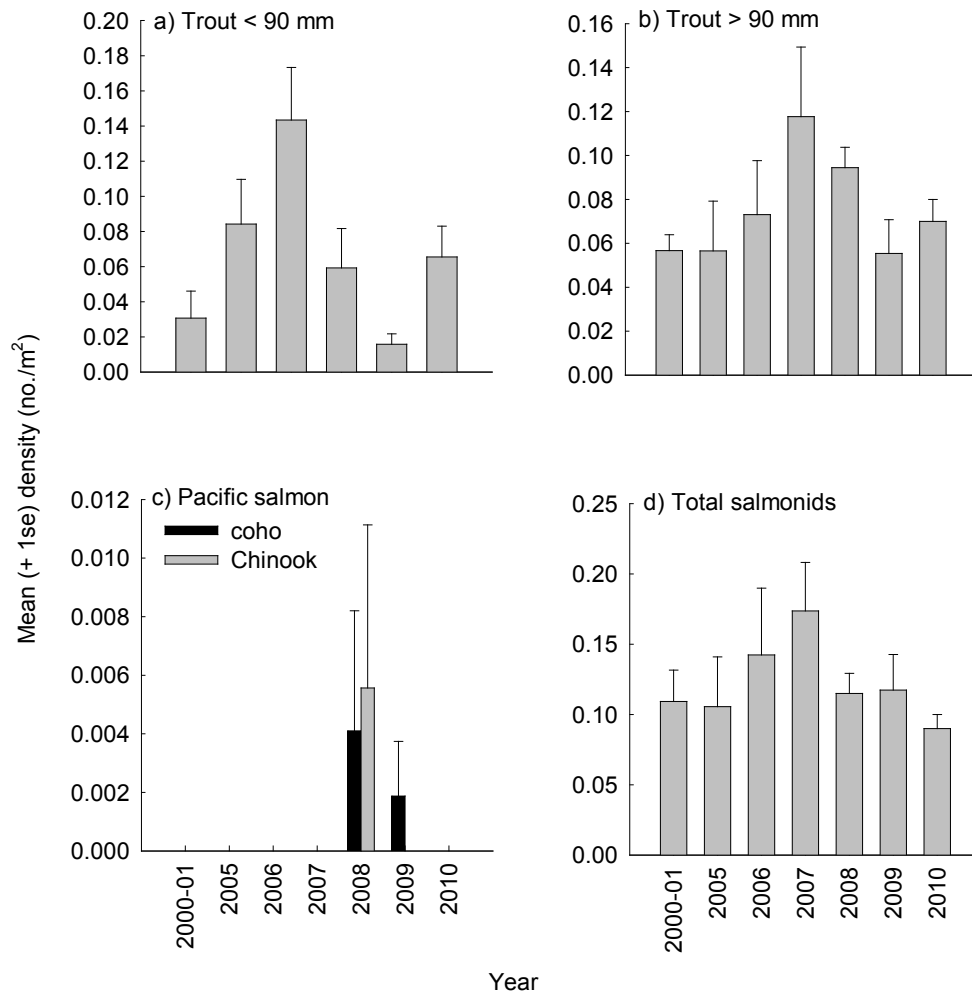


Figure 15. Mean density (± 1 se) of a) small trout (≤ 90 mm), b) large trout (> 90 mm), c) juvenile coho (black bar), juvenile Chinook (grey bar), and d) total salmonids in reach CR9 of the main stem Cedar River, WA.

Coho population growth rate at the reach-scale, defined as change in summer density estimates over time, declined exponentially from CR1 to CR5, followed by an increase at CR6 (Figure 16).

Recolonization by salmon in 2003 has led to a rapid shift in fish community composition (Figure 17). In 2004, coho and Chinook comprised about 18 and 4% of the overall summer fish community, respectively, when averaging across reaches. Since 2007, juvenile coho has dominated the salmonid community in the main stem, comprising 67-81% of total salmonid density, while juvenile Chinook comprised only about 1%.

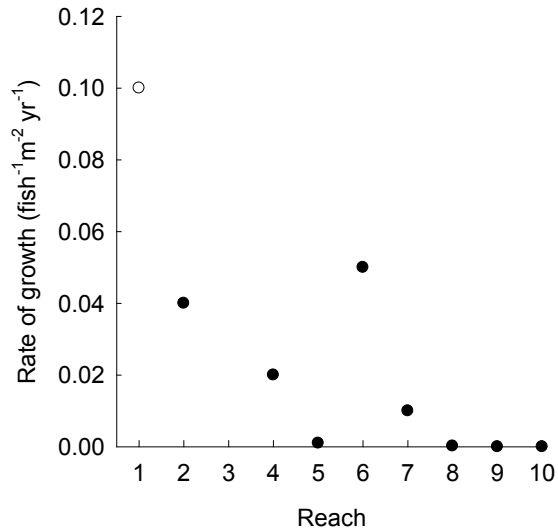


Figure 16. Reach-scale changes in Juvenile coho abundance (fish⁻¹ m⁻² yr⁻¹). Reach CR1 begins about 0.3 km above Landsburg Dam and reach CR10 about 22 km above the dam.

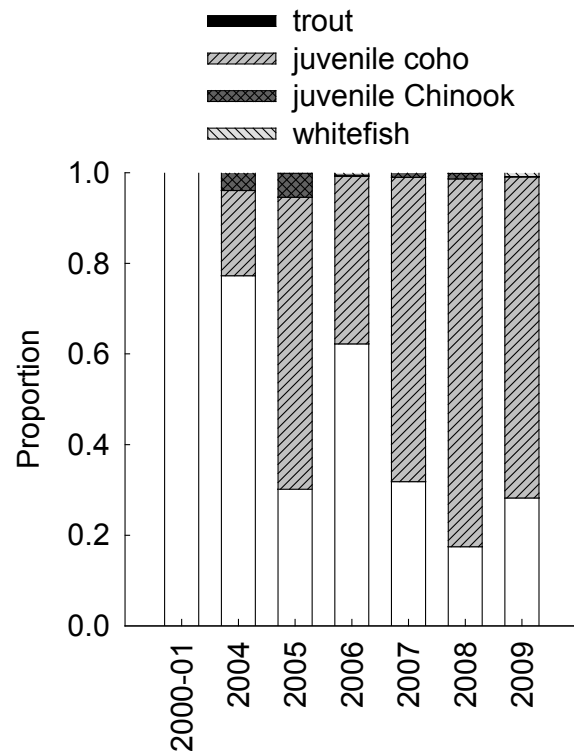


Figure 17. Relative proportions of trout, juvenile coho and Chinook, and whitefish averaged across reaches of the main stem Cedar River, WA.

Similar patterns were observed within individual reaches; however, there was a slower rate of change in the relative density of coho with further distance from the dam (Figure 18a-18d). Specifically, juvenile coho became the most abundant salmonid in CR1 and CR2 by 2005, while this shift did not occur in CR7 until 2007. As mentioned earlier, Pacific salmon have been observed only sporadically in CR9, and no Pacific salmon have been observed in CR10 (~20 km from Landsburg Dam) since the ladder was installed.

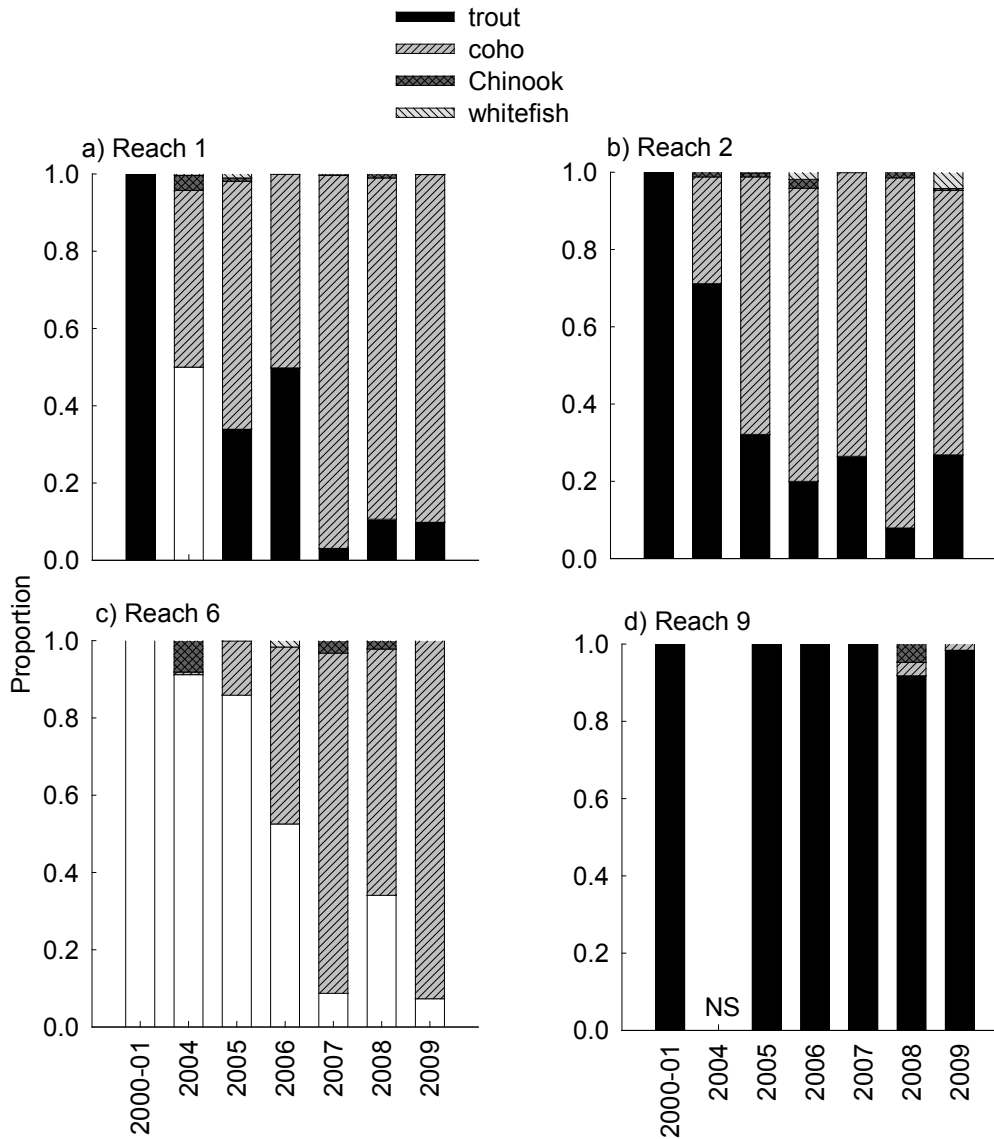


Figure 18. Relative proportion of trout, juvenile coho and Chinook, and whitefish in reaches a) CR1, b) CR2, c) CR6 and d) CR9 of the main stem Cedar River, WA. Reach CR9 was not sampled in 2004.

Similar to past reports, we found considerable variation in fish density among species and size classes at the habitat-unit scale. During summer, small trout (≤ 90 mm), juvenile coho, and juvenile Chinook were the most abundant species in habitats located along stream margins, especially depositional and side channel habitat (Figure 19a-19d) with wood or undercut banks (see below). Large trout (≤ 90 m) were observed in all habitat types, while coho salmon were mostly absent from cascades and step-pools and Chinook from cascades and riffles. Large trout were most abundant in fast-water habitats including step pools and cascades; they were also abundant in pools.

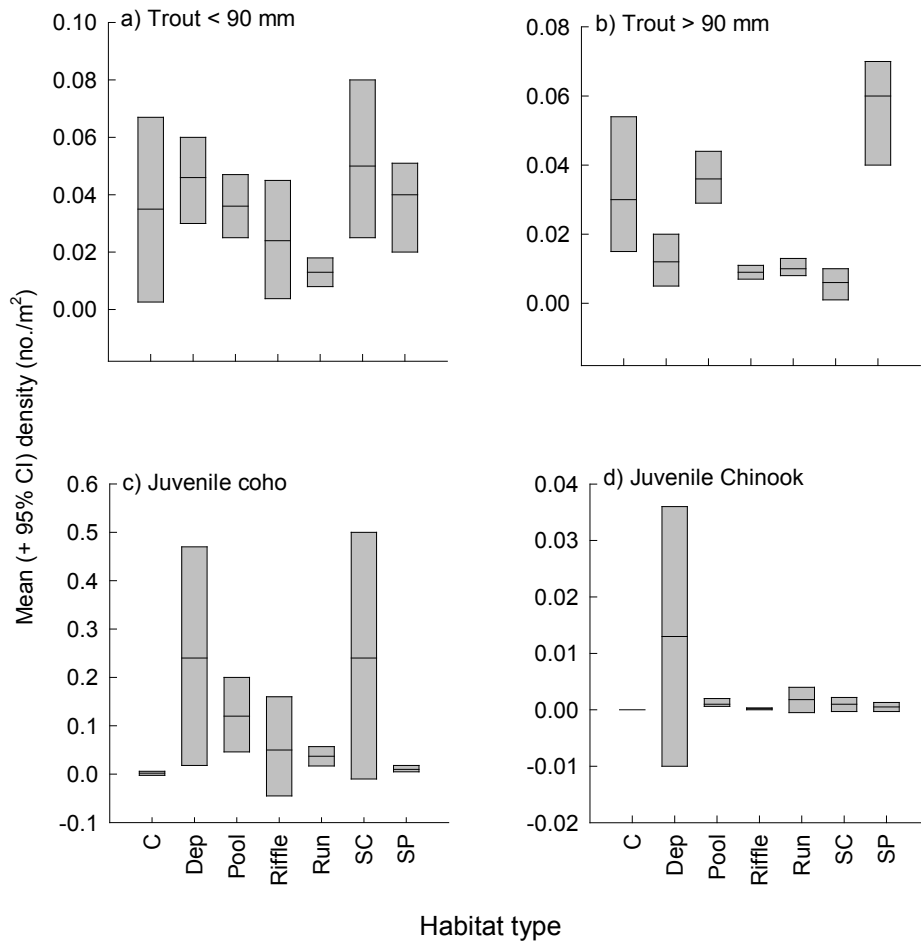


Figure 19. Mean density (number/m² ± 95% CI) of a) small trout (≤ 90 mm), b) large trout (> 90 mm), c) juvenile coho, and d) juvenile Chinook during summer 2005-2009.

Habitat-specific patterns were somewhat similar in winter (Figure 20a-20d), with the following exceptions: small trout were absent from runs and side-channels, large trout were observed at higher densities in depositional and side channels, and juvenile Chinook were more abundant in side-channels than in other habitat types.

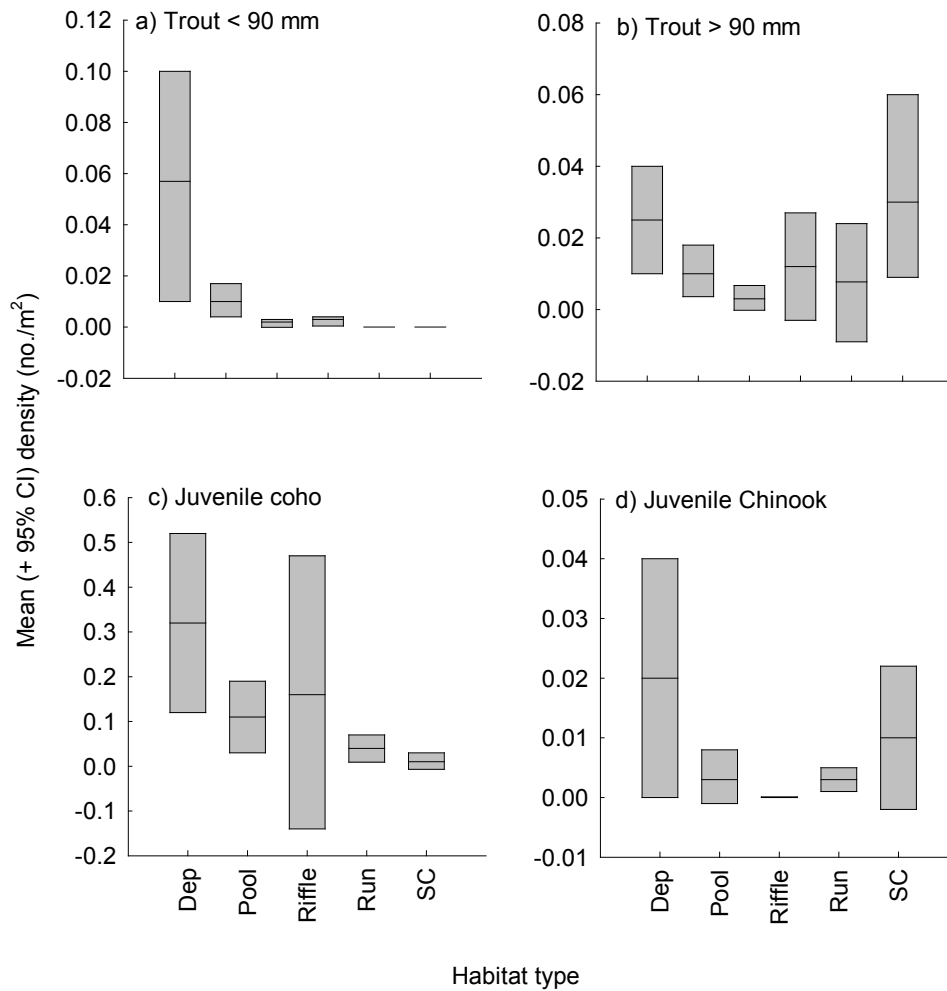


Figure 20. Mean density (number/m² ± 95% CI) of a) small trout (≤ 90 mm), b) large trout (> 90 mm), c) juvenile coho, and d) juvenile Chinook during winter 2005-2009.

Density and Species Composition in Rock Creek—When averaged across reaches, temporal trends in fish density in Rock Creek generally mirrored those in the main stem (Figure 21a-21f). For example, trout density has exhibited no statistical trends with time: small trout (≤ 90 mm) densities have ranged from about 0.07 fish/m² in 2005 to 0.14 fish/m² in 2008-2009, while large trout (> 90 mm) densities have ranged from 0.04 to 0.08 fish/m². In contrast, juvenile coho density has increased relatively rapidly since recolonization, at rates of 0.13 fish⁻¹ m⁻² yr⁻¹ in reach 1 (RC1) and 0.05 fish⁻¹ m⁻² yr⁻¹ in RC3 (Table 9). Juvenile Chinook densities increased from 2006, when they were first observed in Rock Creek, to 2008; however, Chinook were not observed during 2009 or 2010. Overall, total fish density has nearly doubled from 0.2 fish/m² in 2000-2001 to 0.45 fish/m² in 2008-2009.

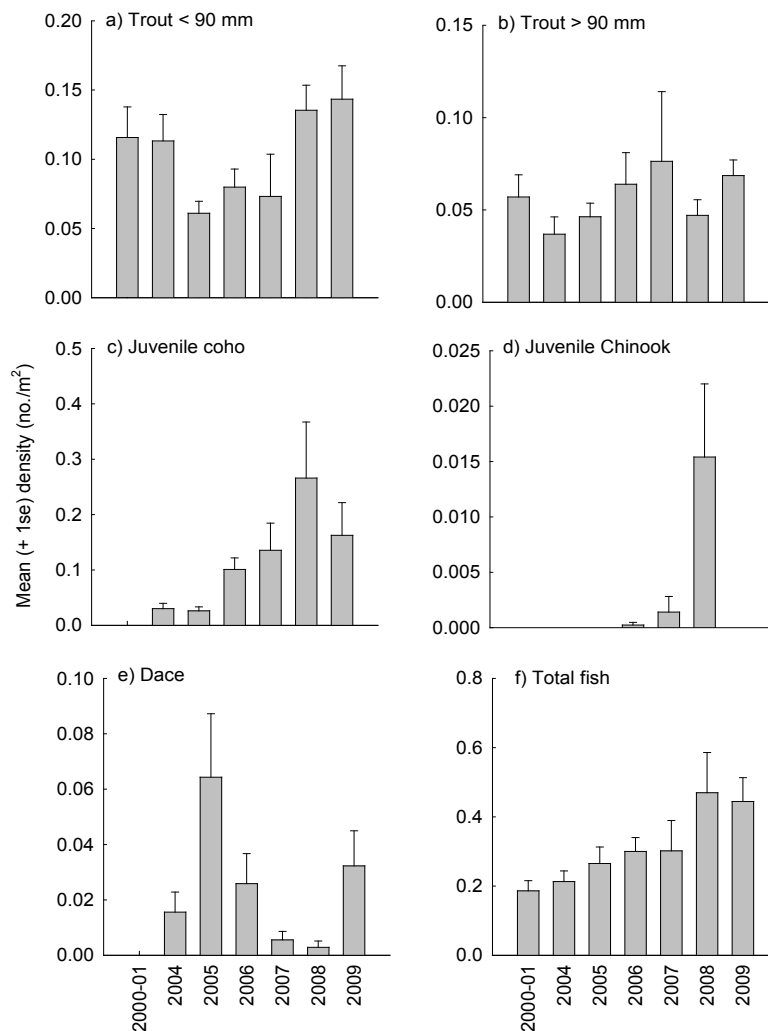


Figure 21. Mean density (± 1 se) of a) small trout (≤ 90 mm), b) large trout (> 90 mm), c) juvenile coho, d) juvenile Chinook, e) speckled, and f) total fish (excluding sculpin) across reaches in Rock Creek, 2000-2009.

Table 9. Simple linear regression models describing the association between Rock Creek fish density (number/m²) and time within reaches RC1-RC3 during summer. Density estimates were based on snorkel surveys of replicate pool (*n* ~5 per reach) habitats within each reach. Year 1 for trout responses represented data averaged across 2000 and 2001 and collected before the ladder was installed. 2004 represented year 1 for salmon responses. The last year of this time series included 2009.

Reach	Response	Intercept (1 se)	Slope (1 se)	R ²	P value
1	Trout ≤ 90 mm	-74 (24)	0.04 (0.01)	0.16	<0.01
	Trout > 90 mm	-17 (8)	0.008 (0.004)	0.09	<0.001
	Juvenile coho	-263 (79)	0.13 (0.04)	0.18	<0.001
3	Juvenile coho	-94 (3)	0.05 (0.02)	0.16	<0.01

Spatial expansion of juvenile coho in Rock Creek was limited by a culvert located ca. 2.5 km from the confluence of the main stem; juvenile coho were not observed past that point until spring 2008 (Figure 22). Because they were young of the year, these individuals were likely a result of adult coho spawning above the culvert in reach RC4 during the previous winter.

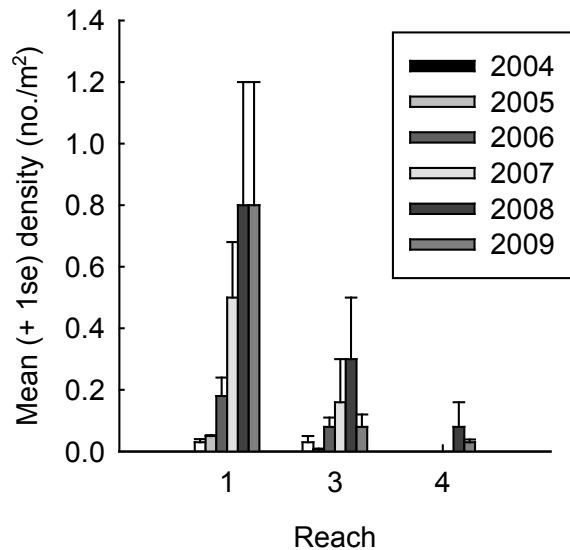


Figure 22. Mean density (+ 1se) of juvenile coho in reaches 1, 3 and 4 of Rock Creek since 2004. Reach 1 begins at the confluence of Rock Creek with the main stem Cedar River and ends ca. 800 m upstream, reach 3 spans from ca. 1600 to 2400 m from the confluence, and reach 4 spans from 2,400 to 4,500 m from the confluence.

Species composition. Changes in fish composition observed in Rock Creek were similar to those observed in the main stem Cedar River, as the relative proportion of Pacific salmon has increased over time. However, Chinook salmon were less important to salmonid community composition in Rock Creek than in the main stem (Figure 23). The relative abundance of juvenile coho in RC1 increased from about 20% in 2004 to 65% of total salmonid density in 2006. The relative abundance of juvenile coho in RC3 ranged from a low of 1.5% in 2005 to 65% in 2007. The other abundant species in RC3 was speckled dace, which reached a peak of about 50% relative abundance in 2005.

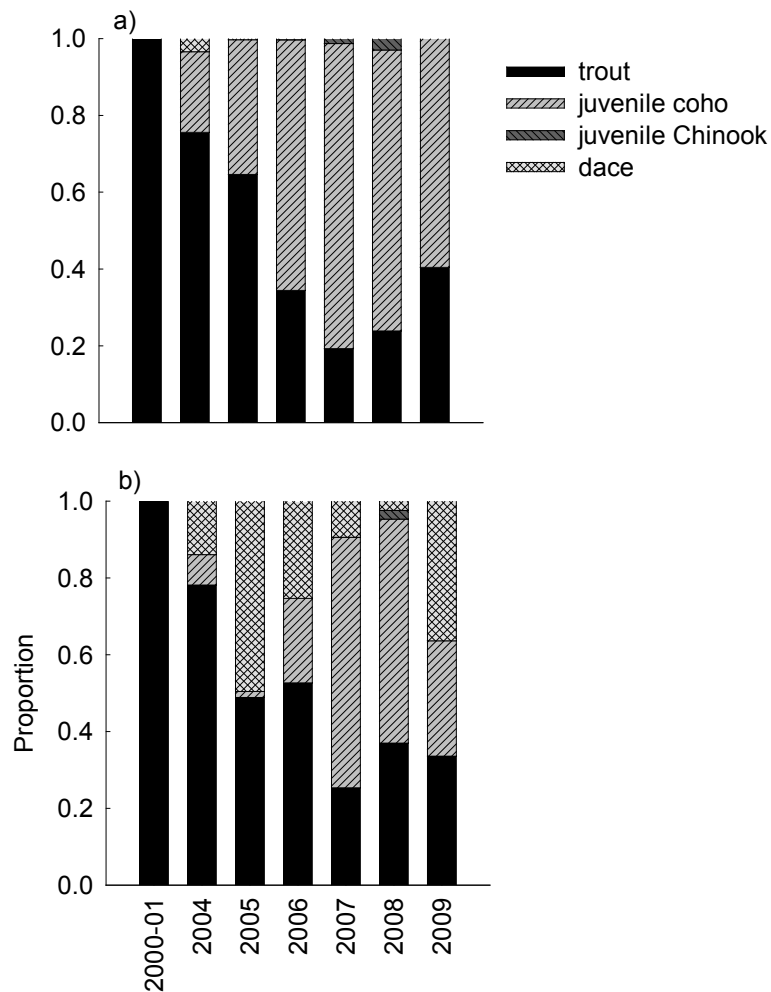


Figure 23. Relative proportion of trout, juvenile coho and Chinook and dace in reaches a) RC1 and b) RC3 of Rock Creek, WA.

Snorkel surveys of upper and lower Rock Creek, which drains into the Cedar River below Landsburg Dam, began in 2007. These surveys allowed for a comparison of fish populations above and below the dam. Results of these surveys showed that salmon and trout densities were similar above and below the dam in summer 2007 and 2009 (Figure 24a-24d). For example, in summer 2007, mean juvenile coho density was about 0.8 fish/m² in upper Rock Creek and 0.6 fish/m² in lower Rock Creek (Figure 24c).

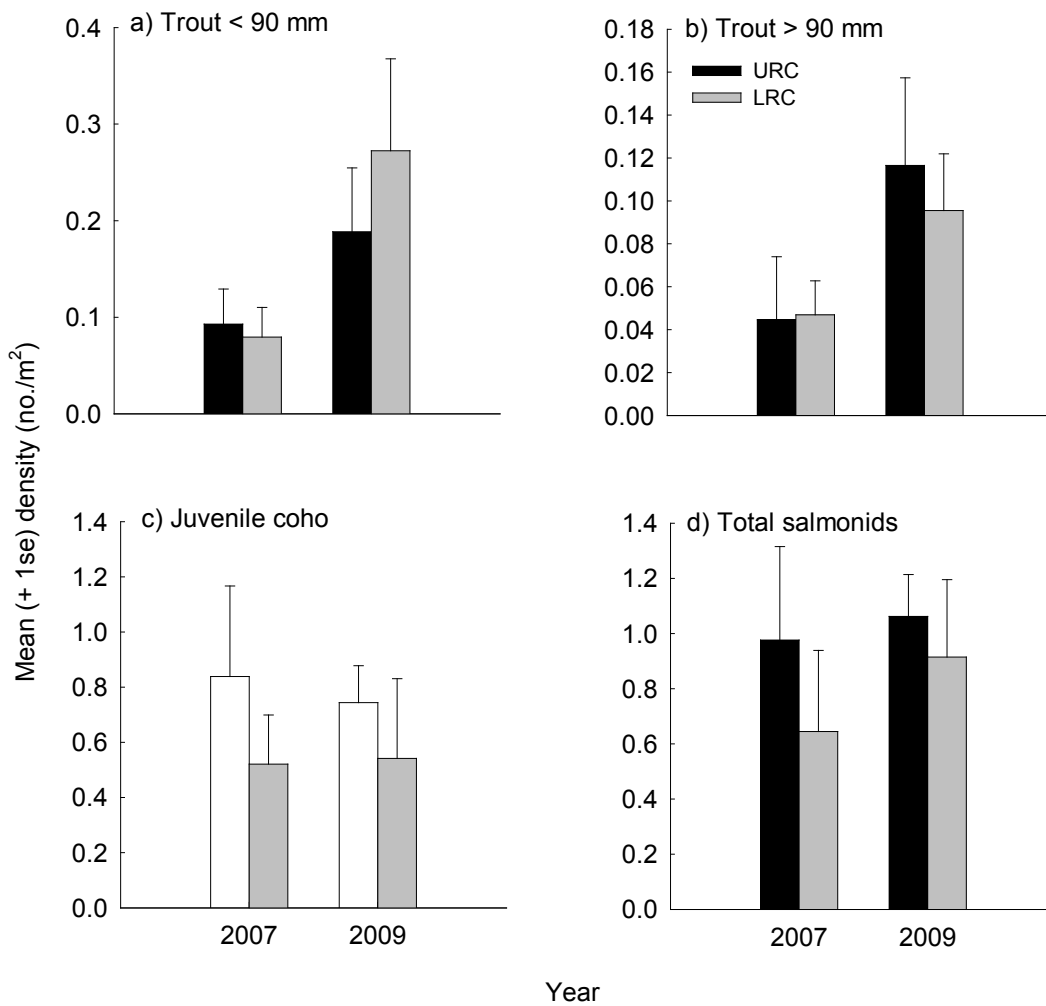


Figure 24. Mean density (number/m² ± 1 se) of a) small trout (≤ 90 mm), b) large trout (> 90 mm), c) juvenile coho, and d) total salmonids in Rock Creek above (URC) and below (LRC) Landsburg Dam in summer 2007 and 2009. Density was estimated by snorkel surveys.

Density in Williams Creek—In Williams Creek, no Pacific salmon have been observed in reach 3 (WC3) since the ladder was installed, confirming that a natural barrier exists in the reach immediately upstream from the confluence of Williams Creek with the Cedar River. Small trout (≤ 90 mm) densities ranged from about 0.07 to 0.2-0.3 fish/m² (Figure 25a-25b), while large trout (> 90 mm) increased in density by a factor of five, from 0.02 fish/m² in 2000-2001 to 0.10 fish/m² in 2009.

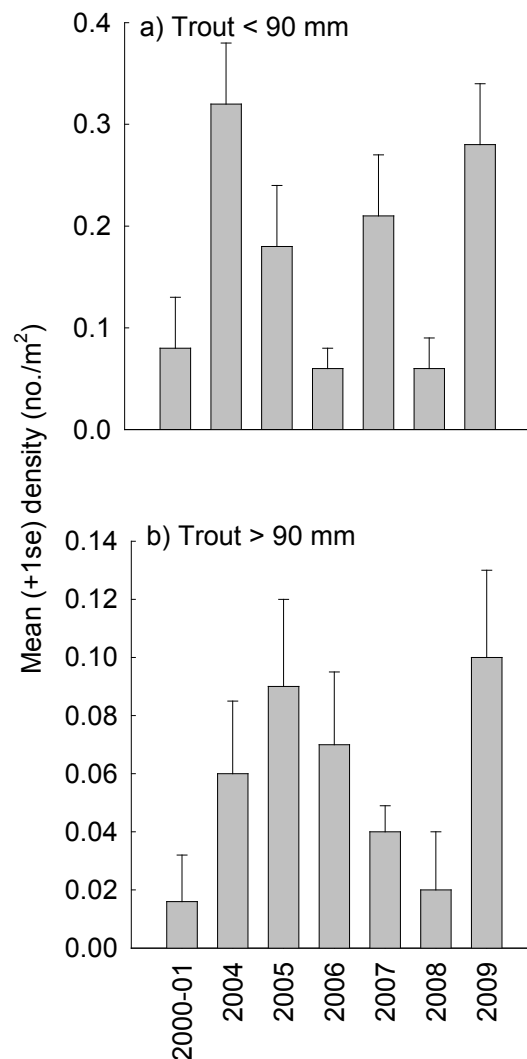


Figure 25. Mean (+ 1se) density of a) small trout (≤ 90 mm) and b) large trout (> 90 mm) reach 3 of Williams Creek, WA.

Effect of Habitat on Abundance—During each summer survey, we found significant positive correlations between habitat structure, primarily habitat attributes defined as fish cover (in m²), and resident and anadromous salmonid abundance in the main stem Cedar River (Table 10). For example, in summer 2007 large trout (> 90 mm) and juvenile coho were positively correlated with single logs ($r = 0.3$; $P < 0.05$). Juvenile coho abundance was also positively correlated with debris jams ($r = 0.3$, $P < 0.05$). Similarly, juvenile coho and Chinook abundance were positively correlated with debris jams in summer 2008 ($r = 0.4$; $P < 0.01$).

Table 10. Pearson correlation coefficients describing the relationship between physical habitat variables (single logs were >10 cm dia and 1 m long) and fish response during summer surveys in 2005-2009. All coefficients were significantly different than zero at $P < 0.05$, and those marked with an asterisk at $P < 0.01$.

Fish response	Habitat variable	Year	Correlation coefficient
Trout ≤ 90 mm	Single log	2005	0.14
Trout > 90 mm	Single log	2005	0.2*
Juvenile coho	Single log	2005	0.1
Juvenile coho	Undercut bank	2006	0.3*
Juvenile coho	Root wad	2006	0.1
Juvenile coho	Single log	2006	0.4*
Juvenile Chinook	Single log	2006	0.15
Trout > 90 mm	Debris jam	2006	0.3*
Juvenile coho	Debris jam	2006	0.4*
Juvenile Chinook	Undercut bank	2007	0.3*
Trout >90 mm	Single log	2007	0.3*
Juvenile coho	Single log	2007	0.3
Juvenile coho	Debris jam	2007	0.3*
Juvenile coho	Debris jam	2008	0.4*
Juvenile Chinook	Debris jam	2008	0.4*
Trout ≤90 mm	Single log	2009	0.3*
Juvenile coho	Debris jam	2009	0.5*
Juvenile Chinook	Debris jam	2009	0.2
Juvenile coho	Single log	2010	0.2
Juvenile Chinook	Single log	2010	0.4*
Juvenile coho	Debris jam	2010	0.5*

The area of undercut banks (defined as stream banks which overhang the water surface and are held together by plant roots) was also positively correlated with fish abundance during some surveys: in 2007, juvenile Chinook abundance was positively correlated with undercut banks ($r = 0.3$, $P < 0.01$). Fish abundance was also positively correlated with the amount of cover area during winter: in 2008 both size classes of trout, as well as juvenile coho and Chinook abundance were positively correlated with debris jams (Table 11).

Table 11. Pearson correlation coefficients describing the relationship between physical habitat variables (single logs were >10 cm diameter and 1 m long) and fish response during winter surveys in 2007-2009. All coefficients were significantly different than zero at $P < 0.05$ and those with asterisk at $P < 0.01$.

Fish response	Habitat variable	Year	Correlation coefficient
Juvenile coho	Debris jam	2007	0.4*
Juvenile Chinook	Single log	2008	0.5*
Trout ≤ 90 mm	Debris jam	2008	0.2
Trout > 90 mm	Debris jam	2008	0.2
Juvenile coho	Debris jam	2008	0.3*
Juvenile Chinook	Debris jam	2008	0.2

Simple linear regression models were used to examine further the functional relationship between juvenile coho abundance during summer and habitat cover (in m^2) provided by wood (sum of single log and debris jam areas; Table 12). Juvenile coho abundance was a positive function of wood cover during almost every summer survey since 2004, with variation in wood cover explaining 17-32% of juvenile coho abundance.

Table 12. Simple linear regression models describing the association between juvenile coho abundance and wood cover (m^2) in individual habitat units during summer surveys in the main stem Cedar River, WA.

Year	Number of observations	Intercept ($\pm 1se$)	β ($1\pm se$)	R^2	P -value
2006	162	6.6 (2.0)	0.44 (0.06)	0.26	<0.001
2007	67	5.7 (3.4)	0.21 (0.06)	0.17	<0.01
2008	104	41.3 (6.6)	0.73 (0.16)	0.17	<0.001
2009	113	11.6 (5.4)	1.0 (0.14)	0.32	<0.001
2010	140	26.1 (9.2)	1.2 (0.17)	0.28	<0.001

Abundance vs. Prey Availability—During summer 2007, invertebrate drift was collected in four reaches of the main stem Cedar River (CR1, CR2, CR4, and CR6) and in two reaches of Rock Creek (RC1, RC3). These samples were collected coincident with snorkel surveys and mark-recapture collections of juvenile coho and resident trout, allowing us to examine the relationship between fish and prey availability. The biomass of drifting invertebrates in the water column measured at the reach scale (i.e., multiple drift samples collected across each reach) was positively correlated with reach-scale total salmonid abundance (Pacific salmon and resident trout; Figure 26; $r = 0.9$; $P < 0.001$).

We also examined average growth rates of multiple individual fish captured and recaptured within each reach. These growth rates indicated a similar relationship between prey availability and juvenile coho growth rate measured at the reach-scale after accounting for total salmonid density in that reach. Specifically, coho growth rate during summer was positively associated with invertebrate drift biomass when total salmonid density was included in the model as a covariate (ANCOVA, where coho growth rate was $109 \times (\text{drift biomass}) - 5.1 \times (\text{total salmonid density})$; $R^2 = 0.94$; $P < 0.01$; $n = 6$).

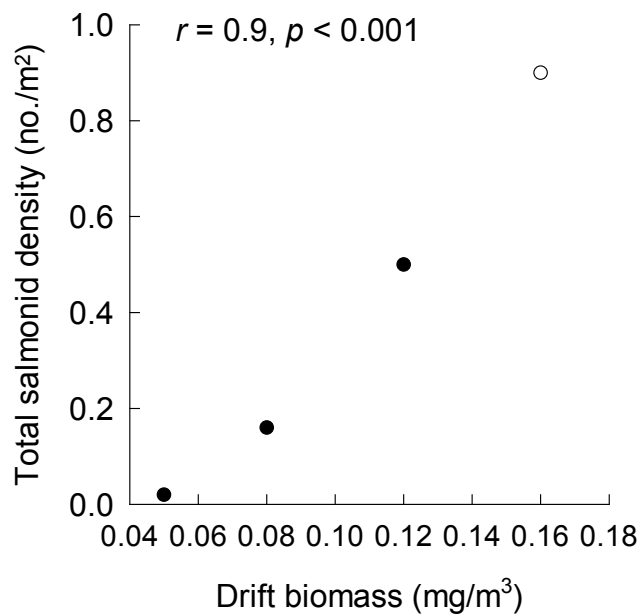


Figure 26. The correlation (Pearson's) between mean reach-scale total salmonid density and invertebrate drift biomass during summer 2007.

3.0. ECOSYSTEM STUDIES

3.1. Carcass Analog and Small Wood Experiments

Methods

An experiment was conducted during summer 2007 to assess further the effects of salmon carcasses on the Cedar River food web (section 3.2); this work complements the fall/winter study conducted by Cram (2009). The experiment was conducted between 18 July and 31 August 2007 (45 days total) in 16 experimental streams located on a 200 m² grassy opening. Incidental sunlight was high in this area due to an unobstructed southern exposure.

Experimental streams (4.8 m long × 0.3 m wide) were constructed of cinder-block rows, with each row covered by pond-liner material and partially filled with gravel (10-30 mm median grain size; Cram 2009). One cinder block and three large cobbles (~64-100 mm median grain size) were placed in each stream to serve as cover for fishes. Habitat in each stream was comprised of three pools (mean depth 22 cm) and two riffles (depth 15 cm); pools were deeper, slower velocity habitats compared to riffles.

Water was gravity transported (temperature range 10-14°C, mean 12°C) from the Cedar River to experimental streams. The intake pipe for river water was covered by a mesh screen (mesh opening 1.75 cm) that restricted immigration of juvenile fishes but allowed for import of organic detritus and natural populations of algae, bacteria, and stream invertebrates. Plastic pipes carried water to a primary head tank, which acted as a settling basin and reservoir, feeding water to channels. Gate valves were used to control flow (~1.0 L/s) into each channel.

Water was turned on ~45 days prior to day zero (18 July) of the experiment, allowing for natural colonization of biofilm and invertebrates. Juvenile coho salmon (mean ±1 se, length 66.0 ±1.5 mm, weight 4.1 ±0.3 g) and sculpin (length = 55.4 ±2.9 mm, weight = 2.2 ±0.5 g) were collected from the Cedar River. One individual of each species was placed into each experimental channel and allowed to acclimate to their surroundings for 3 d. Coho and sculpin densities in channels were within the range observed in Rock Creek (0.70 fish/m²; Kiffney et al. 2002, 2009). There were no significant differences among treatment fish in initial weight or length ($P > 0.2$). Fish emigration was restricted by wire screen placed at the downstream end of each channel. Scavengers and predators were excluded by 2.4-cm mesh netting, which fully enclosed channels but had little effect on ambient light.

Carcass analogs, which were shaped into small briquettes ($\sim 4 \times 4$ cm), were used to mimic pulsed subsidies provided by spawning anadromous fish (Wipfli et al. 2004; Kohler et al. 2007). Carcass analogs were manufactured from adult Chinook salmon (*O. tshawytscha*) and marine bone meal (Bio-Oregon, Inc., Warrenton, Oregon), and contained 2.3% P, 10.9% N, 14.6% fat, and 67.9% protein by mass. On day 0 of the experiment (18 July 2007), analogs were added to the upstream end of randomly selected streams at density of 0.6 kg/m^2 . This density was generally lower than that used in other experimental studies (e.g., 1.8 kg/m^2 , Wipfli et al. 2003) but was within the range observed in British Columbia and Alaska streams with healthy salmon populations (Chaloner et al. 2004; Johnston et al. 2004).

To vary habitat structure, four pieces of small wood (diameter ~ 6 -7 cm and length ~ 15 -18 cm) were evenly distributed along the length of eight randomly selected channels the day water was turned on. Wood was placed at a ~ 45 -degree angle to the channel edge so as not to span the entire channel width. The four treatment channels were designated as C, no wood or carcass analog; +W, wood added; +A, carcass analogs added, or +WA, wood and carcass analogs added, and each was replicated four times.

To quantify the main and interactive effects of habitat structure (wood) and resource subsidies (carcass analogs) on nutrients, primary producers and consumers, and fish predators, we used a completely randomized design and a 2×2 treatment structure with four replicates per treatment ($n = 16$ experimental units). A 2×2 analysis of variance (ANOVA) was used to model treatment effects on biofilm biomass, net invertebrate emigration rate, and fish growth rate and body size because these factors were measured only once.

To quantify the main and interactive effects of resource subsidies and habitat structure, we measured total and dissolved nitrogen and phosphorus in water, biofilm biomass, benthic and drifting invertebrate abundance and biomass, and fish growth. Water for nutrient analysis was collected from the downstream end of each channel. Total nutrients were unfiltered, while dissolved nutrients were collected by pouring water through a $0.45\text{-}\mu\text{m}$ filter (Nalgene cellulose acetate membrane filters, Fisher Scientific). Samples were frozen until analysis (School of Ocean and Fisheries, University of Washington, Seattle, WA); analyses included total nitrogen (N), dissolved nitrate-nitrogen (NO_3^-), nitrite-nitrogen (NO_2^-), ammonium (NH_4^+), total phosphorus, and soluble reactive phosphorus (SRP).

Water chemistry and benthic invertebrate populations were sampled twice from the same stream channel during the experiment (days 14 and 45), so a 2×2 mixed-model repeated measures ANOVA was used for these data (stream as a random

effect, and wood and analogs fixed effects). There were no significant interaction terms ($P > 0.2$); therefore, models were analyzed with only main effects.

Unglazed ceramic tiles (108 cm²) were used as a substrate to sample biofilm and invertebrate populations; tiles are readily colonized by stream algae and bacteria, and primary consumers (Kiffney et al. 2003). Although tiles are selective for certain organisms, and thus do not reflect the entire benthic community, they provided a uniform surface that minimized variability and allowed for comparison among streams and treatments.

Eight tiles were evenly split between pools and riffles. On days 14 and 45, two tiles were randomly selected from one pool and riffle and processed for biofilm (day 45 only), ash-free dry mass (represents all benthic organic matter), chlorophyll a (represents algal biomass), and invertebrate abundance and biomass. All invertebrates on tiles were removed before scrubbing the tile with a wire brush and scraping with a flat blade.

Distilled water was used to rinse attached material into sieve, with the liquid slurry collected in a basin. This slurry was frozen until processing (see Kiffney et al. 2003, 2005 for further details). All invertebrates collected in the sieve were transferred to 95% ethanol until processing. A dissecting microscope was used to identify (genus or family for all groups except Chironomidae and Simuliidae) and count invertebrates in the sample (Merritt and Cummins 2004). Head capsule width was measured using an ocular micrometer attached to the dissecting scope; published regressions were used to convert head capsule width to biomass (Benke et al. 1999; Burgherr and Meyer 1997; Hodar 1997; Meyer 1989; P. Kiffney and S. Naman unpublished data).

On day 44, invertebrate immigration and emigration rates were quantified by placing drift nets (250- μ m mesh) over inflow pipes and below the outflow so that the entire volume of water in a channel could be filtered. Nets were retrieved 24 h later, and all captured invertebrates were stored in 95% ethanol and processed as tile invertebrates. Net emigration rate (number invertebrates emigrating - number immigrating) was used to model treatment effects (Melody and Richardson 2004). Per capita emigration rates (number of invertebrates emigrating per channel/total number of invertebrates in channel; Richardson 1991) showed the same patterns as net emigration rates, but were more variable.

On day 45, 15 coho and 12 sculpin were captured and euthanized with an overdose of MS-222; the lower recapture rate of sculpin was likely due to their benthic and cryptic nature, but also could have been a result of escaping channels or mortality. Each fish was weighed (± 0.1 g) and measured (fork length, ± 1.0 mm). Stomach samples were also removed from coho for diet analysis. Relative growth rates were calculated

using the following formula: $\text{change in length or mass} = ((x_{\text{final}} - x_{\text{initial}}) / (x_{\text{initial}})) / 45 \text{ d}$ where x represents mass (g) or length (mm) at the beginning (initial) and end (final) of the experiment.

Simple linear regression was used to model the relationships between nutrient chemistry and invertebrate populations, and invertebrate populations and fish growth and body size. Chironomidae larvae, pupae, and adults (drift only) were observed in experimental streams, providing an opportunity to quantify the relative importance of multiple factors on life stage abundances. Therefore, multiple regression was used to model the relative importance of benthic Chironomidae larval abundance (i.e., on tiles), total phosphorus and total benthic primary consumer abundance (excluding Chironomidae) on the number of benthic Chironomidae pupae ($n = 16$). A similar approach was used to assess the relative importance of these factors on net emigration of Chironomidae adults from channels.

Results

Carcass analogs and small wood had complex but non-additive effects on the Cedar River food web in experimental streams. Carcass analogs increased the availability of nutrients, including total nitrogen and phosphorus, dissolved NH_4^+ , and soluble reactive phosphorus (SRP) in the water column (Figure 27a-27d). On day 45, total nitrogen was about 1.4 times higher in channels with carcass analogs compared to those without. Carcass analogs had even larger effects on dissolved NH_4^+ , which was ~2.1 times higher in channels with analogs. Furthermore, dissolved NH_4^+ and SRP levels were generally higher on day 45 compared to day 14 as evidenced by the significant day effect.

Sixteen different taxa were observed on tiles, with Baetidae mayfly nymphs (Ephemeroptera) and Chironomidae larvae (Diptera) comprising about 11 and 60% of total benthic invertebrate biomass, respectively. Biomass of most taxa was higher on day 45 than on day 14; for example, Baetidae biomass was two times higher on day 45 than on day 14 (Figure 28a-28d).

There was no evidence that wood influenced benthic invertebrate populations, whereas analog carcasses had positive effects on three taxa (Chironomidae larvae and pupae, *Atherix* spp. larvae, and Baetidae nymphs, RM-ANOVA, $P < 0.05$) as well as total invertebrate biomass (Figure 29). For instance, Chironomidae pupal biomass was ~four times higher in analog treatments at the end of the study. Average size (mg) of Chironomidae pupae and Simuliidae was also significantly larger in analog channels: mean size of Chironomidae pupae was about twice as high in channels with analog carcasses (mean \pm 1se, 0.64 ± 0.04 , $n = 35$) than those without (0.34 ± 0.03 , $n = 46$).

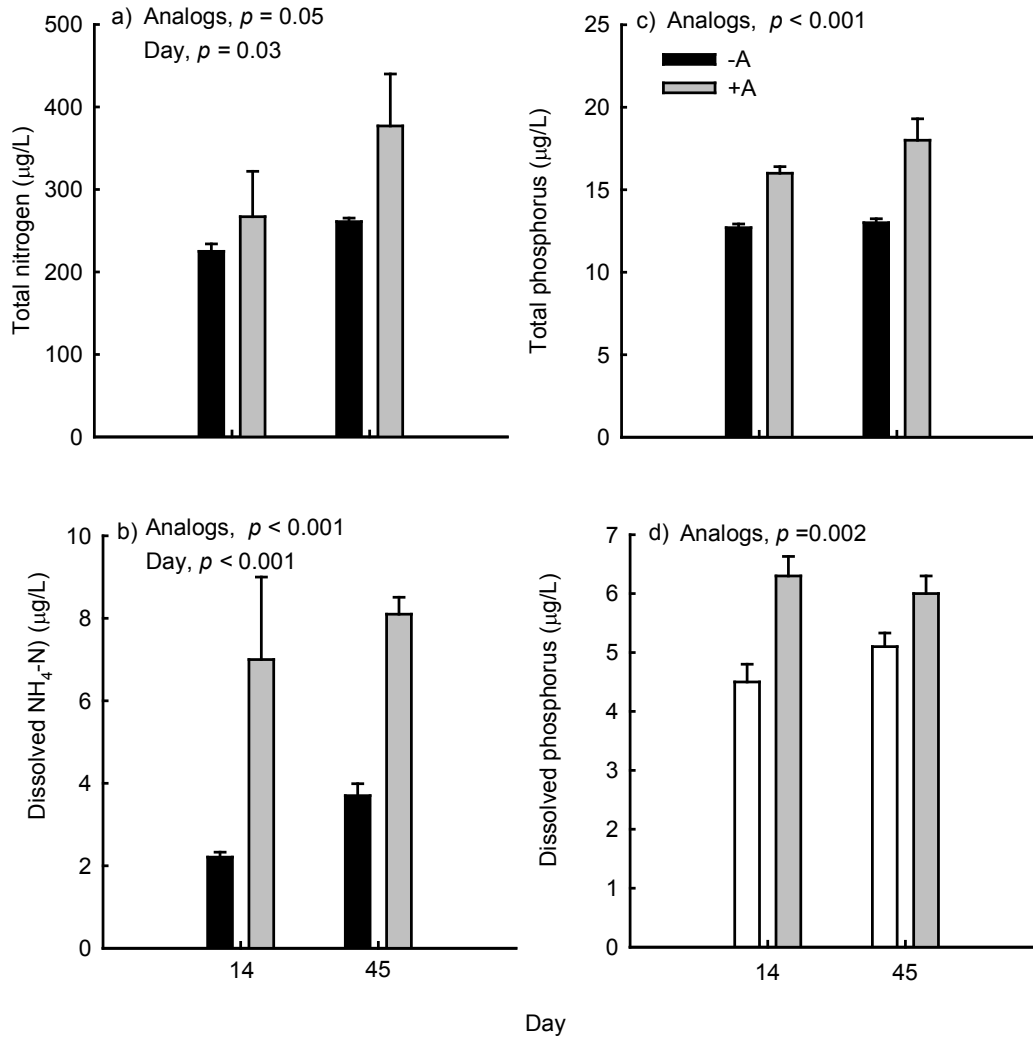


Figure 27. Concentrations (µg/L) of a) total nitrogen, b) ammonium, c) total phosphorus and d) soluble reactive phosphorus (SRP) on days 14 and 45 for experimental channels without (-A, black bar) and with carcass analogs (+A, grey bar).

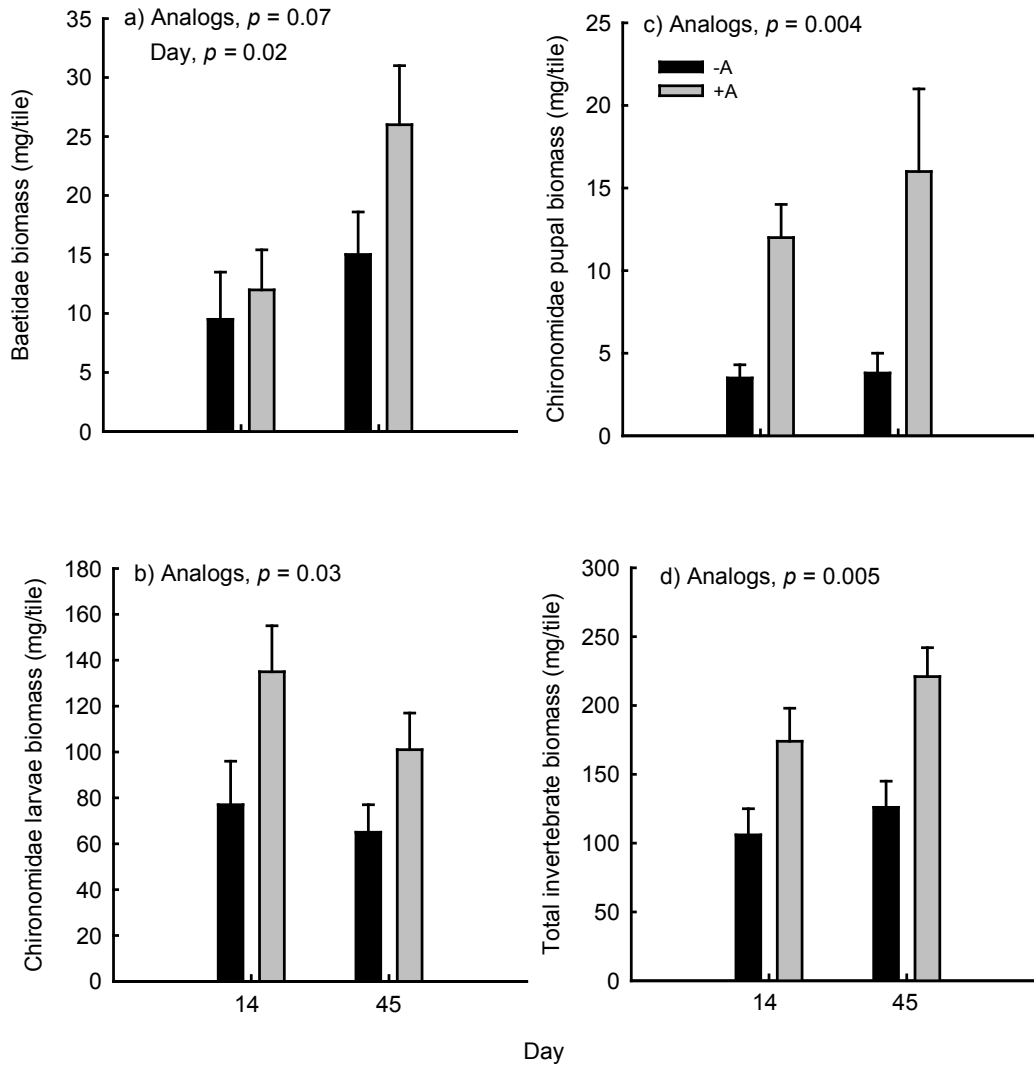


Figure 28. Benthic biomass (mg/tile) of a) Baetidae nymphs, b) Chironomidae larvae, c) Chironomidae pupae and d) total invertebrates on days 14 and 45 for experimental channels without (-A, black bar) and with analogs (+A, grey bar).

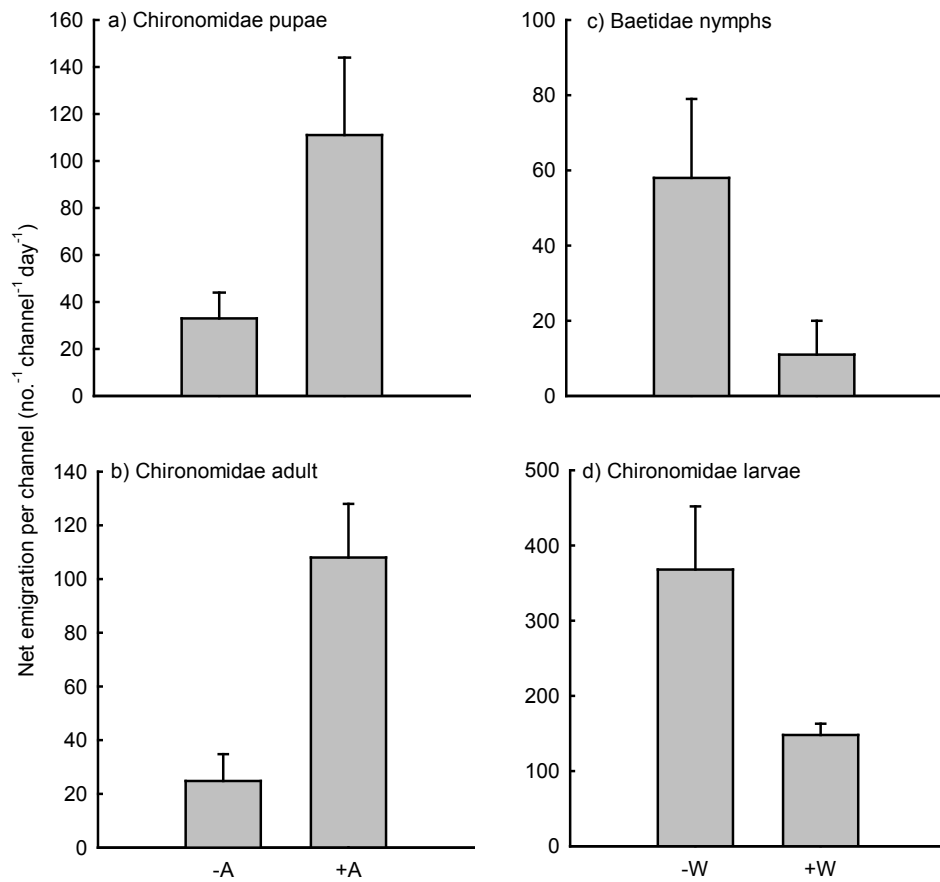


Figure 29. Net emigration rate (total emigrating from channel-total immigrating into channel) (no.⁻¹ channel⁻¹ d⁻¹) of a) Chironomidae pupae, b) Chironomidae adults, c) Baetidae nymphs, and d) Chironomidae larvae in analog channels with and without analogs ($\pm A$) and wood ($\pm W$) (n = 8 replicates per treatment).

Thus, both increased abundance and greater individual size contributed to a total benthic biomass that was ~ 1.8 times higher in analog-amended channels on day 45.

Evidence that resource subsidies indirectly affected select primary consumers through bottom-up effects was evident in the positive relationship between total phosphorus and Chironomidae pupae and adults. On day 14, a two-variable model that included Chironomidae larval abundance and total phosphorus ($\mu\text{g/L}$) explained 70% of the variation in Chironomidae pupal abundance on tiles (Table 13).

Table 13. Parameter estimates (± 1 se) and coefficients of determination for regression models. Parameter estimates with an asterisk did not overlap zero. Model for total benthic biomass included a higher-order term. TP = total phosphorus ($\mu\text{g/L}$).

Intercept (1 se)	$\beta_1 \times x_{i1}$	$\beta_2 \times x_{i2}$	Adjusted R^2
Total benthic biomass (mg/tile)^a			
-43 (100)	$16 (7.2) \times \text{TP}^*$	$-13 (4.5) \times \text{TP}^{2*}$	0.43
Chironomidae pupae benthic biomass (mg/tile)			
$-38.5 (12.7)^{*a}$	$0.04 (0.006) \times \text{Chironomidae larvae}^*$	$2.8 (0.8) \times \text{TP}^*$	0.71
$-20.6 (11.3)^b$	$2.5 (0.7) \times \text{TP}^*$		0.42
Chironomidae adult emigration (number⁻¹ channel⁻¹ d⁻¹)			
-147 (70.5)	$2.6 (1.1) \times \text{Chironomidae benthic pupae abundance}^*$	$11.4 (5.0) \times \text{TP}^*$	0.66
Coho relative growth rate (g⁻¹ g⁻¹ d⁻¹)			
0.001 (0.003)	$0.00008 (0.00003) \times \text{Adult Chironomidae emigration}^*$		0.27
Coho mean weight (g)			
$4.0 (0.5)^*$	$0.014 (0.006) \times \text{Adult Chironomidae emigration}^*$		0.34
Coho mean weight (g)			
$3.4 (0.3)^*$	$0.20 (0.03) \times \text{Chironomidae benthic pupal biomass}^*$		0.71

^a Day 14, ^b Day 45

Invertebrate emigration rates did not differ across treatments; in contrast, net emigration rate was higher from carcass analog-amended channels than non-amended channels for Chironomidae pupae and adults ($P < 0.07$ for pupae and $P < 0.006$ for adults; Figure 29a and 29b). For instance, adult Chironomidae emigration was 4.5 times higher in analog treatment channels. A two-variable model that included benthic Chironomidae pupal abundance and total phosphorus explained $\sim 70\%$ of the variation in adult Chironomidae emigration rate (Table 13). Although larger benthic populations of baetid nymphs and chironomid larvae were observed in analog-amended channels, these differences did not affect their emigration rates. Baetidae emigration rate was 80% lower ($P < 0.1$) and Chironomidae emigration 60% lower ($P < 0.07$) in channels with wood compared to channels without wood (Figure 30c and d), however.

Coho growth rate and final mass were positively affected by carcass analogs (Table 14); for instance, relative change in length was four times higher and final mass 1.6 times higher in analog-amended channels. These increases were a function of prey availability, since relative growth rate and final mass were significantly and positively associated with adult and pupal Chironomidae emigration rate and benthic biomass (Table 14; Figure 30a-30c). The link between analogs, select invertebrate populations, and fish performance was evident in diet analysis, which showed that juvenile coho in analog channels consumed ~3 and 16 times the biomass of Chironomidae pupae and adults, respectively, as coho in channels without analogs. There was no evidence that analogs or wood affected sculpin individual traits.

Table 14. Relative change in coho weight and length (e.g., relative length = ((final length-initial length)/initial length)/(initial length)/study duration), and biomass and C¹³ and N¹⁵ isotope levels in channels without and with analogs at the end of the experiment. *T*-values represent results of a two-way ANOVA without the interaction term: * = *P*-value < 0.1, ** = *P*-value < 0.01.

Response	Coho salmon		<i>t</i> -value
	-A	+A	
Relative length (mm ⁻¹ mm ⁻¹ d ⁻¹)	0.0015 (0.0004)	0.004 (0.0005)	-3.14**
Relative weight (g ⁻¹ g ⁻¹ d ⁻¹)	0.003 (0.009)	0.01 (0.008)	-1.78*
Biomass	3.8 (0.3)	6.2 (0.3)	-4.86**
C ¹³ (‰)	-23.4 (0.1)	-21.0 (0.2)	-8.55**
N ¹⁵ (‰)	5.6 (0.2)	8.8 (0.3)	-9.17**

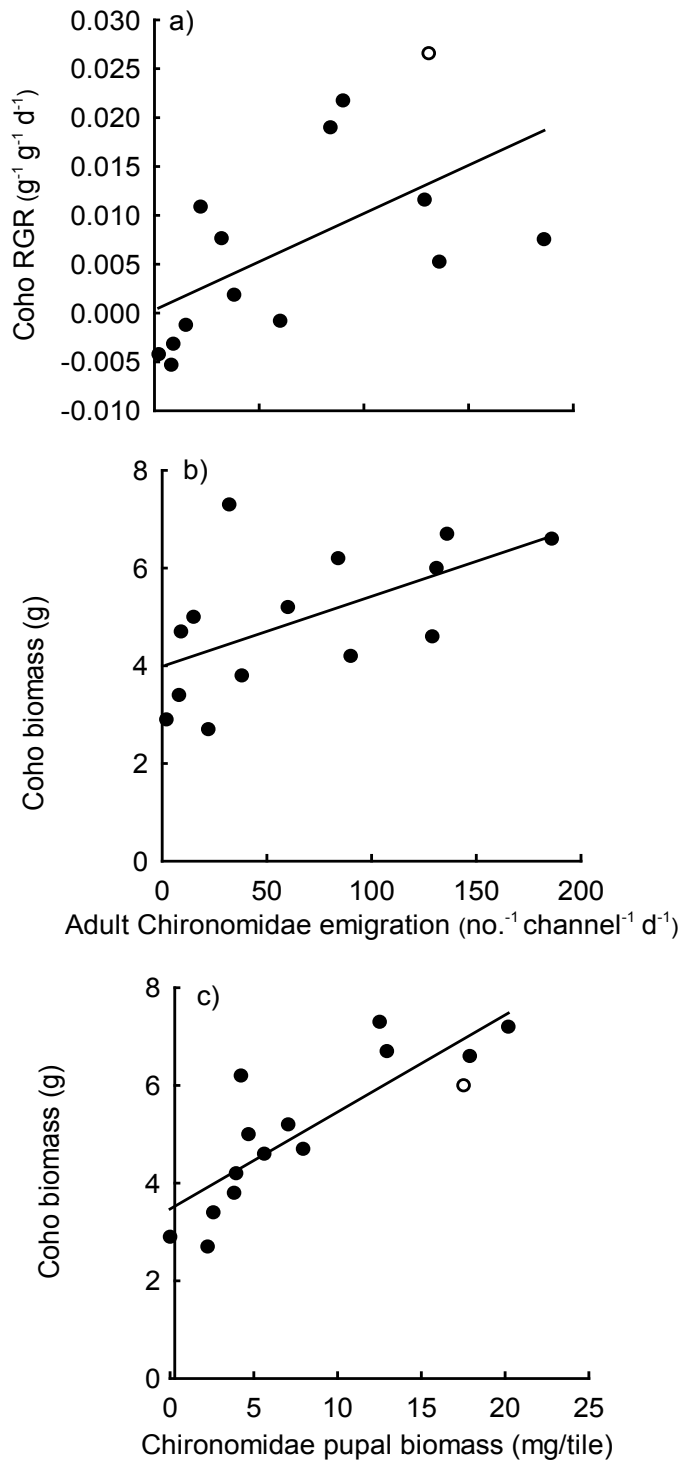


Figure 30. Relationships between adult Chironomidae net emigration ($\text{no.}^{-1} \text{channel}^{-1} \text{d}^{-1}$) and a) juvenile coho growth rate ($\text{g}^{-1} \text{g}^{-1} \text{d}^{-1}$) and b) final mass (g) and c) Chironomidae pupal benthic biomass (mg/tile) and coho final mass (see Table 2 for parameter estimates and associated regression statistics).

3.2. Adult Salmon Biomass Input

We calculated annual adult salmon inputs (kg) above Landsburg Dam from 2003 to 2009 by using counts at the ladder (e.g., Faulds and McDowell 2009) and assuming an average weight of 11 kg for adult Chinook and 3.6 kg for adult coho (Gresh et al. 2000). To estimate total nitrogen (N) and phosphorus (P) inputs provided by adult salmon, we assumed that individual fish were composed of 30% N and 3.5% P by weight.

Simple linear regression and Pearson's correlation coefficient were used to quantify the relationship between total inputs of biomass, N, and P provided by adult salmon Chinook and coho into the Cedar River above Landsburg and time since recolonization.

Results showed that annual biomass inputs of adult coho and Chinook (kg/m²) have generally increased over time. Correlations between time and the metrics of coho biomass input, Chinook biomass input, total salmon biomass input (Chinook + coho), total N, and total P were statistically significant and positive (Table 15). Adult coho inputs are increasing at a rate of 468 kg/year. Moreover, in 2009, adult Chinook inputs were 1.7 times higher and adult coho inputs 14.5 times higher than in 2003.

Table 15. Biomass input (kg) of adult coho, adult Chinook, total adult salmon input, total nitrogen (N) and total phosphorus (P) above Landsburg Dam since summer 2003. Totals were based on number of fish within each species that passed above the dam at the fish ladder. Biomass estimates were based on average size for each species (11 kg for Chinook and 3.6 for coho). N and P estimates were based on the assumption that each adult salmon was 30% N and 3.5% P by mass. Columns with an asterisk indicate the relationship between year and input was positively correlated (Pearson's correlation coefficient at $P < 0.05$).

Year	Biomass input to the Cedar River above Landsburg Dam (kg)				
	Coho biomass	Chinook biomass	Total biomass*	Total N*	Total P*
2003	118	869	987	298	34
2004	248	561	809	245	28
2005	425	759	1,184	358	41
2006	435	2,002	2,436	738	85
2007	353	4,367	4,719	1,430	165
2008	643	1,606	2,248	681	78
2009	1,690	1,518	3,215	974	112

3.3. Diet Content Analyses

Methods

In 2000, 2001, and 2004 stomachs were dissected from sacrificed fish; contents were preserved in 95% ethanol until processing. In 2007-2009, we used gastric lavage to collect diets from fish stomachs (Bowen 1996). Medical syringes and large-gauge needles were used to pump water into the stomach and flush out stomach contents into a plastic tray. Typically, a stomach was flushed two to three times or until it was empty. A subset of fish were sacrificed each year to test lavage efficiency; we found this method to be 95-100% effective at removing all stomach contents. Stomach contents were processed under a dissecting microscope, with each item first classified as either of aquatic or terrestrial origin and then identified to at least the level of order (e.g., Diptera, Ephemeroptera).

Many items in stomachs were partially digested; these items were a challenge to classify, but we attempted to categorize them to the lowest taxonomic level possible. In some cases, classification was not possible; therefore, these items were identified as “unidentified diet items.” If possible, fish in diets were assigned as either salmonids or sculpin. If only bones remained, they were identified as fish. All identifiable diet items were then counted. Furthermore, the head capsule of each identified invertebrate item was measured to the nearest 0.1 mm. This value was then used in body size-biomass regression relationships to estimate biomass of each invertebrate and vertebrate in a diet sample (Benke et al. 1999; Burgherr and Meyer 1997; Hodar 1997; Meyer 1989; S. Naman unpublished data).

Information on isotopes from stomach content analyses were reported in detail by Kiffney et al. (2006).

Results

Since 2000, the stomach contents of 1,263 fish (trout, sculpin, coho and whitefish) have been examined. The size of fish examined ranged from 25 to over 400 mm. We found that piscivory was generally limited to fish larger than 120 mm (Figure 31a); the relative proportion of piscivory ranged from 0% in 2004 to 4% in 2001, and averaged ca 2% (Figure 31b). No Pacific salmon were found in fish diets.

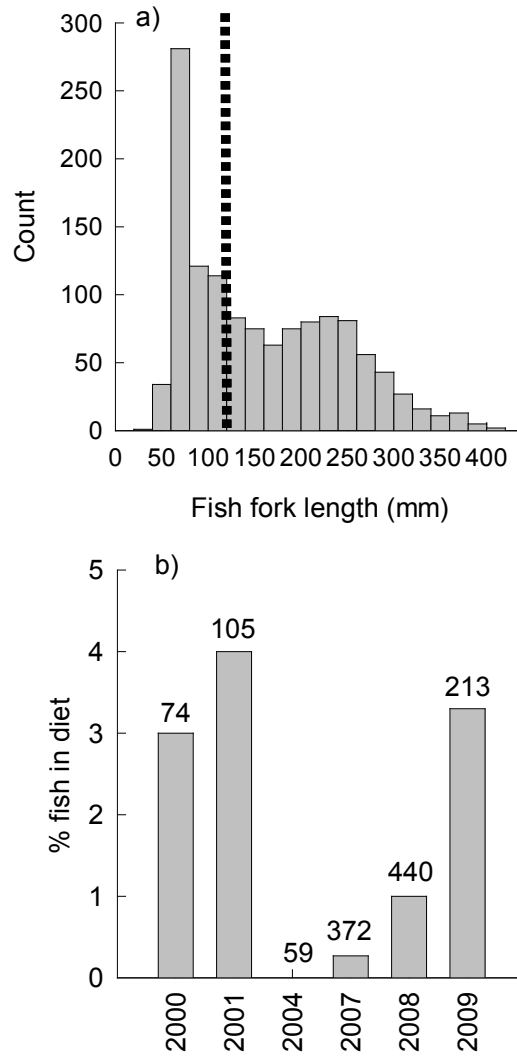


Figure 31. a) Size-frequency histogram of fish sampled for diet contents during 2000-2001, 2004, and 2007-2009 (dotted line indicates the size where fish became predators of other fish) and b) percent of fish sampled that had fish in their diets. Number above bar represents sample size for that year.

Of stomach samples collected since 2004, immature aquatic invertebrates made up about 50% (by biomass) of juvenile coho diets (coho sampled were 70-120 mm fork length), with the remaining 50% split between adult aquatic and terrestrial invertebrates (Figure 32). Large rainbow and cutthroat trout (>90 mm) had similar amounts of food in their stomachs, with cutthroat trout larger than 120 mm primarily eating other fish (also by biomass), followed by immature aquatic and terrestrial invertebrates. Diet contents of rainbow trout were relatively evenly split among the four diet categories. Sculpin (30-150 mm), trout fry (≤ 90 mm), and whitefish (all >300 mm) primarily ate immature aquatic invertebrates.

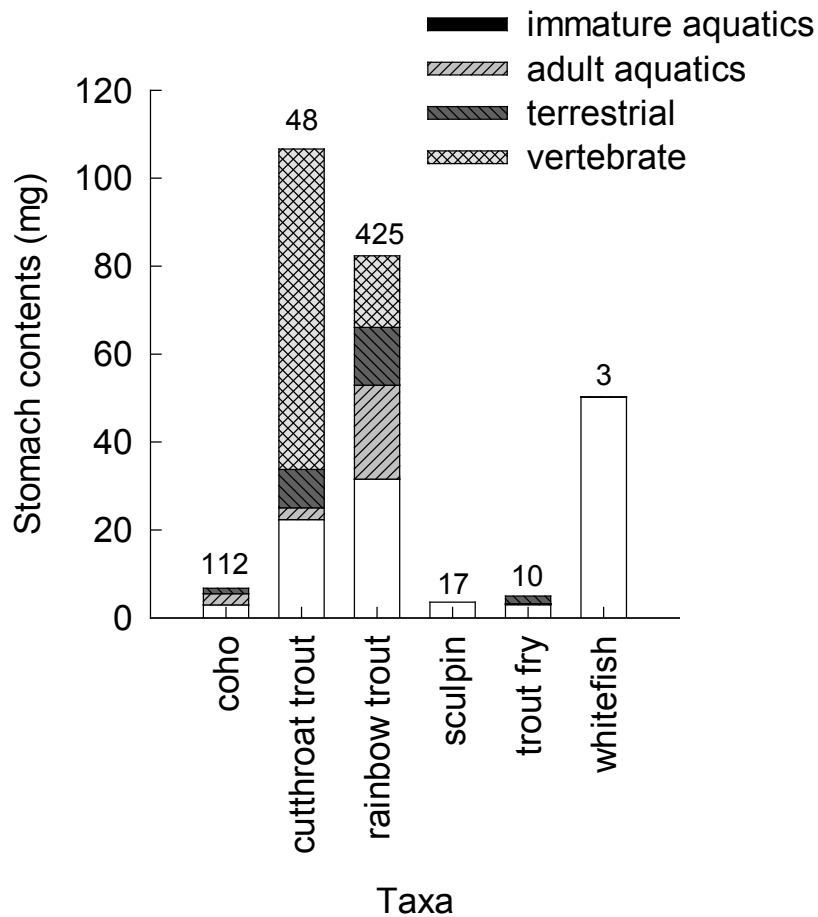


Figure 32. Average biomass (mg) for major diet items in fish stomachs collected from the main stem Cedar River during 2004, and 2007-2009. Number above bar represents sample size per taxa.

3.4. Carbon and Nitrogen Isotopes

Although salmon flux into the Cedar River above the dam has been increasing over time, there was mixed evidence to indicate whether N and C isotopic values have been increasing at sites accessible to salmon, with considerable variation among reaches sampled (Figure 33).

We used *t*-tests to determine whether levels of N¹⁵ and C¹³ differed in fish tissue collected before (2000-2001) vs. after (2004, 2007-2009) fish ladder installation/recolonization. We predicted that N¹⁵ and C¹³ should be higher with the return of spawning salmon.

Across all years sampled, N¹⁵ values in large trout (>90 mm) collected from Rock Creek (RC1) and the main stem Cedar River (CR1 and CR6) were higher than in those collected from Taylor Creek (TC2), which is a natural barrier to salmon. However, these values showed no significant trend with time. Moreover, on average, fish from Rock Creek were more enriched in N¹⁵ than fish from other sites. Similar patterns in N¹⁵ values were observed for sculpin and small trout (≤90 mm).

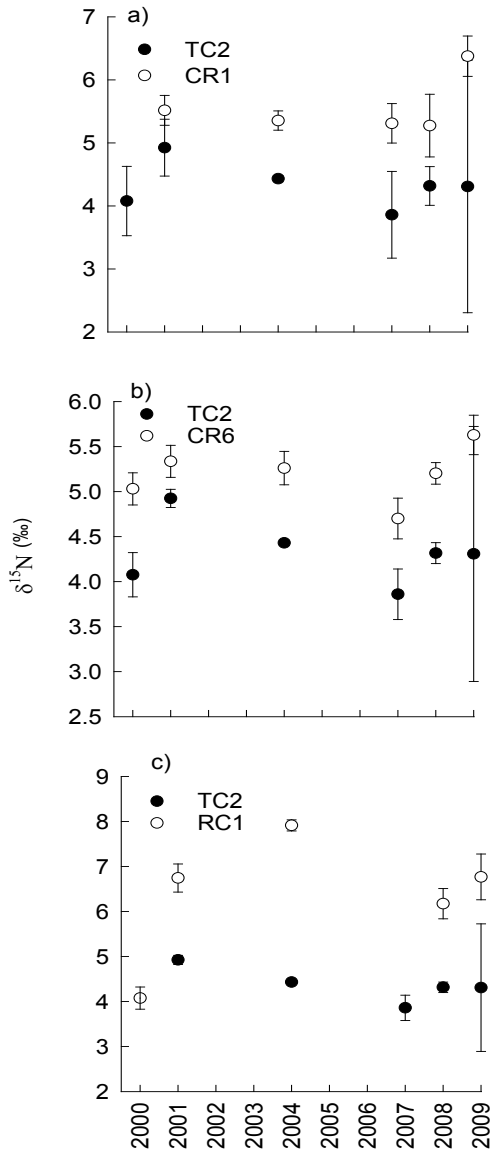


Figure 33. Mean (\pm 1se) $\delta^{15}\text{N}$ in large trout in a) CR1, b) CR6, and c) RC1 since 2000 relative to reach 2 of Taylor Creek (TC2), which was above a natural barrier to adult Pacific salmon.

Although there was little evidence for trends in isotopic values in resident fish over time with increasing biomass flux of adult Pacific salmon, a comparison of isotope levels averaged across the years before (2000, 2001) vs. after (2004, 2007, 2008, 2009) the ladder was installed showed significant differences in C^{13} and N^{15} for some species and reaches. For example, large trout from CR1 were more enriched in C^{13} after the ladder was installed than before (Figure 34a), as were sculpin and small trout (data not shown). There were no differences in fish isotope levels before vs. after the ladder at TC2.

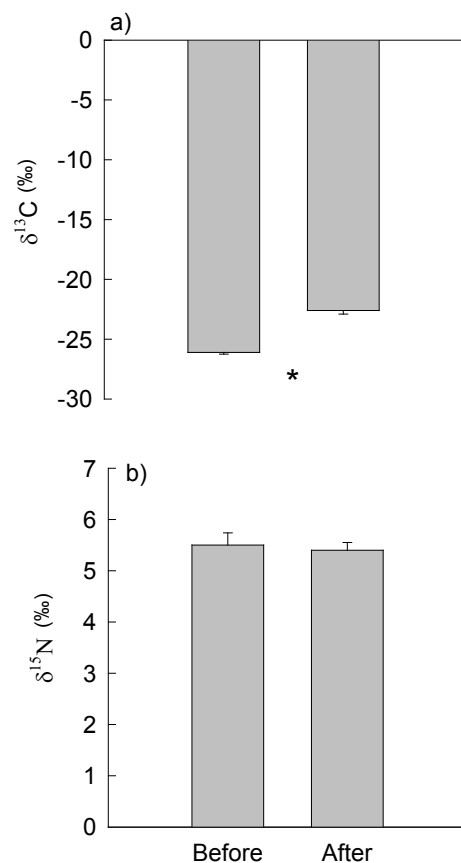


Figure 34. Mean (± 1 se) a) δC^{13} and b) N^{15} in large trout (> 90 mm) from reach CR1 of the main stem Cedar River. “Before” represents fish collected during 2000 and 2001 and “After” represents fish collected in 2004 and 2007-2009. Asterisk indicates a significant difference between means ($P < 0.05$).

Comparing N^{15} levels of fish collected in 2008 from below and above Landsburg Dam provided a different perspective on isotope levels as a function of anadromy (Figure 35a-35c). Specifically, anadromous fish have only recently returned to sites above Landsburg after about a 100-year absence, while sites below Landsburg (CRB) have experienced continual but fluctuating populations of anadromous fish. Sculpin collected from below Landsburg (CRB) had N^{15} values that were almost twice as high as those of sculpin collected from the main stem reach immediately above Landsburg Dam (CR1, the reach with highest cumulative number of adult salmon redds; Figure 29a), while sculpin from RC3 exhibited N^{15} levels similar to sculpin from CRB. A similar pattern was observed for small trout (≤ 90 mm), but only one individual was collected from below the dam (Figure 35b). Furthermore, large trout (>90 mm) from CRB had N^{15} levels that were two to three times higher than those of large trout above the dam (Figure 35c).

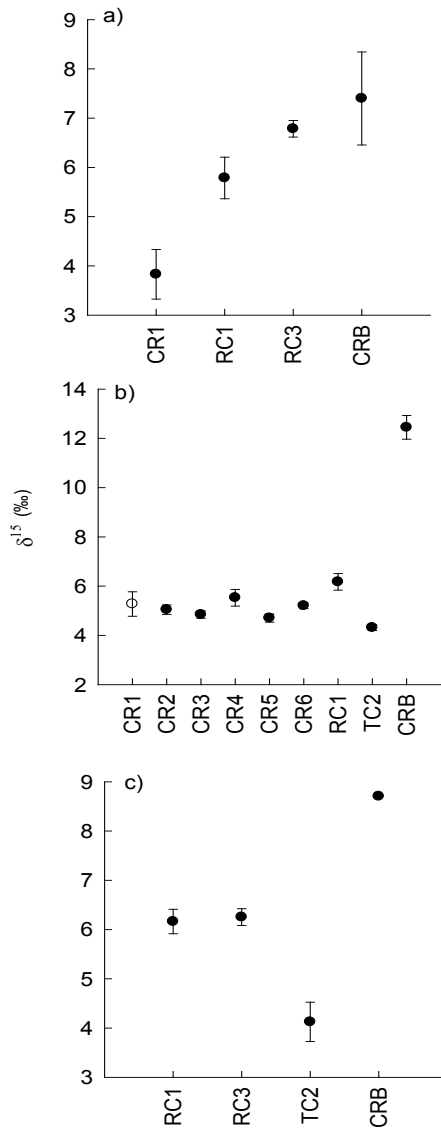


Figure 35. Mean levels of $\delta^{15}N$ in a) sculpin, b) small trout, and c) large trout collected in 2008. Cedar River reaches CR1-CR6 were above Landsburg Dam. Reach CRB was below the dam, where fish were collected by King County (Dr. Hans Berge, personal communication). Rock Creek reaches RC1 and RC3 were above the dam, and TC2 represents a reach in Taylor Creek above the dam and a natural barrier to adult Pacific salmon.

DISCUSSION

Recolonization by Juvenile Pacific Salmon

Density and Habitat Use

Among fish captured by electrofishing and hook and line angling on Rock Creek in 2008 and 2009, absolute and relative abundance and species composition remained similar to previous years, suggesting stable populations of most fish species. There were, however, some notable exceptions to this general pattern: in 2009, largemouth bass (2 individuals) were documented for the first time in Rock Creek, and juvenile coho salmon densities continued to increase relative to other species, exceeding cutthroat trout for the first time.

The presence of largemouth bass in Rock Creek was likely the result of a large flood event in January 2009 that led to the reconnection of Walsh Creek and Walsh Lake, which were previously known to contain bass, with Rock Creek enabling greater exchange of fish populations between the two watersheds. Densities of bass in 2009 in Rock Creek were too low to observe any ecological impacts on native species; however, it is unknown whether bass populations in Rock Creek will increase over time, potentially leading to negative ecological impacts on native species. At present, this risk appears to be relatively low in much of Rock Creek and the Cedar River, where habitat suitability, including temperature regimes, are suboptimal for warm-water species.

The trend of increasing juvenile coho densities in Rock Creek indicates continuing population growth above Landsburg Dam. The common obligate stream-rearing during the juvenile life stage, which is shared by coho salmon and trout and which includes overlaps in resource use, suggests an increasing potential for interference or exploitative competition between these species (Keeley 2001; Harvey et al. 2005; Rosenfeld et al. 2005). Consequent declines in cutthroat abundance or summer growth rates, however, have not been observed in Rock Creek, suggesting that interspecific resource competition with coho is not limiting trout growth or abundance. This may be due to sufficient habitat, resource partitioning between species (e.g. Bisson et al. 1988; Glova 1984), or population densities too low to observe negative density-related effects.

Ontogenetic shifts in microhabitat use by different age classes of cutthroat and coho, coupled with differences in mean size between the two species at a given age and time of year, may also reduce competition or mitigate density effects by aiding in habitat partitioning (McMichael and Pearsons 1998; Rosenfeld and Boss 2001). The ability to

make statistical inferences, either from seasonal growth patterns of coho and cutthroat trout during winter and spring in Rock Creek, or from seasonal and annual growth of rainbow trout in the Cedar River, was limited by small sample sizes and the resultant inability to control for factors like initial fish size. However, no obvious temporal trends were apparent.

Fish movements observed through remote PIT-tag detections and physical recaptures in 2008 and 2009 in Rock Creek were similar to those observed in previous years. The frequency of both upstream and downstream movement was highest for all species during fall, likely reflecting movement by juveniles both in and out of Rock Creek in search of overwintering habitat. Movement of coho salmon and trout was generally lowest during the low-flow period from late spring through summer: the lowest rates of upstream movement occurred in late spring/early summer, while the lowest rates of downstream movement occurred during late summer.

One notable exception to these patterns, which was consistent with previous years, was the high frequency of downstream movement by coho during May, which is the peak month of transition to the smolt stage for coho throughout the region. Additionally, the annual frequency of PIT-tag detections declined among all species as the distance from initial tagging location to the antenna array increased. This relationship was consistent between years, potentially indicating interannual stability in migration rates or survival.

Implementing PIT-tag technology in the Cedar River has allowed us to document several key findings. Perhaps the most important were habitat use, movement, growth, and survival of juvenile coho and trout. Despite the absence of significant use of Rock Creek by spawning coho until fall 2009, juvenile coho rapidly colonized this tributary and have continued to increase in abundance, density, and spatial distribution. The use and contribution of newly opened habitats is important to understanding how salmon populations respond to restoration actions.

An equally important finding was the absence of demonstrable negative impacts of salmon recolonization on extant trout populations. Although this result was not necessarily unexpected, it is important for resource managers contemplating the removal of migration barriers to aid Pacific salmon in areas where other important fish populations reside. Further deployment of PIT-tag monitoring systems across the watershed will allow us to gain critical information in the future on specific variables associated with growth, movement, and survival of all salmonids, and will allow us to better understand how populations respond to this large-scale restoration action.

With the planned restoration actions at the confluence of Walsh and Rock Creeks,

PIT tagging and remote detection antennas will continue to provide valuable information about the benefits of these restoration actions on fish survival and the continued growth and spatial expansion of colonizing salmon populations.

Trends in Community Structure

We observed relatively rapid changes in fish density and community structure following recolonization by Pacific salmon above Landsburg Dam. These changes reflect two of the unique life history traits of salmon that make them excellent colonizers: a small portion of fish that stray from natal habitats and high reproductive capacity. Coho salmon were mostly responsible for nearly the fourfold increase in total salmonid density by 2010 relative to before the ladder was installed; however, Chinook salmon, speckled dace, and whitefish also made small contributions to population and community level changes.

Before installation of the fish ladder, the salmonid population above Landsburg Dam was dominated by resident trout, with rainbow trout most abundant in the main stem Cedar River and cutthroat trout dominant in its tributaries (Riley et al. 2001). These distribution patterns were similar to those of other rivers in the region, where cutthroat trout tend to occupy small tributary or headwater streams and rainbow trout (or steelhead) are more commonly found in main stem areas or larger tributaries (e.g., Hartman and Gill 1968; Behnke 1992). Average trout density in the Cedar River prior to ladder installation was 0.06 fish/m², which fell at the low end of the range of trout densities reported in other studies in the Pacific Northwest (Riley et al. 2001).

Despite the fact that the Puget Sound region has much lower populations of Pacific salmon relative to Alaska or to historic conditions (e.g., Gresh et al. 2000), recolonization of the Cedar River above Landsburg Dam by coho and Chinook has led to a rapid increase in total salmonid density (including both trout and salmon). These changes in density were mostly due to coho salmon. Density increases were observed in the main stem Cedar River up to CR8, which is about 18 km upstream from Landsburg Dam. So far, we have observed salmon in the lower part of CR 9, but at low abundances and only in 2008 and 2009. This high-gradient, cascade reach also appears to be a partial barrier to Pacific salmon, as there have been no confirmed sightings of coho or Chinook in CR10.

The main stem reach with the largest change in coho salmonid abundance was CR1 followed by CR6, CR2, and CR4 (Figure 16). Relatively large increases in coho abundance in CR1 and CR2 supported the hypothesis that recolonization rates will be highest in habitats closest to the source population (i.e., below Landsburg Dam; Simberloff and Wilson 1969). However, distance from the source population did not

explain all of the observed spatial variation in recolonization rates, such as the large increases in coho abundance at CR6, which is about 10 km upstream from Landsburg Dam. These increases suggested that CR6 possesses productive fish habitat. Overall, these are relatively low-gradient reaches with side-channels and other habitat types that provide relatively high-quality habitats for both spawning and rearing for river-rearing salmonids (Rosenfeld et al. 2000, 2008; Burnett 2001).

Similar distribution patterns were observed in Rock Creek, where coho densities increased at a relatively high rate in reach RC1 (closest to main stem and dam) and RC3, but coho were observed in reach RC4 (furthest from main stem and dam) only as recently as spring 2009. The relatively low juvenile densities observed in RC4 were also likely a result of a culvert on the 41 road, which restricted upstream movement of adult and juvenile coho until 2009, when adult coho apparently spawned immediately above the culvert. This observation was based on the fact that young-of-the-year coho were observed in RC4 during the 2009 spring snorkel survey; these coho were not likely to have been able to swim from nest sites below the culvert. To date, no Pacific salmon have been observed in Rock Creek above the large wetland complex.

Although coho populations have been generally increasing since recolonization, juvenile Chinook densities have been more variable. Highest Chinook densities were observed in summer 2008 (0.015 fish/m²), which corresponded to the large number of adults returning in 2007. We predict that use of Rock Creek by Chinook will occur during years with large adult returns, similar to those observed in 2007, because of increased competition for spawning sites at CR1. Minimal use of Rock Creek by Chinook may be expected, given that surveys have occurred mostly during summer, when most juvenile Chinook have migrated to saltwater, and that Rock Creek is a relatively small system with flows that may restrict adult Chinook. However, these patterns partially reflect adult returns of Chinook, which have been more variable than those of coho.

Abundance estimates of Cedar River juvenile coho from snorkel surveys during the past few years suggest that the population may have reached a saturation point, and that some factor or factors may be limiting further population growth. For example, in CR1 and CR2, coho density has remained relatively stable since 2007 except for high density in 2008. We have a relatively short time-series, so these patterns can certainly change; however, factors that might constrain juvenile density include adult population size, predation, competition with resident fishes, food availability, or physical habitat (temperature, flow, or habitat complexity). There has been little evidence that predation by resident trout or sculpin is great enough to constrain salmon abundance (see below).

As mentioned above, our data showed little evidence that competition with

resident fishes has affected coho density or vice versa. Specifically, if competition with resident fish was occurring, it might be manifested by changes in abundance, growth, or survival, yet there has been little change in resident trout density in the main stem or Rock Creek as coho density increased. Although we have little quantitative evidence that competition or predation are affecting salmon, correlative analyses and experiments suggest that both habitat structure and prey availability might be constraining coho populations.

We consistently observed high densities of juvenile salmonids (trout, coho and Chinook) along margins of the main stem Cedar River that possessed downed wood or undercut banks. This observation was supported by the consistent (every year since 2005) positive correlation between summer juvenile coho density and wood or undercut banks (Table 10). Similar, but less consistent correlations were also observed for juvenile Chinook and resident trout. Correlations between wood and undercut banks and fish were evident during winter surveys as well. Taken together, these results suggest that juvenile salmonid abundance in the main stem Cedar River is limited by the quantity of river edge habitat that has either wood or undercut banks.

Many others have found salmonid abundance to be positively associated with wood cover (Roni and Quinn 2001; Rosenfeld et al. 2000; Solazzi et al. 2000; Pess et al. in press), although some have found no association (Spalding et al. 1995; Stewart et al. 2009). Previously, we noted much less downed wood in the Cedar River than in other similar-sized rivers in Western Washington (Fox and Bolton 2007); this is likely a result of the confined, relatively high-gradient morphology of the main stem. Low levels of instream wood in the main stem may also be a result of reductions in natural recruitment due to past logging and removal of downed wood to limit impacts on the Landsburg Diversion Dam during large floods. Overall, our findings suggest that increases in wood cover, especially along channel margins, will increase rearing habitat for juvenile salmonids.

In addition to strong evidence of habitat limitation in the Cedar River, we found multiple lines of evidence that food abundance constrains salmon populations. The first line of evidence was the strong correlation between invertebrate drift biomass or density and reach-scale total salmonid density (salmon + trout) in the main stem during summer 2007. Similar relationships have been observed for coho (e.g., Giannico 2000) and other fish species (e.g., Thompson et al. 2001). A second line of evidence was the positive association between juvenile coho growth rate during summer and reach-scale drift biomass after controlling for reach-scale salmonid density. The third line of evidence comes from the experimental stream study, where juvenile coho final mass and growth rate were positively correlated with biomass of drifting adult Chironomidae. Rosenfeld et al. (2005) also observed that juvenile coho growth rate was positively associated with

drift abundance in experimental channels. Thus, along with habitat complexity, limited prey availability might also be constraining juvenile fish populations.

Coho salmon have rapidly emerged as a dominant species in the Cedar River and Rock Creek. Juvenile coho abundance increased from about 40% of total summer salmonid density in 2004 to about 80% in 2009. Averaged across reaches, coho comprised about 70% of total salmonid abundance. Similar changes were observed in Rock Creek, where coho now comprise about 60% of total water-column fish density. Other, less dramatic changes in fish community composition were also observed. Although they make up a small proportion of total salmonid density, mountain whitefish has increased in abundance since 2004. Recently, speckled dace has increased in relative abundance in Rock Creek, especially in reaches RC3 and RC4. This may reflect the increased hydrologic connection between the Walsh Lake subbasin and Rock Creek following the 2009 winter floods.

Chinook salmon remains a relatively small, but consistent component of the overall fish community in the main stem; however, Chinook has been relatively rare in Rock Creek, and was observed only in 2007 and 2008. In addition, during summer 2009 we observed one Pacific lamprey and three large (ca. 600-700 mm) adult bull trout in the main stem in reach CR5. Their origin was unknown: the bull trout could have migrated up the fish ladder or could have been washed over the Chester Morse Dam during winter floods, while the lamprey most likely migrated through the fish ladder. An adult steelhead was also observed for the first time in the main stem during summer 2010. These observations suggest that the fish community is still in a state of flux, with new species being observed, but at extremely low abundances.

Despite the large and rapid increases in juvenile coho densities, we observed little evidence for change in resident trout populations in the mainstem Cedar River. This was in agreement with findings from Rock Creek. For example, in CR1, which has experienced some of the highest densities of juvenile coho, density of large trout (>90 mm) before ladder installation was estimated at ca. 0.02 fish/m², and as of 2010, density of this size class was virtually unchanged. We speculate that the relatively large and underutilized habitat in the Cedar River above Landsburg Dam allows for trout populations to coexist with Pacific salmon without negative impacts. In addition, trout and coho exhibit distinct morphological and ecological differences that allow them to exploit different habitat types. This was especially the case for large trout, which were most abundant in fast and deep-water habitat types (step pool, pools), whereas juvenile coho and Chinook were most abundant in depositional and side-channel habitats.

Ecosystem Studies

Carcass Analog and Small Wood Experiments

The experimental stream study clearly demonstrated the link between nutrients and energy provided by salmon carcass analogs, prey availability, and individual traits of juvenile coho. Increased growth of salmon appeared to have been a result of nutrient limitation at lower trophic levels: nitrogen and phosphorus concentrations in channels with salmon analogs were significantly higher than in control channels. Similar effects of adult salmon on water chemistry have been observed in other studies (e.g., Claeson et al. 2006; Tiegs et al. 2009).

In addition, we observed significantly higher benthic insect and drift biomass in streams with carcass analogs. Higher rates of insect drift were in turn strongly associated with coho growth rate and body mass. A number of studies have shown that body size is an important predictor of survival. For example, Pess et al. (in press) found that freshwater survival of juvenile coho in Rock Creek, a tributary to the Cedar River, was positively associated with body size. A unique aspect of our experimental study is that we observed salmon carcass effects at relatively low levels of biomass (0.6 kg/m^2); a meta-analysis of salmon impacts on freshwater ecosystems (i.e., water chemistry, algae, invertebrates, fish, and stable isotopes) found no effects at low biomass loading levels ($0.1\text{-}1.0 \text{ kg/m}^2$).

These results suggests that the main stem Cedar River is potentially nutrient limited, and that larger returns of adult salmon may alleviate this limitation, thereby increasing benthic production and food for drift-feeding fishes. Nitrogen:phosphorus (N:P) ratios suggest that the Cedar River and tributaries are primarily P-limited. Phosphorus is also of concern in terms of potential impacts on algal productivity in Youngs Lake, which is also P-limited. In a previous study conducted during fall/early winter, we found that salmon biomass loads up to 4 kg/m^2 had positive but relatively small effects on nutrient concentrations including P (Cram 2009).

Thus, the experimental results, combined with the positive associations between drift biomass and fish growth and density that we observed in the field, strongly suggest that increased prey availability can increase growth and body size of juvenile fishes, potentially leading to higher rates of ocean survival. Furthermore, these benefits can occur at relatively low biomass loadings of ca. 0.6 kg/m^2 , which are much higher than current loadings. Adult Chinook returns in 2007 were the highest to date, with the highest reach-scale salmon biomass loadings of 0.0066 kg/m^2 found in CR1 (based on redd surveys). This loading was approximately 91 times lower than the experimental loading rate of 0.6 kg/m^2 .

Adult Salmon Biomass Input

Installation of the fish ladder was followed by a relatively rapid recolonization of accessible habitat in the Cedar River and Rock Creek by coho and Chinook salmon. However, there was little quantitative evidence that current adult returns are large enough to elicit any sort of ecosystem effect. Adult salmon biomass inputs over Landsburg Dam have been increasing at rate of 468 kg/year, or 21 kg/km (there is 22 km of main stem habitat). However, these densities, on an areal basis, are orders of magnitude lower than those observed in western Washington streams with relatively large populations of coho or chum salmon (e.g., Honea 2006). For example, Volk (2004) estimated that Griffin Creek, a tributary to the Snoqualmie River, has an annual average input of coho salmon of around 1,355 kg/km, which is over 63 times greater than current annual adult inputs observed to the Cedar River main stem.

Diet Content Analysis

The number of fish that were sampled for diets over a 6-year period was large (1,263) and included a variety of size classes and species. Fish were able to consume other fish after attaining a size of 125 mm fork length, and this size was smaller than reported for salmonids by Keeley and Grant (2001). They reviewed a variety of studies that examined salmonid diets and reported that salmonids began eating fish at 270 mm in streams, 150 mm in lakes, and 80 mm in the ocean. The reason for the discrepancy between these findings and ours was unclear. On average, we found piscivory higher during 2000-2001 (3.5 ± 0.5 , $n = 2$) than during the years following installation of the fish ladder (1.4 ± 0.7 , $n = 4$), but this difference was not statistically significant. Of fish found in diet samples, 60% were salmonids (all trout) with sculpin making up the remaining 40%.

Carbon and Nitrogen Isotopes

Theoretically, because adult salmon are more enriched in the heavier isotopes of C and N relative to freshwater ecosystems, an increased flux of marine-derived nutrients from spawning salmon should lead to higher levels of C^{13} and N^{15} in the freshwater food web. Thus, these isotopes have been used in a number of studies to demonstrate the ecosystem effects that spawning salmon can have on aquatic and terrestrial ecosystems (Bilby et al. 1996; Chaloner and Wipfli 2002). However, in the present study, evidence of an ecosystem effect of salmon recolonization, as represented by changes in levels of C and N isotopes, was mixed.

Two lines of evidence suggested no ecosystem effect. First, when looking at all years of isotope sampling, there was no evidence of a temporal increase in stable isotope levels in fish or other organisms corresponding to increases in the flux of salmon-derived nutrients above the dam. Second, fish collected from the Cedar River below the dam, which has experienced continuous exposure to anadromous fish populations, were significantly more enriched in N^{15} and C^{13} relative to fish above the dam. Specifically, N^{15} levels in sculpin from below the dam were about two times higher than those in sculpin collected from CR1, where adult carcass inputs were highest (K. Burton, Seattle Public Utilities, unpublished data).

Evidence for a potential adult carcass effect was observed in the higher levels of C^{13} and N^{15} in some fish when averaging across years before vs. after fish ladder installation. These higher isotope values for years following installation of a fish passage facility may reflect a signal from salmon inputs or may have resulted from the high variability in isotope levels observed in 2009. Additional years of isotope data should clarify whether salmon are actually affecting ecosystem processes.

Although temporal patterns in C and N isotopes were mixed, there were clear and consistent spatial differences. Specifically, organisms collected in Rock Creek were more enriched in N^{15} relative to sites on the main stem or reach TC2 of Taylor Creek. In some cases, isotope levels in organisms collected from Rock Creek were similar to those measured in streams with continuous exposure to anadromous fish populations (e.g., in the Cedar River Basin). This result was intriguing because these differences were apparent before salmon recolonized the Cedar River above Landsburg Dam.

It has been shown in Alaska that channel geomorphology can affect isotope levels through the process of denitrification. Specifically, isotope levels in low-gradient channels with abundant wetlands and no salmon can mimic isotope levels observed in salmon-spawning streams because of high rates of denitrification (Pinay et al. 2003). Rock Creek is a relatively low-gradient channel with a large wetland complex located approximately 4 km upstream from its confluence with the Cedar River. Therefore, the relatively high N^{15} levels measured in fish and other organisms in lower Rock Creek may have resulted from high rates of denitrification in this wetland complex.

In addition, isotope levels in stream biota from Taylor Creek reach TC2 were lower than those from main stem Cedar River or Rock Creek sites. The reasons behind this difference were not clear; however, we hypothesize that lower isotope levels at TC2 were partially a result of a "salmon legacy." Before the construction of Landsburg Dam, anadromous salmonids had access to all main stem habitat up to Cedar Falls (a natural migration barrier) as well as Rock Creek, the Walsh Lake subbasin, and the lower 200 m of Taylor Creek. TC2 is above a natural migration barrier for salmon; thus, higher

isotope levels in biota from main stem sites relative to TC2 may be partially a result of the historical legacy of salmon that spawned in main stem sites but were absent from TC2.

Overall, these data suggested relatively low rates of piscivory, but rates may be higher in spring as alevin emerge from the gravel to initiate feeding. Fish sampled in spring at Landsburg Dam ($n = 40$) had consumed aquatic insects, but none had consumed fish. Tabor et al. (2004) examined the diets of 599 fish (445 cottids, 154 trout) from the Cedar River below Landsburg Dam from January to April and found that 1.3% contained juvenile Chinook. Using bioenergetic models, they estimated that this consumption rate would lead to the loss of 24,000 juvenile Chinook or 27% of the run in 2000. Tabor et al. (2004) also examined historical diet studies and found that of 4,346 fish sampled 0.3% contained juvenile Chinook. Both of these values fall within the range we observed.

Isotopic data suggested that the influx of nutrients and energy from marine sources (i.e., salmon flesh, eggs, juveniles or via bottom-up processes) to resident fish above Landsburg Dam was minimal. Isotope levels in fish reflect what they have eaten over the previous months, while diet samples reflect only a snapshot of consumption. Therefore, the combination of diet and isotopic analyses suggested that resident fish in the Cedar River were consuming low amounts of energy or nutrients derived from marine or salmon sources.

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APPENDIX

Study Summary

This multi-year study, with the generous support of Seattle Public Utilities, the Cedar River Anadromous Fish Commission, and the National Marine Fisheries Service, has provided substantial insight into the response of coho and Chinook salmon, and other fish species to installation of the Landsburg Dam fish ladder. In addition, we have gained knowledge of the ecological requirements of resident and anadromous salmonids in the upper Cedar River watershed. Finally, this work has highlighted the importance of salmon on the resident ecosystem. Appendix Table 1 provides a detailed list of activities across the life of the study.

Some major accomplishments and findings include the following:

- 1) Documented coho colonization of Rock Creek, the Walsh Lake subbasin and the main stem Cedar River, and colonization of Rock Creek and the main stem by Chinook salmon
- 2) Quantified habitat variables associated with fish abundance, growth and survival at the habitat unit and reach scale
- 3) Documented anadromy in *O. mykiss* including the presence of an adult steelhead in summer 2010
- 4) Documented the presence of bull trout (*Salvelinus confluentus*) and Pacific lamprey (*Lampetra tridentate*) in the main stem Cedar River during summer 2009
- 5) Documented the presence of large-mouth bass (*Micropterus salmoides*) in Rock Creek during summer 2009 and 2010
- 6) Completed a second experiment on the effects of salmon carcasses on the Cedar River food web
- 7) Completed four M.S. theses and one Ph.D. dissertation, with one M. S. and Ph.D. in progress
- 8) Submitted and published the following manuscripts:
 - i. Anderson, J., P. Kiffney, G. Pess, and T. Quinn. 2008. Distribution and growth of juvenile coho salmon (*Oncorhynchus kisutch*) during colonization of newly accessible habitat. Transactions of the American Fisheries Society 137: 722-781.

- ii. Kiffney, P.M., G. Pess, J. Anderson, P. Faulds, K. Burton and S. Riley. 2009. Changes in fish communities following recolonization of the Cedar River, WA, USA by Pacific salmon after 103 years of local extirpation. *River Research and Applications* 25: 438-452.
 - iii. Kiffney, P.M., G. Pess, J. Anderson, P. Faulds, K. Burton and S. Riley. 2009. Changes in fish communities following recolonization of the Cedar River, WA, USA by Pacific salmon after 103 years of local extirpation. *River Research and Applications* 25: 438-452.
 - iv. Pess et al.. In press. The influence of body size, habitat quality, and competition on the movement and survival of juvenile coho salmon during the early stages of stream re-colonization. *Transactions of the American Fisheries Society*
 - v. Cram et al. (submitted) Effects of salmon loading during fall and winter on Cedar River food webs. *Hydrobiologia*.
- 9) Presented numerous talks at local and national meetings on the recolonization study
- 10) Submitted proposals to the Environmental Protection Agencies Puget Sound Technical Investigations (February 2010) and the National Science Foundation's Long-term research in biology program (July 2010)

Appendix Table 1. Summary of sample categories and type, years and locations for the Cedar River salmon recolonization project from 2000-2009. Abbreviations: CR = the main stem Cedar R from Cedar Falls to above Landsburg Dam (Figure 1); RC = Rock Creek from confluence with main stem to Kerriston Road; WC = confluence of main stem to 500 m upstream confluence; TC = confluence to USGS flow gauge; LRC = Rock Creek below Landsburg Dam to about 100 m upstream; LCR = about 500 to 1000 m below Landsburg Dam on main stem Cedar River.

Category	Sample type	Years sampled	Streams sampled
Water temperature	Point measurements	November 2000 to October 2005 May 2005 to June 2006	CR, RC, WC, TC
	Continuous measurements	October 2007 to August 2009 January 2000 to December 2001; November 2004-October 2005; October 2007, December 2007	CR, RC, TC
Water chemistry Habitat	Grab samples	Summer 2000, 2001, 2005-2010; Summer 2000-2002, 2004-2010; Fall 2004-2010 (tributaries only); Winter 2007-2009	CR, RC, WC, TC
	Surveys	Spring 2005-2010; Fall 2004-2010; Summer 2005-2010	CR, RC
Fish populations	Snorkel surveys	October 2000-2001; October 2004; June, July, and October 2007-2009	CR, RC, WC, TC, LRC (2007-2009), LCR (2007-2009)
	Mark-recapture	July 2005, 2007 and 2008 (not processed) June 2009 (tributaries only, not processed)	RC, CR (summer 2007-2009)
Diet	Gastric lavage and fish mortalities	October 2000-2001, 2004, 2007, 2009	CR, RC, TC
Drift	Drift nets	October 2000-2001, 2004, 2007, 2009	CR, RC, TC, WC
Isotopes	Riparian plants	October 2000-2001, 2004, 2007, 2009	CR, RC, TC, LCR (2007), LRC (2007, 2009)
	Biofilm	October 2000-2001, 2004, 2007, 2009	CR, RC, TC, LCR (2007), LRC (2007, 2009)
	Aquatic invertebrates Fish	October 2000-2001, 2004, 2007, 2009 October 2000-2001, 2004, 2007-2009	CR, RC, TC, LCR (2007), LRC (2007, 2009) CR, RC, TC, LCR (2008)