This article was downloaded by: [National Forest Service Library] On: 11 December 2013, At: 10:22 Publisher: Taylor & Francis Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information: <u>http://www.tandfonline.com/loi/utaf20</u>

## Riverscape Patterns among Years of Juvenile Coho Salmon in Midcoastal Oregon: Implications for Conservation

R. Flitcroft <sup>a</sup> , K. Burnett <sup>a</sup> , J. Snyder <sup>b</sup> , G. Reeves <sup>a</sup> & L. Ganio <sup>c</sup>

 $^{\rm a}$  U.S. Department of Agriculture Forest Service Research Lab , 3200 Jefferson Way Southwest , Corvallis , Oregon , 97331-8550 , USA

<sup>b</sup> Department of Biology, Western Oregon University, 345 North Monmouth Avenue, Monmouth, Oregon, 97361, USA

<sup>c</sup> Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, Oregon, 97331, USA Published online: 11 Dec 2013.

To cite this article: R. Flitcroft, K. Burnett, J. Snyder, G. Reeves & L. Ganio (2014) Riverscape Patterns among Years of Juvenile Coho Salmon in Midcoastal Oregon: Implications for Conservation, Transactions of the American Fisheries Society, 143:1, 26-38

To link to this article: <u>http://dx.doi.org/10.1080/00028487.2013.824923</u>

#### PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <a href="http://www.tandfonline.com/page/terms-and-conditions">http://www.tandfonline.com/page/terms-and-conditions</a>

#### ARTICLE

### **Riverscape Patterns among Years of Juvenile Coho Salmon** in Midcoastal Oregon: Implications for Conservation

#### **R. Flitcroft\* and K. Burnett**

U.S. Department of Agriculture Forest Service Research Lab, 3200 Jefferson Way Southwest, Corvallis, Oregon 97331-8550, USA

#### J. Snyder

Department of Biology, Western Oregon University, 345 North Monmouth Avenue, Monmouth, Oregon 97361, USA

#### G. Reeves

U.S. Department of Agriculture Forest Service Research Lab, 3200 Jefferson Way Southwest, Corvallis, Oregon 97331-8550, USA

#### L. Ganio

Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, Oregon 97331, USA

#### Abstract

Patterns of salmon distribution throughout a riverscape may be expected to change over time in response to environmental conditions and population sizes. Changing patterns of use, including identification of consistently occupied locations, are informative for conservation and recovery planning. We explored interannual patterns of distribution by juvenile Coho Salmon *Oncorhynchus kisutch* in 11 subbasins on the midcoast of Oregon. We found that juvenile Coho Salmon distribution expanded and contracted around stream sections that were continuously occupied (core areas). Timing of expansion or contraction was synchronous among subbasins and appeared to be related to the size of the parental spawning run. Juvenile distribution expanded from core areas when adults were abundant and contracted into core areas at lower adult abundances. The "intrinsic potential" of stream sections to support high quality habitat for Coho Salmon also appeared to inform distribution patterns. In most subbasins, when populations expanded, they moved into areas of high intrinsic potential. We identified areas that were consistently used by juvenile Coho Salmon which may be important target locations for conservation and restoration. Our study contributes to the body of work that seeks to explain the processes behind spatial and temporal patterns of freshwater habitat use by salmonids in the Pacific Northwest, thereby enhancing understanding of the complexity of biological and environmental interactions over broad scales.

Knowledge of habitat use by juvenile salmonids is generally based on investigations that focus on sample sites at scales of habitat units (tens of meters) or stream reaches (perhaps hundreds of meters). These fine-scale approaches effectively identify habitat characteristics amenable for different life stages of salmonids (Quinn and Peterson 1996) and establish seasonal site fidelity and movement characteristics of juveniles (Nickelson et al. 1992; Bell et al. 2001). However, in recent years, a call for broad-scale analysis that explores riverscape-scale processes and patterns has been echoed by aquatic ecologists (Fausch et al. 2002; Wiens 2002). Analysis at the riverscape scale allows for exploration of processes that function at broad

<sup>\*</sup>Corresponding author: rflitcroft@fs.fed.us

Received April 25, 2013; accepted July 2, 2013

scales that may help explain patterns observed at fine scales. This reflects the data input at riverscape scales that is meant to be fairly continuous, or comprehensive, throughout all stream sections in a chosen watershed.

Patterns at one spatial scale may not translate into the same pattern at a different spatial scale (Wiens 1989; Fukushima 2001). Habitat occupancy by juvenile salmonids at microsite and reach scales is not random. Rather, habitat use at these fine scales has been shown to be related to season of the year (Nickelson et al. 1992), locations of habitat forming features (Montgomery et al. 1996; Benda et al. 2004), and proximity among seasonal habitats (Flitcroft et al. 2012). Much work has been done in aquatic systems to model and understand the geomorphic processes of stream habitat creation (Beechie and Sibley 1997), distribution (Benda et al. 1998, 2004; Burnett et al. 2007), and the effect of human uses on the availability, diversity, and quality of stream habitat (Wang et al. 1997; Fausch et al. 2002). Due to predictable patterns of geomorphology and hydrology, recent models of salmonid habitat characteristics have been developed at watershed scales (Benda et al. 2007). The question arises as to whether this predictability is also found in patterns of juvenile fish distribution at riverscape scales, and whether broad-scale habitat use patterns change over time.

The riverscape template of salmonid habitat types and quality associated with geomorphology and underlying geology may not be the only influence on interannual patterns of fish distribution. Other factors also may be important in explaining interannual distribution patterns of juvenile salmonids at riverscape scales. These may include population density (Grant and Kramer 1990), hydrologic regime (Poff et al. 1997), or location of spawning parents (Einum et al. 2008). However, little work examining interannual patterns of juvenile salmonids at riverscape scales has been completed. At subbasin and basin scales, ecological investigation often focuses on habitat or geomorphic associations with fish occurrence because inventories of the species of interest are time consuming or unavailable (Fausch et al. 2002; McMillan et al. 2013).

Analysis of riverscape-scale patterns of stream occupancy by juvenile salmon over time may advance our understanding of the forces that drive habitat use at watershed scales. We address this issue by comparing subbasin-scale distribution patterns of juvenile Coho Salmon *Oncorhynchus kisutch* in western Oregon across multiple years. Coho Salmon are broadly distributed across the coastal-draining stream systems in the Pacific Northwest (Sandercock 2003). Although juvenile Coho Salmon may move during any time of the year (Kahler et al. 2001; Ebersole et al. 2006, 2009; Pess et al. 2011; Reeves et al. 2011), summer distributions are important because juveniles are assumed to move least during this season (Nickelson et al. 1992). Therefore, summer surveys were used to assess variation of interannual distribution.

We focused on three specific research questions: (1) are there differences in the extent of juvenile Coho Salmon distribution among 4 years within river systems in midcoastal Oregon; (2) are juvenile Coho Salmon patterns of interannual distribution throughout stream networks centered on consistently used sections of stream, or core areas; and (3) does the intrinsic potential of a stream to support Coho Salmon inform interannual patterns of juvenile distribution. We examined a variety of potentially correlated factors that may influence interannual summer distribution by juvenile Coho Salmon, including the size of parental spawning runs, seasonal streamflow, patchiness of juvenile Coho Salmon density, and subbasin size.

#### **METHODS**

*Study site.*—Interannual distribution patterns of juvenile Coho Salmon were determined in 11 subbasins of the Alsea and Siletz River basins (1,785 and 1,964 km<sup>2</sup>, respectively), in the mid-Oregon Coast Range (Figure 1; Table 1). Both the Alsea

TABLE 1. Interannual variation in distribution patterns of juvenile Coho Salmon documented in 11 subbasins located on the mid-Oregon coast. Stream length used is the total number of stream kilometers where juvenile Coho Salmon were observed throughout the entire subbasin (no entry indicates no survey).

			Stream length used (km)			
Subbasin	Basin	Area (km <sup>2</sup> )	1998	1999	2001	2002
Canal Creek	Alsea River	33.0	12.7		15.6	19.5
Cedar Creek	Siletz River	33.4		4.4	18.7	18.8
Sams Creek	Siletz River	37.7		25.2	25.4	28.9
Fall Creek	Alsea River	71.8	19.3		17.9	19.1
North Fork (NF) Alsea River	Alsea River	73.5	31.5		31.8	33.8
Sunshine Creek	Siletz River	77.0	15.6	12	18.6	15.4
Upper Drift Creek	Alsea River	79.7		35.5	37.8	42.7
Rock Creek	Siletz River	104.7	21.1	21.2	38	41.8
Lobster Creek	Alsea River	143.7	49.1	49.5	65.8	70.7
SF Alsea River	Alsea River	158.8	22.3		34.4	34.4
Five Rivers	Alsea River	300.0	74.9		89	108
Average across all subbasins		30.8	24.6	35.7	39.4	



FIGURE 1. Subbasins selected for analysis of the distribution of juvenile Coho Salmon in the midcoast of Oregon between 1998 and 2002.

and Siletz River basins are in the vegetation zone for western hemlock *Tsuga heterophylla* (Franklin and Dyrness 1988). Fire (Spies et al. 1988), timber harvest (Kennedy and Spies 2004; Wimberly and Ohmann 2004), and agricultural uses have modified the landscape (Nonaka and Spies 2005). The geology of the Siletz River is principally volcanic, while the Alsea River is characterized by sandstone (Madin 2009). The climate of this area is mild maritime; rain is the dominant form of precipitation, occurring primarily during the winter (Redmond and Taylor 1997).

Juvenile Coho Salmon data.-To assess annual distribution, locations of juvenile Coho Salmon for the years 1998, 1999, 2001, and 2002 were compiled from snorkel surveys conducted by the MidCoast Watershed Council, Newport, Oregon. Not all 11 subbasins were surveyed in every year (Table 1), but all subbasins had survey information for at least 3 of 4 years analyzed. Surveys from 2000 were not used because accurate field maps necessary for georeferencing the data were unavailable. Every fifth pool was snorkeled, and all observed fish were counted in one pass. Pool length and width were recorded to facilitate calculation of fish density. Other habitat types such as riffles were not sampled because Coho Salmon are known to occur predominantly in pools in this region (Nickelson et al. 1992). Surveys were conducted from the stream mouth upstream, and included all tributaries thought to be used by rearing juvenile Coho Salmon during the summer field season (June through September). Surveys were ended when crews observed no juvenile Coho Salmon for five snorkeled pools. This distance was meant to approximate a stream reach beyond which it is unlikely juvenile Coho Salmon would be found. Therefore, this end point was interpreted to be the end of juvenile Coho Salmon distribution for a given year.

We georeferenced the snorkel survey data to facilitate calculation of metrics to describe how much of the stream system was occupied by juvenile Coho Salmon in a given year. The juvenile snorkel survey data set was attached to digital hydrography using the Arc Info dynamic segmentation protocol (ESRI 2006). The digital hydrography for the Alsea and Siletz River basins was generated from 10-m digital elevation models (DEMs; Miller 2003; Clarke et al. 2008) and obtained for this study from the data set available for all streams in western Oregon (http://www.fsl.orst.edu/clams/). Control points located approximately every 0.5 km were the basis for spatially referencing the surveys to the digital data set. The start of the survey and the end point of the survey were of critical importance for the interpretation of areas of use. Therefore, end points were referenced with great detail to promote the greatest accuracy. However, we anticipate that some error in the identification of the end point may be present in the georeferenced data set. This error is associated with crew misidentification of location or the spatial inaccuracy of the DEMs. We were unable to quantify this error for our analysis.

Interannual distribution of juvenile Coho Salmon: differences among years in area used.—Maps of juvenile Coho Salmon distribution were created that display distributions of fish in the streams for each year. The upstream end of juvenile Coho Salmon presence for all surveyed streams was the basis for calculating the total number of stream kilometers used per year, per subbasin. Summary information was collected to a tenth of a kilometer in resolution, reflecting the accuracy of field measurements and the accuracy of the spatial linework. Error in geospatial location in the field or in the georeferencing was certainly present in our data set. However, quantification of that error was not possible. Therefore, we chose to summarize the distance measures at the fairly coarse resolution of one tenth of a kilometer.

In the four largest subbasins (Rock Creek, Lobster Creek, South Fork [SF] Alsea, and Five Rivers), juvenile Coho Salmon were not observed throughout the main stem in 1998 and 1999. In these subbasins, we identified the start of summer stream occupancy by the presence of juvenile Coho Salmon in the main stem. In all other subbasins, in all other years, juvenile Coho Salmon were observed starting at the stream mouth. The distribution of juvenile Coho Salmon was continuous among surveyed pools for most years. However, occasionally, a pool would be surveyed that did not contain juvenile Coho Salmon. Such a pool was included in length of stream used by juvenile Coho Salmon if juvenile Coho Salmon were documented both upstream and downstream of the pool.

To test whether the mean length of stream used by juvenile Coho Salmon averaged over subbasins differed among years, an unbalanced repeated-measures ANOVA was conducted (SAS 2003). In this test, data from different subbasins are assumed to be independent, but data from each subbasin are assumed to be correlated through time. Therefore, subbasin forms the unit of replication. Given the multiple comparisons, significance was determined from a Bonferroni-corrected alpha ( $\alpha = 0.0125$ ). Differences between pairs of years among subbasins in the mean annual distribution length (km) for juvenile Coho Salmon was described by Tukey–Kramer multiple-comparison tests (SAS 2003).

Adult Coho Salmon.-Variation in juvenile Coho Salmon distribution may be influenced by the abundance of spawners in the previous year. Annual basin-scale estimates of spawning Coho Salmon abundance were available for the Alsea and Siletz River from the Oregon Department of Fish and Wildlife's Salmonid Survey Program (http://oregonstate. edu/dept/ODFW/spawn/index.htm). These estimates were based on spawning ground surveys of sites selected using a spatially distributed, probability-based survey protocol. Spawning survey locations were regularly revisited by field crews during the spawning season to count spawning fish and redds (Jacobs and Nickelson 1998). In all years except 1997, the number of spawning fish, regardless of origin (wild or hatchery), were estimated. Only estimates of the number of wild spawning fish were available from the 1997 spawning season (effectively parents of 1998 summer juveniles). Wild fish were identified by the absence of hatchery identification markings (adipose or maxillary clip) or PIT tags.

As the number of spawning Coho Salmon increases, the density of fish on the spawning grounds would also increase, potentially encouraging individuals to occupy other spawning habitat locations. This density-dependent relationship may influence the observed use of stream habitat by juvenile Coho Salmon. The finest resolution available of adult spawning run sizes is the basin. Therefore, we plotted the number of spawning Coho Salmon with the average number of kilometer of stream occupied by their progeny the following summer.

Movement of adult Coho Salmon into freshwater to spawn is associated with adaptation to seasonal flow regime (Sandercock 2003). In Oregon, the timing of the Coho Salmon run is associated with fall precipitation events (Weitkamp et al. 1995) that increase streamflow levels, allowing adults access to upstream habitats. It is possible that high flow levels may allow adults access to reaches located further in the stream network to spawn than low flow levels. This may affect the observed distribution of juveniles the following summer. The months of October through March encompassed all documented spawning in either the Alsea or Siletz basins during our study period (1997–2001). Average monthly streamflow data were available at the basin scale for the Siletz and Alsea River basins. This information was acquired from the U.S. Geological Survey Water Resources of Oregon (http://waterdata.usgs.gov/or/nwis/monthly?). We graphed the estimated size of the spawning run with streamflow during the run for the Alsea and Siletz basins.

*Core areas.*—Core stream areas were identified as the contiguous portion of the surveyed stream in each subbasin that was used in every year. This allowed us to describe and compare interannual variation of the proportion of stream kilometers used that were within the core area and outside the core area over the sample period. We were also interested in the location of core areas within the river network and how core areas may be related to groupings of juvenile Coho Salmon.

The term "patch" is generally used to describe areas of similar habitat or landscape (Clark 2010). In this project, rather than habitat, we were interested in the length of groups of juvenile Coho Salmon and refer to this as a patch. We were interested in whether patches were of similar sizes among subbasins and among years within subbasins. We quantified the patch size of juvenile Coho Salmon by analyzing patterns of spatial autocorrelation in the density of juvenile Coho Salmon at each snorkeled pool. This was done by generating variograms, designed for stream networks, for each subbasin and each year (Ganio et al. 2005).

Before calculating the variograms, we removed the relationship of fish density with distance between its location and the stream mouth in order to meet the assumptions of a stationary process. We did this by regressing fish density on the distance and obtaining the estimated residuals to use in the variogram calculation. The robust variograms allow for the estimation of the interval (estimated variogram range) in which survey points exhibit spatial autocorrelation, in this case due to the density of fish. Because the range was estimated, it included an unquantifiable amount of error. Therefore, no statistical tests were completed using this metric as a dependent variable, and we summarized the results qualitatively.

Habitat intrinsic potential: delineating areas of high intrinsic potential.—Fish distribution data were collected without accompanying data describing habitat quality of the channel. Therefore, we used intrinsic potential (IP; Burnett et al. 2007) when examining interannual patterns of juvenile Coho Salmon distribution. Intrinsic potential describes the capacity of streams to provide rearing habitat for Coho Salmon and was modeled from mean annual streamflow, valley constraint, and channel gradient in conjunction with the hydrography for the Alsea and Siletz River basins (Burnett et al. 2007; Clarke et al. 2008). Values of intrinsic potential can range from 0 to 1. We measured the annual length of stream classified as high (>0.75) IP and calculated the percentage of available juvenile Coho Salmon habitat within a subbasin that was high IP using a geographic information system (ESRI 2006) and digital hydrography. Available juvenile Coho Salmon habitat was conservatively defined as all the stream length in a subbasin below a gradient of 7% (Burnett et al. 2007).

Comparing juvenile Coho Salmon habitat potential between the Alsea and Siletz basins.—The Alsea and Siletz basins differ by geology, which has been shown to influence the development of stream habitat types in the Oregon Coast Range (Hicks and Hall 2003). Before we could compare among all subbasins in the Alsea and the Siletz, we attempted to detect differences in mean intrinsic potential for juvenile Coho Salmon between these two basins that may influence fish distribution. We compared (*t*-tests) the mean length of streams with a high IP designation per subbasin, between the Alsea and Siletz basins. We also compared (*t*-tests) the mean percent of available juvenile Coho Salmon habitat in high IP per subbasin between subbasins in the Alsea and Siletz basins.

Comparing juvenile Coho Salmon habitat potential among all subbasins—We anticipated that in years when fewer stream kilometers were occupied, a higher proportion of occupied areas would have a high IP than in years when more stream kilometers were occupied. Hence, we predicted IP might be related to core area usage. Annual summaries were made in each subbasin of the length of occupied stream with high IP, the percent of occupied habitat with high IP, and the percent of high IP habitat occupied. To provide context for comparisons among subbasins, we also summarized the total percent of all juvenile Coho Salmon habitat within a subbasin with high IP and the number of stream kilometers with high IP. We also calculated Ivlev's electivity values for each year (Ivlev 1961). While alternative indices are available (e.g., Manly et al. 1993), this metric was chosen for its simplicity and compatibility with our data set given that areas of high IP are not rare in any study subbasin and that the amounts are constant over time. Therefore, we used Ivlev's electivity values to compare the amount of high IP used with the total length of high IP that is available using

$$E = \frac{r - p}{r + p}$$

where r is the percentage of habitat used with high IP and p is the percentage of high IP among all habitat throughout the watershed.

#### RESULTS

#### Interannual Distribution of Juvenile Coho Salmon

Stream lengths used by juvenile Coho Salmon in subbasins varied among years from 4.4 to 108 km, with interannual variation in a single subbasin spanning over 20 km (Table 1). Unbalanced repeated-measures ANOVA results supported this observation and indicated significant differences among years in the mean annual stream length used (P < 0.001 with 22 df for each year [1998, 1999, 2001, and 2002]). Tukey–Kramer multiple-comparison tests indicated that the mean for the length of stream used differed in each of the six pairwise year comparisons except between 1998 and 1999 and between 2001 and 2002 (Table 2).

A density-dependent relationship may exist between the size of the adult Coho Salmon spawning population and the number of spawning sites that are occupied. This may, in turn affect the number of stream kilometers used by juvenile Coho Salmon the following summer. Because comprehensive surveys of spawning Coho Salmon were unavailable, we plotted the size of the spawning Coho Salmon population with the average number of stream kilometers used in the Alsea and Siletz basins, respectively (Figure 2). In the Alsea basin, as the size of the spawning population of Coho Salmon increased, so did the average number of stream kilometers used by juvenile fish the following summer. In the Siletz basin the relationship was weaker; however, more stream kilometers were used by juvenile Coho Salmon in 2001 and 2002 than in 1998 or 1999.

The number of spawning adults and available streamflow during spawning may affect the habitats adults can access, thereby influencing the distribution of juveniles observed in the following summer. Interannual counts of wild spawning Coho Salmon varied over time in the Alsea and Siletz basins (Figure 3). The number of spawning adult Coho Salmon in the Alsea increased between 1997 (parents of juvenile fish observed in summer

TABLE 2. Tukey–Kramer multiple-comparison tests for differences between years in the mean subbasin length (km) of stream used by juvenile Coho Salmon in 11 subbasins located on the mid-Oregon coast. Each comparison has 22 df, and a blank indicates that this comparison was not made (for instance, 1998 was compared with 1999, but the reverse comparison is redundant and not presented).

	(Differ	Tukey–Kramer a rences in juvenile Coho Salmon me	djusted P-value can stream length used [km] $\pm$ 95%	% CI)
	1998	1999	2001	2002
1998		$0.78(-2.42 \pm 5.27)$	$0.05 (6.37 \pm 4.75)$	$0.01~(10.02~\pm~6.04)$
1999			$<0.01~(8.79~\pm~4.50)$	$<0.01~(12.44~\pm~5.87)$
2001				$0.22 (3.65 \pm 3.80)$



FIGURE 2. Estimated run size of spawning Coho Salmon in the Alsea or Siletz basins, plotted against the average stream kilometers used by their progeny the following summer.

1998) and 2001 (parents of juvenile fish observed in summer 2002). The Siletz also saw lower numbers of spawning fish in 1997 and 1998 than in 2000 and 2001. Streamflow during spawning in both basins was considerably lower during October 2000 through March 2001 than in the period of highest streamflow during the spawning run, October 1997 through March 1998 (Figure 3).

#### **Core Areas**

Delineation of areas that were used by juvenile Coho Salmon during all of the survey years juxtaposed with areas used only



FIGURE 3. Spawning run size of Coho Salmon in the Alsea and Siletz River basins compared with streamflow during parental spawning season (October through March).

occasionally support the concept of core areas (Figure 4). We quantified the stream length inside and outside the core area, for each year in each subbasin (Table 3). Core areas comprised the majority of stream lengths used in all subbasins except Cedar and Rock creeks in 2001 and 2002. Further, in years when fewer stream kilometers were occupied, more occupied length centered in the core than in years when more stream length was used. Likewise, variability in the percent of stream length used outside the core was greatest in 2001 and 2002, when more of the stream was used.

Variogram range sizes, used to suggest patch sizes, varied within subbasins among years and were more variable in larger subbasins than smaller ones (Figure 5). In addition, the estimated variogram range size appears to be smaller in small subbasins compared with larger subbasins.

#### Habitat Intrinsic Potential

Although the Alsea and Siletz basins have different underlying geologies that may influence habitat suitability, neither the mean total quantity (km) of stream length with a high IP designation ( $T_9 = 0.363$ ; *P*-value = 0.72) nor the mean percent of available juvenile Coho Salmon habitat in high IP ( $T_9 =$ 0.853; *P*-value = 0.42) differed between the basins. Thus, all subsequent comparisons are among subbasins.

To explore our interest in the connection between areas with the capacity to support highly suitable habitat and stream occupancy, we summarized fish use of high IP areas over time. The shortest length of habitat used with a rating of high IP occurred in either 1998 or 1999 for all subbasins (Table 4). This is consistent with the shortest length of stream used for all subbasins, which occurred in either 1998 or 1999 (Table 1). Subbasins varied in the percent of all habitat used with a designation of high IP; the highest percent was in either in 1998 or 1999 for seven subbasins (Canal Creek, Cedar Creek, Sunshine Creek, Upper Drift Creek, Rock Creek, Lobster Creek, and Five Rivers; Table 5). Lowest length of stream occupied in high IP and the highest percent of habitat used in high IP coincided for five subbasins (Canal Creek, Cedar Creek, Sunshine Creek, Upper Drift Creek, Five Rivers; Tables 4, 5). For all subbasins, the percent of available high IP used was highest in either 2001 or 2002 (Table 4). In 6 of the 11 subbasins, at least 90% of high IP habitat was used in the years of the most extensive fish distribution (Table 4). Ivlev's electivity index (E) values support juvenile selection of high IP areas. For all subbasins in all years (with the exception of SF Alsea in 1998), values for E were positive (Table 5). Further, some subbasins have more high IP habitat than others (Table 6).

#### DISCUSSION

Our study of interannual variability in juvenile Coho Salmon distribution across entire subbasins enables us to describe a complicated story of habitat use and relationships in fish distribution between cohorts. We identified patterns of interannual variation



FIGURE 4. Interannual distribution of juvenile Coho Salmon among 11 subbasins in midcoastal Oregon, which included core areas where fish were found every year and areas of expansion outside the core that were used less frequently.

Subbasin		Length (km) used outside the core (%)					
	Core length (km)	1998	1999	2001	2002		
Canal Creek	11.6	1.1 (9)		4.0 (26)	7.9 (41)		
Cedar Creek	4.4		0 (0)	14.3 (76)	14.3 (76)		
Sams Creek	21.7		3.4 (14)	3.7 (14)	7.1 (25)		
Fall Creek	15.9	3.5 (18)		2.0 (11)	3.2 (17)		
NF Alsea River	24.1	7.4 (24)		7.7 (24)	9.7 (29)		
Sunshine Creek	11.1	4.4 (28)	0.9 (7)	7.4 (40)	4.2 (28)		
Upper Drift Creek	32.5		2.9 (8)	5.3 (14)	10.2 (24)		
Rock Creek	15.3	5.7 (27)	5.9 (28)	22.7 (60)	26.5 (63)		
Lobster Creek	39.1	10.0 (20)	10.4 (21)	26.7 (41)	31.7 (45)		
SF Alsea River	18.8	3.3 (15)	· · ·	15.4 (45)	15.4 (45)		
Five Rivers	66.7	8.3 (11)		22.3(25)	41.3 (38)		
Mean % and SE		$(19) \pm 7$	$(13) \pm 5$	$(34) \pm 10$	$(39) \pm 12$		

TABLE 3. The length of stream used by juvenile Coho Salmon in every year, inside and outside areas used in every year, and core areas (and as a percent of total) for 11 subbasins on the mid-Oregon coast (blanks under years indicate no survey).

in the distribution of juvenile Coho Salmon. Across subbasins, we found synchrony in patterns of expansion and contraction around core areas over time. Elements of this synchrony appear to be related to habitat characteristics and to the overall size of the adult spawning run.

# Interannual Distribution of Juvenile Coho Salmon and Core Areas

Interannual variation in spatial patterns of juvenile Coho Salmon distribution appeared to be centered on core areas. Across subbasins, map and statistical analysis of juvenile Coho Salmon distribution indicate statistically significant differences in the number of stream kilometers used among years and between years within subbasins. In all subbasins but one, juvenile Coho Salmon use of stream kilometers was highest in 2001 or 2002. Further, in all subbasins, a set of core areas were used over time.

Two possible ideas that may contribute to an explanation of juvenile Coho Salmon distribution patterns are related to the behavior of spawning parents. One alternative is the hypothesis that in years of high flow during the spawning run, adults migrate farther upstream, thereby resulting in a positive relationship



FIGURE 5. Juvenile Coho Salmon estimated variogram range for 1998, 1999, 2001, and 2002 in subbasins of the Alsea and Siletz River basins. Each point is an annual estimate of variogram range size. Variograms were calculated from fish density data in snorkeled pools, detrended for distance of the pool to the mouth of each stream.

	Length of habitat used with high IP (km)				Available high IP used (%)			
Subbasin	1998	1999	2001	2002	1998	1999	2001	2002
Canal Creek	3.2		3.3	3.4	89.2		92.1	94.9
Cedar Creek		1.0	2.4	2.4		37.8	92.3	92.3
Sams Creek		13.6	14.2	15.5		83.7	87.5	95.4
Fall Creek	1.2		1.2	1.5	80.2		80.2	100
NF Alsea River	21.2		22.2	22.7	75.5		78.9	81
Sunshine Creek	6.6	5.5	7.5	6.4	74.6	63.2	85.4	72.8
Upper Drift Creek		14.4	14.2	15.5		82.9	82.1	89.2
Rock Creek	12.8	14.8	20.9	21.8	40.9	47.2	66.7	69.5
Lobster Creek	24.8	28.3	35.7	35.2	65.9	74.9	94.6	93.3
SF Alsea River	7.3		18.2	18.2	31.3		77.7	77.7
Five Rivers	44.0		44.2	48.8	83.7		84.1	92.8

TABLE 4. The length (km) of habitat used with a designation of high IP for juvenile Coho Salmon and the percent of available high IP used each year for 11 subbasins on the mid-Oregon coast (blanks indicate no survey).

between water flow during spawning and juvenile distribution the following summer. This explanation does not appear to be supported by the data from our study subbasins. Rather, greater stream lengths and the broadest distribution of juvenile Coho Salmon into upstream areas were documented in 2001, the year corresponding to the lowest flow during the spawning run of the previous year, compared with 1998, the year with the highest flow conditions during the spawning run of the previous year.

Alternatively, the size of the spawning population may influence the distribution of adults; larger populations would be more broadly distributed across available spawning habitat than smaller populations. In our subbasins, we observed that lower spawning run sizes were present in the Alsea and Siletz River basins in the first 2 years of the study than in the latter 2 years. Smaller run sizes in the early years correspond with more limited juvenile distribution and greater use of core areas. Larger spawning run sizes correspond with greater stream length used and both upstream and downstream expansion out of core areas. Juvenile Coho Salmon have limited mobility between the time of alevin emergence and summer low-flow conditions due to a combination of poor mobility and spring flow conditions (Ottaway and Forrest 1983). Therefore, it is possible that distribution of juvenile Coho Salmon in the summer reflects the spawning patterns of their parents. Such a link was found by Teichert et al. (2011) for Atlantic Salmon *Salmo salar*. Evidence of distribution restricted to core area in years of low spawning population size was documented for Chinook Salmon *O. tshawyscha* (Isaak and Thurow 2006). At fine spatial scales, Einum et al. (2008) found that patterns

TABLE 5. The percent of habitat used with a designation of high IP for juvenile Coho Salmon and the Ivlev electivity index for high IP habitat each year for 11 subbasins on the mid-Oregon coast. The Ivlev electivity index can range between -1 and 1, with positive values indicating that areas of high IP were selected for, while negative values indicating they were selected against. Values close to zero indicate no preference for or against areas of high IP (blanks indicate no survey).

	Percent of habitat used with high IP				Ivlev electivity index for high IP habitat used			
Subbasin	1998	1999	2001	2002	1998	1999	2001	2002
Canal Creek	25.2		21.1	17.4	0.35		0.28	0.18
Cedar Creek		22.1	12.7	12.7		0.52	0.29	0.29
Sams Creek		54.1	56.0	53.8		0.13	0.14	0.12
Fall Creek	6.3		6.9	5.0	0.22		0.27	0.11
NF Alsea River	67.2		69.6	67.3	0.27		0.28	0.27
Sunshine Creek	42.1	46.1	40.4	41.7	0.27	0.32	0.25	0.27
Upper Drift Creek		40.5	37.6	36.2		0.43	0.40	0.39
Rock Creek	61.0	69.8	55.0	52.1	0.24	0.31	0.20	0.17
Lobster Creek	50.6	57.1	54.2	49.8	0.13	0.19	0.16	0.12
SF Alsea River	33.0		52.9	52.9	-0.04		0.19	0.19
Five Rivers	58.7		49.6	45.2	0.27		0.19	0.14

TABLE 6. Within each subbasin, the number of stream kilometers within the distribution of Coho Salmon with high IP to support quality habitat for Coho Salmon, and the percent of all stream kilometers within the distribution of Coho Salmon with high IP to support quality habitat for Coho Salmon for each of 11 subbasins on the mid-Oregon coast.

	High IP				
Subbasin	Kilometers available	Percent of al habitat			
Canal Creek	3.6	12			
Cedar Creek	2.6	7			
Sams Creek	16.3	42			
Fall Creek	1.5	4			
NF Alsea River	29.7	39			
Sunshine Creek	8.8	24			
Upper Drift Creek	17.9	16			
Rock Creek	31.3	37			
Lobster Creek	38.5	39			
SF Alsea River	28.7	36			
Five Rivers	56.5	34			

of redd distribution were linked to juvenile distribution and growth in experimental studies of Atlantic Salmon.

## Interannual Distribution of Juvenile Coho Salmon and Habitat Suitability

Our results indicate that the distribution of juvenile Coho Salmon is related to the location of areas with high IP. Areas classified with high IP correspond with geomorphic characteristics in which high quality habitat may naturally develop (Burnett et al. 2007). Geomorphic characteristics have been shown to affect spawning habitat use by Atlantic Salmon (Moir et al. 2004). We found that for most subbasins, the highest percent of high IP stream length used as a proportion of stream length occupied corresponded with the shortest overall stream length occupied. We also saw that for most subbasins, as more stream length was occupied, the percent of available high IP that was used also increased. However, these two general patterns did not hold universally. In some places, areas of high IP may not coincide with current high quality habitat (Burnett et al. 2007). Further, some subbasins had more areas of high IP than others or had different distributions of high IP, making access to areas of high IP potentially more difficult in some locations than in others. Availability and connectivity among the suite of habitat variables needed for the freshwater life stages of Coho Salmon has been shown to be important in explaining juvenile Coho Salmon density (Flitcroft et al. 2012) but is not necessarily represented by the IP metric.

Graphed variation in variogram range sizes of juvenile Coho Salmon indicate that watershed size may also offer insights into patterns of juvenile Coho Salmon distribution. Variograms of subbasins larger than 70 km<sup>2</sup> tended to show greater variation in patch size over time than smaller subbasins. The location of core areas in the four largest subbasins occurred in upstream portions of the river system, core areas in smaller subbasins occurring in the lower portions of the subbasins. These larger subbasins also tended to have more stream length of high IP habitat available and also had larger proportions of high IP habitat compared with all available habitats. This is consistent with the hypothesis that larger subbasins would contain more floodplain habitats than smaller subbasins, thereby changing the spatial configuration of IP among subbasins of different sizes. Larger subbasins may offer juvenile Coho Salmon more options in terms of habitat availability or access to highly suitable habitat than smaller subbasins. Thus, juvenile Coho Salmon in larger subbasins may have more options to respond to annual environmental conditions, and this may result in variation of habitat use and associated patch size over time. However, land use in larger subbasins may be more varied or different from land use in smaller subbasins and may confound the relationship between larger subbasins and habitat diversity in some areas. Geomorphology and stream network configuration have been implicated as important considerations in determining centers of habitat diversity (Benda et al. 2004). Further, barriers to movement may reduce the potential advantages of habitat diversity in some watersheds (Sheer and Steel 2006). Additional analysis that includes the quantification of floodplain morphology and network complexity could further understanding of the differences in habitat availability and diversity that may be related to watershed size.

The context of habitat suitability may be linked in an important way to the distribution of spawning adults. In our study, the lowest quantity of stream length used by juvenile Coho Salmon is associated with the smallest adult spawning run sizes. Historically, spawning by adult Coho Salmon in lower portions of the stream network in low abundance years may have been adaptive because juveniles would have had easy access to highly suitable rearing habitat. However, human management of riverscapes has altered the quality of stream habitats in different parts of the stream network (Sedell et al. 1990; Lichatowich 1999; Trombulak and Frissell 2000). Habitat location within the framework of the entire riverscape has been shown to be important in describing juvenile Coho Salmon density (Flitcroft et al. 2012). In the interests of species conservation and recovery, millions of dollars have been invested in stream habitat restoration projects throughout the Pacific Northwest (ODFW 1997; Bernhardt et al. 2005). Much of the work has been completed on federally or publically owned and managed lands (Bernhardt et al. 2007). These areas often contain the best preserved instream and upslope habitat and are associated with timber holdings (Burnett et al. 2007). These areas are also generally found in the upper elevation portion of river systems, potentially missing core habitat areas identified in this study. These upstream subbasins tend to be relatively small. As noted previously, larger subbasins may afford greater habitat diversity, thereby allowing for population resilience in response to varied environmental conditions. Considering where habitat restoration should occur in order to enhance habitat diversity in core areas and at larger spatial extents may mean looking beyond ownerships and land uses that have been the typical focus for restoration effort.

Studies performed at riverscape scales include the collection and analysis of data throughout a river network (Fausch et al. 2002). Work at this scale can identify patterns of variation and synchrony over large spatial extents that may reflect processes working at multiple spatial scales. In this project, we identified similarities and differences in interannual distribution patterns of juvenile Coho Salmon at subbasin scales. Detection of the patterns that we found would not have been possible using point-based sampling techniques (i.e., generalized random-tessellation stratified [GRTS]) designed by Stevens and Olsen 2004). However, patterns detected using riverscapescale techniques may be able to direct analysis of biological and geomorphic processes in broad-scale monitoring data sets that use spatially randomized point samples. Work that allows riverscape-scale studies to direct process detection at sites within regional sampling frameworks may be an important link towards understanding how processes interact at different spatial extents.

Our study was limited by the inability to find continuous data sets describing spawning distributions of adult Coho Salmon in the same places that we have continuous surveys of juveniles. Two types of Coho Salmon spawning surveys were available through the Oregon Department of Fish and Wildlife for our study area. One set of surveys included long-term monitoring locations in primarily high suitability habitat. The other set of surveys were randomly selected using a rotating panel sampling design and are used to detect trends in the population (Jacobs and Nickelson 1998; Firman and Jacobs 2001). Whereas both of these sampling designs are effective at trend detection, neither detects changes in spawning distribution with great precision (Peacock and Holt 2012). Unfortunately, few of the spawning sites in our study area were surveyed every year, clouding assessments of adult occupancy patterns. Spawning survey data that is available throughout river systems over time has the potential to answer questions regarding processes by which fish chose habitat and are affected by environmental conditions. Detailed analysis of the relationship between adult and juvenile fish habitat use at multiple spatial extents could have been included in this paper if such information was available. Such analysis has the potential to inform stream habitat enhancement and restoration work throughout the range of Coho Salmon. Further research into factors driving distribution patterns of adult spawners and juveniles should expand our understanding of how these fish use available habitat.

Our riverscape model of juvenile Coho Salmon distribution supports the roles of both abundance and core areas, important interacting considerations that may inform natural resource managers concerned with fish restoration or conservation. This result points to the merits of data collection across entire stream networks. Such approaches have been advocated by aquatic ecologists (Fausch et al. 2002; Ward et al. 2002; McMillan et al. 2013), but acquiring continuous survey data continues to be a challenge. Our study demonstrates the utility of such surveys. We were able to analyze multiple spatial scales of organization over time. This allowed for interpretation of relationships that inform an understanding of population-scale use of habitat that is embedded within a stream network. We found that core areas were located in different areas in the river network in larger compared with smaller subbasins. The location of core areas within the river system and their proximity to areas of habitat restoration and protection are important considerations for management. Despite their broad range, Oregon coastal Coho Salmon are listed as threatened under the U.S. Endangered Species Act (Weitkamp et al. 1995). Management and restoration of core areas of salmonid habitats within riverscapes may be the foundation of watershed-scale planning for resilient populations within dynamic environmental conditions. Our study improves understanding of their population ecology and is likely useful to natural resource managers providing stewardship for their ecosystems.

#### ACKNOWLEDGMENTS

We would like to acknowledge the long hours of fieldwork that were necessary to collect the data analyzed in this manuscript. Data collected by snorkel crews supported by the MidCoast Watershed Council and spawning survey crews supported by the Oregon Department and Fish and Wildlife's Salmonid Spawning Survey Program was accurate, well documented, and accessible. Without the vision of the leaders of these programs to gather comprehensive and expensive data sets over a long period of time, analysis such as this would not have been possible. This manuscript was much improved thanks to the thoughtful reviews of Deanna Olson and two anonymous reviewers. Kathryn Ronnenberg and Kelly Christiansen provided important support for graphics, table format, and editorial review. The U.S. Department of Agriculture Forest Service provided funding and support for the analytical portion of this project. Reference to trade names does not imply endorsement by the U.S. Government.

#### REFERENCES

- Beechie, T. J., and T. H. Sibley. 1997. Relationships between channel characteristics, woody debris, and fish habitat in northwestern Washington streams. Transactions of the American Fisheries Society 126:217–229.
- Bell, E., W. G. Duffy, and T. D. Roelofs. 2001. Fidelity and survival of juvenile Coho Salmon in response to a flood. Transactions of the American Fisheries Society 130:450–458.
- Benda, L., D. Miller, K. Andras, P. Bigelow, G. Reeves, and D. Michael. 2007. NetMap: a new tool in support of watershed science and resource management. Forest Science 53:206–219.
- Benda, L., D. J. Miller, T. Dunne, G. H. Reeves, and J. K. Agee. 1998. Dynamic landscape systems. Pages 261–288 *in* R. J. Naiman and R. E. Bilby, editors. River ecology and management: lessons from the Pacific coastal ecoregion. Springer-Verlag, New York.
- Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: how channel networks structure riverine habitats. BioScience 54:413–427.

- Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308:636–637.
- Bernhardt, E. S., E. B. Sudduth, M. A. Palmer, J. D. Allan, J. L. Meyer, G. Alexander, J. Follstad-Shah, B. Hassett, R. Jenkinson, R. Lave, J. Rumps, and L. Pagano. 2007. Restoring rivers one reach at a time: results from a survey of U.S. river restoration practitioners. Restoration Ecology 15:482–493.
- Burnett, K. M., G. H. Reeves, D. J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. Ecological Applications 17:66–80.
- Clark, W. R. 2010. Principles of landscape ecology. Nature Education Knowledge [online serial] 3(10):34.
- Clarke, S. E., K. M. Burnett, and D. J. Miller. 2008. Modeling streams and hydrogeomorphic attributes in Oregon from digital and field data. Journal of the American Water Resources Association 44:459–477.
- Ebersole, J. L., M. E. Colvin, P. J. Wigington Jr., S. G. Leibowitz, J. P. Baker, M. Robbins Church, J. E. Compton, and M. A. Cairns. 2009. Hierarchical modeling of late-summer weight and summer abundance of juvenile Coho Salmon across a stream network. Transactions of the American Fisheries Society 138:1138–1156.
- Ebersole, J. L., P. J. Wigington Jr., J. P. Baker, M. A. Cairns, M. Robbins Church, B. P. Hansen, B. A. Miller, H. R. LaVigne, J. E. Compton, and S. G. Leibowitz. 2006. Juvenile Coho Salmon growth and survival across stream network seasonal habitats. Transactions of the American Fisheries Society 135:1681–1697.
- Einum, S., K. H. Nislow, S. Mckelvey, and J. D. Armstrong. 2008. Nest distribution shaping within-stream variation in Atlantic Salmon juvenile abundance and competition over small spatial scales. Journal of Animal Ecology 77:167– 172.
- ESRI (Environmental Systems Research Institute). 2006. ArcMap, version 9.2. ESRI, Redlands, California.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483–498.
- Firman, J. C., and S. E. Jacobs. 2001. A survey design for integrated monitoring of salmonids. Pages 242–252 in T. Nishida, P. J. Kailola, and C. E. Hollingworth, editors. Proceedings of the 1st international symposium on geographic information systems (GIS) in fishery science. Fishery GIS Research Group, Saitama, Japan.
- Flitcroft, R. L., K. M. Burnett, G. H. Reeves, and L. M. Ganio. 2012. Do network relationships matter? comparing network and instream habitat variables to explain densities of juvenile Coho Salmon (*Oncorhynchus kisutch*) in midcoastal Oregon, USA. Aquatic Conservation 22:288–302.
- Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis.
- Fukushima, M. 2001. Salmonid habitat–geomorphology relationships in lowgradient streams. Ecology 82:1238–1246.
- Ganio, L. M., C. E. Torgersen, and R. E. Gresswell. 2005. A geostatistical approach for describing spatial pattern in stream networks. Frontiers in Ecology and the Environment 3:138–144.
- Grant, J. W. A., and D. L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences 47:1724–1737.
- Hicks, B. J., and J. D. Hall. 2003. Rock type and channel gradient structure salmonid populations in the Oregon Coast Range. Transactions of the American Fisheries Society 132:468–482.
- Isaak, D. J., and R. F. Thurow. 2006. Network-scale spatial and temporal variation in Chinook Salmon (*Oncorhynchus tshawytscha*) redd distributions: patterns inferred from spatially continuous replicate surveys. Canadian Journal of Fisheries and Aquatic Sciences 63:285–296.

- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Translated from the Russian by D. Scott. Yale University Press, New Haven, Connecticut.
- Jacobs, S. E., and T. E. Nickelson. 1998. Use of stratified random sampling to estimate the abundance of Oregon coastal Coho Salmon. Oregon Department of Fish and Wildlife, Report F-145-R-09, Portland.
- Kahler, T. H., P. Roni, and T. P. Quinn. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:1947–1956.
- Kennedy, R. S. H., and T. A. Spies. 2004. Forest cover changes in the Oregon Coast Range from 1939 to 1993. Forest Ecology and Management 200:129– 147.
- Lichatowich, J. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington, D.C.
- Madin, I. P. 2009. Oregon: a geologic history. Oregon Department of Geology and Mineral Industries, Interpretive Map Series 28, Portland. Available: www.oregongeology.org/sub/publications/IMS/ims-028/index.htm. (June 2013).
- Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1993. Resource selection by animals. Chapman and Hill, New York.
- McMillan, J. R., M. C. Liermann, J. Starr, G. R. Pess, and X. Augerot. 2013. Using a stream network census of fish and habitat to assess models of juvenile salmonid distribution. Transactions of the American Fisheries Society 142:942–956.
- Miller, D. J. 2003. Programs for DEM analysis. *In* Landscape dynamics and forest management (CD-ROM). U.S. Forest Service General Technical Report RMRS-GTR-101CD.
- Moir, H. J., C. N. Gibbins, C. Soulsby, and J. Webb. 2004. Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic Salmon (*Salmo salar* L.). Geomorphology 60:21–35.
- Montgomery, D. R., J. M. Buffington, N. P. Peterson, D. Schuett-Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53:1061–1070.
- Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile Coho Salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:783–789.
- Nonaka, E., and T. A. Spies. 2005. Historical range of variability in landscape structure: a simulation study in Oregon, USA. Ecological Applications 15:1727–1746.
- ODFW (Oregon Department of Fish and Wildlife). 1997. The Oregon plan: Oregon coastal salmon restoration initiative. ODFW, Portland.
- Ottaway, E. M., and D. R. Forrest. 1983. The influence of water velocity on the downstream movement of alevins and fry of Brown Trout, *Salmo trutta* L. Journal of Fish Biology 23:221–227.
- Peacock, S. J., and C. A. Holt. 2012. Metrics and sampling designs for detecting trends in the distribution of spawning Pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences 69:681–694.
- Pess, G. R., P. M. Kiffney, M. C. Liermann, T. R. Bennett, J. H. Anderson, and T. P. Quinn. 2011. The influences of body size, habitat quality, and competition on the movement and survival of juvenile Coho Salmon during the early stages of stream recolonization. Transactions of the American Fisheries Society 140:883–897.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47:769–784.
- Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile Coho Salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555–1564.
- Redmond, K., and G. Taylor. 1997. Climate of the coastal temperate rain forest. Pages 25–42 *in* P. K. Schoonmaker, B. von Hagen, and E. C. Wolf, editors. The rain forests of home: profile of a North American bioregion. Island Press, Washington, D.C.

- Reeves, G. H., J. D. Sleeper, and D. W. Lang. 2011. Seasonal changes in habitat availability and the distribution and abundance of salmonids along a stream gradient from headwaters to mouth in coastal Oregon. Transactions of the American Fisheries Society 140:537–548.
- Sandercock, F. K. 2003. Life history of Coho Salmon (Oncorhynchus kisutch). Pages 397–445 in C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.
- SAS (Statistical Analysis Systems). 2003. SAS, version 9.1. SAS Institute, Cary, North Carolina.
- Sedell, J. R., G. H. Reeves, F. R. Hauer, J. A. Stanford, and C. P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14:711–724.
- Sheer, M. B., and E. A. Steel. 2006. Lost watersheds: barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and lower Columbia river basins. Transactions of the American Fisheries Society 135:1654–1669.
- Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in douglas-fir forests of western Oregon and Washington. Ecology 69:1689– 1702.
- Stevens, D. L., Jr., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262– 278.

- Teichert, M. A. K., A. Foldvik, T. Forseth, O. Ugedal, S. Einum, A. G. Finstad, R. D. Hedger, and E. Bellier. 2011. Effects of spawning distribution on juvenile Atlantic Salmon (*Salmo salar*) density and growth. Canadian Journal of Fisheries and Aquatic Sciences 68:43–50.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.
- Wang, L., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries 22(6):6–12.
- Ward, J. V., K. Tockner, D. B. Arscott, and C. Claret. 2002. Riverine landscape diversity. Freshwater Biology 47:517–539.
- Weitkamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples. 1995. Status review of Coho Salmon from Washington, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-24.
- Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.
- Wiens, J. A. 2002. Riverine landscapes: taking landscape ecology into the water. Freshwater Biology 47:501–515.
- Wimberly, M. C., and J. L. Ohmann. 2004. A multi-scale assessment of human and environmental constraints on forest land cover change on the Oregon (USA) Coast Range. Landscape Ecology 19:631–646.

38