

Do network relationships matter? Comparing network and instream habitat variables to explain densities of juvenile coho salmon (*Oncorhynchus kisutch*) in mid-coastal Oregon, USA.

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ABSTRACT

1. Aquatic ecologists are working to develop theory and techniques for analysis of dynamic stream processes and communities of organisms. Such work is critical for the development of conservation plans that are relevant at the scale of entire ecosystems. The stream network is the foundation upon which stream systems are organized. Natural and human disturbances in streams alter the configuration of stream habitats such as pools, riffles, and glides across seasons, decades, or centuries. Thus, native aquatic species have developed mechanisms for adapting to the dynamic configuration of habitats in stream networks.

2. At different spatial scales, stream network structure informs habitat connectivity for aquatic-obligate species. The movement of aquatic species both upstream and downstream is limited by stream channels and may be modified by the downstream flow of water, nutrients, and physical materials such as wood and substrate. Analysing streams as networks offers a realistic and holistic perspective for assessing movement and distribution by freshwater aquatic species in response to life-history needs and environmental conditions.

3. In this study, network analysis was facilitated by automating, in a Geographic Information System, the calculation of network distances and variables that represent spatial configuration. A comparison between traditional instream habitat variables and network variables for juvenile coho salmon (*Oncorhynchus kisutch*) in seven sub-basins of Oregon's mid-coast over a 5-year period revealed that network variables perform better at explaining juvenile coho salmon density than instream habitat variables. Moreover, analysis of network distances among seasonal habitats indicates that juvenile coho salmon density may be higher where the distance between critical seasonal habitats is short. This work furthers aquatic conservation, management, and restoration by including analysis of the proximity and connectivity among aquatic freshwater habitats.

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INTRODUCTION

Scientists have begun to advocate river-scale management and research (Schlosser, 1995; Poff *et al.*, 1997; Fausch *et al.*, 2002; Palmer *et al.*, 2005) as the focus of aquatic conservation shifts from

individuals to populations, species, and ecosystems (Scott *et al.*, 1987; Lichatowich *et al.*, 1995; Schlosser and Angermeier, 1995; Thurow *et al.*, 1997). Even with the call for river-scale management in trying to rehabilitate aquatic ecosystems and threatened species (Schlosser, 1991; Fausch *et al.*,

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2002; Lake *et al.*, 2007), restoration continues to target habitats specific to single species, life-history stages, or locations within a river network (Nickelson *et al.*, 1992; Tippery *et al.*, 2010). Current approaches to stream restoration have cost billions of dollars and have not recovered threatened or endangered aquatic species (Ruckelshaus *et al.*, 2002). Resilience in native species is now thought to be associated with habitat diversity throughout stream systems (Bisson *et al.*, 2009; Bottom *et al.*, 2009). Directing stream restoration toward the diversity, availability, and connectivity of habitats can help system capacity to recover and support diverse life histories and more resilient populations (Frissell *et al.*, 1986; Ebersole *et al.*, 1997). This will require considering habitat availability and connectivity, species distribution patterns, and habitats for all life-history stages at multiple spatial scales throughout entire stream networks (Schlosser, 1995; Rabeni and Sowa, 1996).

River-scale analysis for ecological conservation requires an understanding of conditions within the complex structure of river networks. Rivers have been predominantly conceptualized as linear (Vannote *et al.*, 1980) and studied either as lines or points. These approaches have informed aquatic ecology by relating aquatic community composition, structure, and functioning at a location to biophysical conditions at that location on a stream (Naiman *et al.*, 1987). However, the architecture of stream systems is not strictly linear. Most streams are networks, with many having a dendritic topology formed by branching and interconnecting water channels. Research at the scale of river networks, or including components of network relationships, is becoming more common (Campbell Grant *et al.*, 2007; Ebersole *et al.*, 2009; Fullerton *et al.*, 2010). Dendritic channel structures have higher extinction vulnerability than linear structures for aquatic-dependent metapopulations (Fagan, 2002). To expand conservation programmes to the scale of river systems, simple tools and techniques that describe relationships between aquatic species and the dendritic river network must be available and interpretable. Network relationships can include the spatial location and connectivity among stream habitats, movement pathways available to aquatic species, and the biogeomorphic characteristics inherent to different locations within a stream system (Vannote *et al.*, 1980; Frissell *et al.*, 1986; Montgomery and Buffington, 1997; Montgomery *et al.*, 1999).

Work in aquatic ecology at the scale of entire river networks offers the opportunity to explore processes

and patterns unique to river systems. Because a river system is embedded in a landscape, some physical characteristics or processes, such as the rate of wood input from fallen trees following fire, may be similar on land and in the stream. However, movement pathways and connections within a river system differ from those on land principally due to directions of flow (physical and biological), and the hierarchical organization of stream channels (Strahler, 1952; Frissell *et al.*, 1986). The structure of a river system can be described as a network with unique characteristics and considerations. As with landscape features, the distance between points may not always describe dissimilarity, but connectivity for most stream processes is provided only along the river channel. How distance metrics are interpreted in river systems is complicated because stream habitats are embedded in both a landscape and a riverscape (*sensu* Fausch *et al.*, 2002). For example, two stream habitats (Figure 1, sites 2 and 3) may be near one another in two-dimensional Cartesian space and share similar physical characteristics (depth, amounts of large wood, substrate composition) that result from being embedded in similar landscapes (rock type, vegetation, disturbance history, or land use) (Gresswell *et al.*, 2006; Lowe *et al.*, 2006). However, the two habitats may be far apart in network distance space, or effectively isolated, depending on whether the branches of the river network are connected. Similarly, two stream habitats (Figure 1, sites 1 and 4) may be relatively close in stream network space, but because they are located in different portions of the stream network (site 1 is in the headwaters, site 4 is in the valley floodplain), the habitat they contain may be quite different. In a stream network, being physically close in the landscape does not necessarily translate into connection or access for aquatic species.

In order to explore how aquatic species use an entire river system, the analysis coupled Geographic Information Systems (GIS) and non-parametric statistical techniques. The primary goal of this work was to advance understanding about how instream habitat and stream network parameters influence spatial and temporal distributions of juvenile coho salmon (*Oncorhynchus kisutch*), to inform conservation. Instream habitat parameters, such as substrate and habitat type, are commonly collected during stream surveys (Hankin and Reeves, 1988; Hughes and Peck, 2008; Roper *et al.*, 2010); stream network parameters, such as the proximity between seasonal habitats, can be readily derived from available spatial data. Three objectives were explored

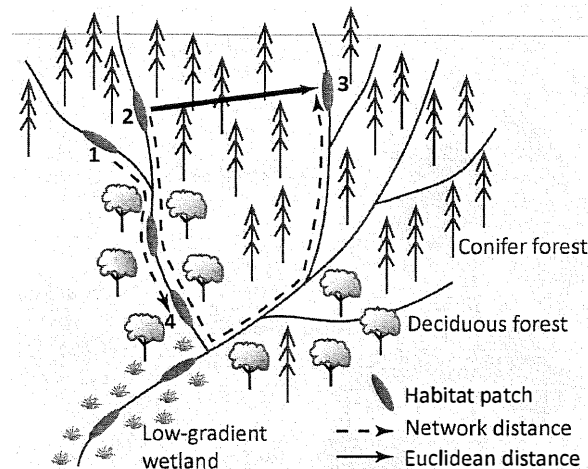


Figure 1. Contrasting interpretation of distance measures in a stream system: the shortest Euclidean distance is not the shortest network distance.

in this project that use stream network variables to analyse the distribution and density of juvenile coho salmon in seven sub-basins of Oregon's mid-coast over a 5-year period at two spatial extents. Coho salmon were selected owing to their wide distribution, their imperilled status, and the strong societal interest in restoring habitat for the species. The three analytical objectives were: (1) to compare the effectiveness of instream and stream-network variables for explaining variation among sites in the density of juvenile coho salmon; (2) to explore whether densities of juvenile coho salmon differ among sub-basins, differ within sub-basins among years, and exhibit inter-annual variability; and (3) to compare the effectiveness of instream habitat and stream-network variables to distinguish sub-basins where densities of juvenile coho salmon decreased or increased between 2001 and 2002. In addition, a network perspective was considered in several aspects of aquatic conservation and restoration.

METHODS

Study area

Sub-basins selected for analysis were located in the Alsea (area = 1785 km²) and Siletz (area = 1964 km²) river basins in the mid-Oregon Coast Range (Figure 2). Selected sub-basins included three in the Alsea drainage: Five Rivers (300 km²), South Fork Alsea (159 km²), and Upper Drift Creek (80 km²); and four in the Siletz: Rock Creek (105 km²), Cedar Creek (33 km²), Sams Creek (38 km²), and Sunshine Creek (77 km²). Populations of coho salmon and

their habitats have been studied extensively in these areas. The headwaters of both basins are located in the Oregon Coast Range and exist within predominantly coniferous forests. Although agriculture is an important lowland land-use, timber harvest is the chief economic activity in the area and the dominant land-use at higher elevations. The geology of the Siletz River is principally volcanic, while the Alsea is characterized by sandstone. The climate of this region is mild maritime, with precipitation generally occurring as rain during the winter months (Redmond and Taylor, 1997).

Data

Instream data were assembled from a wide variety of sources and analysed at two spatial scales: the site scale, corresponding to an individual pool habitat unit (a snorkelled pool), between 5 and 25 m in length; and the sub-basin scale, corresponding to an entire catchment network, and ranging in area between 33 and 300 km². Using a GIS, all datasets were attached to stream hydrography from 10-m digital elevation models (DEMs) (Miller, 2003; Clarke *et al.*, 2008).

Juvenile coho salmon dataset

Counts of juvenile coho salmon for the years 1998, 1999, 2001, and 2002 came from snorkel surveys conducted for the Oregon Mid-coast Watershed Council (Table 1). Data from 2000 were excluded because field maps necessary for georeferencing were unavailable. During each summer field season (June to September), every fifth pool in a sub-basin was

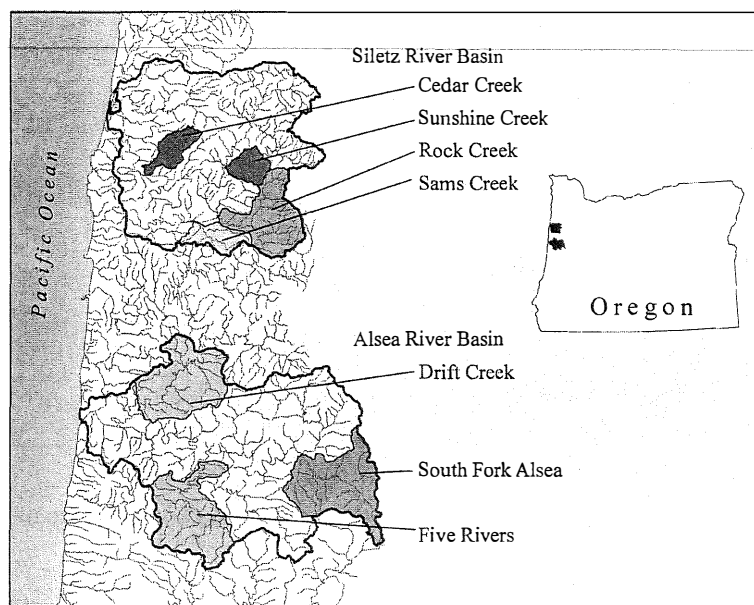


Figure 2. Highlighted sub-basins in the Alsea and Siletz River basins included in an analysis of multiple spatial scales over time that incorporated a stream network framework.

Table 1. Summary table for the seven sub-basins of interest on the mid-coast of Oregon

Sub-basin	Year	Number of sites	Total number of coho counted	Mean density per site	SD of coho density
Alsea Basin					
Upper Drift Creek (79.7 km ²)	1999	124	1317	0.28	0.68
	2001	193	18 548	1.21	1.12
	2002	194	11 392	1.25	1.70
S.F. Alsea (158.8 km ²)	1998	123	259	0.10	0.18
	2001	85	1181	0.39	0.56
	2002	134	2132	0.69	1.13
Five Rivers (300.0 km ²)	1998	63	449	0.06	0.07
	2001	81	3479	0.44	0.46
	2002	90	4249	0.87	1.32
Siletz Basin					
Cedar Creek (33.4 km ²)	1999	15	84	0.02	0.04
	2001	46	3287	0.38	0.32
	2002	56	1824	0.24	0.23
Sams Creek (37.7 km ²)	1999	94	728	0.15	0.18
	2001	99	5394	0.83	0.55
	2002	98	4027	0.80	0.64
Sunshine Creek (77.0 km ²)	1998	112	2266	0.60	0.72
	1999	74	464	0.37	0.56
	2001	110	4938	0.92	0.84
	2002	129	5983	1.38	1.39
Rock Creek (104.7 km ²)	1998	66	22	0.00	0.01
	1999	70	50	0.01	0.05
	2001	60	1661	0.14	0.16
	2002	56	638	0.07	0.13

surveyed by two or three snorkellers, depending on river size. Surveys began at the stream mouth, continued to the headwaters, and included all tributaries. For each stream, a survey ended after no

juvenile coho salmon were observed in five consecutively snorkelled pools. This survey distance encompassed approximately 25 pool habitat units, and thus a reach of stream beyond which

juvenile coho salmon are unlikely to move. For this research, a snorkel site refers to surveyed pools. Snorkel sites were analysed by sub-basin for Cedar Creek ($n=117$); Rock Creek ($n=252$); Sams Creek ($n=291$); Sunshine Creek ($n=425$); Drift Creek ($n=511$); Five Rivers ($n=234$); and South Fork Alsea ($n=342$).

Field crews marked the location of snorkel sites that corresponded with identifiable features such as tributaries, road crossings, or railroad lines on 1:24 k topographic maps. The locations were the basis for georeferencing streams surveyed to the hydrography using an ArcInfo (version 9.2, ESRI, 2006) dynamic segmentation protocol with calibration points at least every 500 m along the stream linework. Snorkel crews estimated the length and width of each pool but collected no other descriptive information. Summer fish surveys are important because juveniles are assumed to move less during the summer than other seasons (Nickelson *et al.*, 1992; Kahler *et al.*, 2001). Snorkel estimates in each site were compared over time based on final GIS maps (for example: Figure 3).

Instream habitat

Fine-scale data on summer instream habitat were acquired from the Oregon Department of Fish and Wildlife Aquatic Inventories Program (AIP). Field crews collected data by walking from the stream mouth to the headwaters, recording several physical habitat parameters, and identifying discrete habitat unit types (Moore *et al.*, 1997). Field surveys from 1997 to 2002 were pieced together because all streams for a sub-basin were never surveyed in a single year.

Analysis considered 13 biologically relevant instream habitat variables (Table 2). For example, juvenile coho salmon densities are generally greater where large wood is abundant; percentage of sand as a measure of fine-grained material can decrease juvenile survival to emergence (Bryce *et al.*, 2008, 2010); and gravels are necessary for spawning (Groot and Margolis, 1991; Bilby and Bisson, 1998).

Network position and connectivity

Network variables represent the location of a site within the stream network, or the connectivity among habitats in the stream channel. Several variables describing position within the stream network (Table 2) were modelled from 10-m DEMs while delineating hydrography (Clarke and Burnett, 2003; Miller, 2003; Clarke *et al.*, 2008). Connectivity among adequate habitats was defined as the distance along the stream network between snorkel sites and seasonal (spawning, summer refuge, and winter rearing) habitats identified from the AIP instream habitat surveys. 'Adequate' habitat was defined based on ODFW benchmarks (Appendix 1) for site-specific habitat features (Foster *et al.*, 2001): (1) adequate spawning habitat was defined as riffle units with $\geq 50\%$ gravel and $\leq 8\%$ silt; (2) adequate summer refuge habitats are pools ≥ 0.5 m in depth; and (3) adequate winter rearing habitats are off-channel areas (backwater pools, alcoves, and isolated pools). A map was created of each seasonal habitat type. The network distances between each snorkel site and the closest adequate seasonal habitat were calculated with the

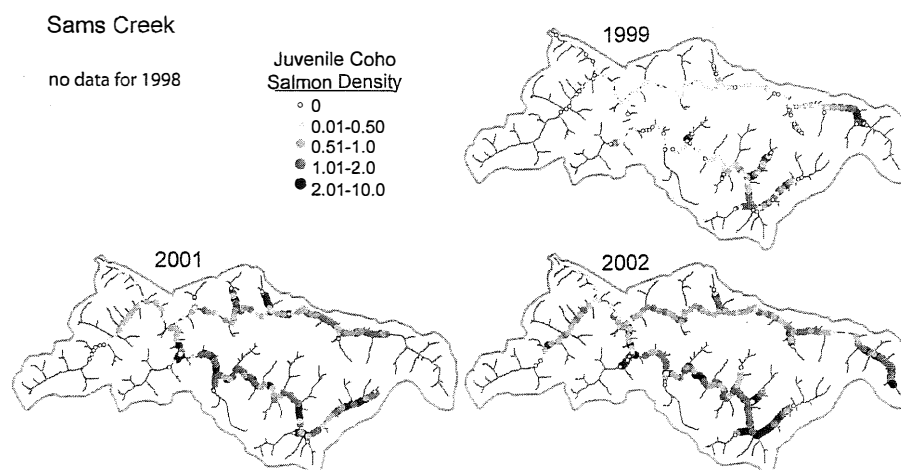


Figure 3. Juvenile coho density in each snorkelled pool by year in the Sams Creek catchment.

Table 2. Variables in the instream habitat and network datasets with source information

Variable	Units	Source Dataset	Measurement Type
<i>Instream habitat dataset</i>			
Slope*	%	ODFW AQI	Field estimated
Shade	%	ODFW AQI	Field estimated
Depth		ODFW AQI	Field estimated
% sand in substrate*	%	ODFW AQI	Field estimated
% gravel in substrate*	%	ODFW AQI	Field estimated
% cobble in substrate*	%	ODFW AQI	Field estimated
% boulder in substrate*	%	ODFW AQI	Field estimated
% bedrock in substrate*	%	ODFW AQI	Field estimated
Boulder count	Count	ODFW AQI	Field estimated
Active bank erosion	%	ODFW AQI	Field estimated
% undercut bank	%	ODFW AQI	Field estimated
Number of pieces of wood*	Count	ODFW AQI	Field estimated
Key pieces of wood*	Count	ODFW AQI	Field estimated
<i>Network position</i>			
Stream order	Strahler	Clarke <i>et al.</i> 2008	DEM derived
Basin area	km ²	Clarke <i>et al.</i> 2008	DEM derived
Maximum gradient downstream	Gradient	Clarke <i>et al.</i> 2008	Modelled
<i>Network connectivity</i>			
Distance to 'adequate' spawning habitat	m	ODFW AQI	Calculated
Distance to 'adequate' winter rearing habitat	m	ODFW AQI	Calculated
Distance to 'adequate' summer habitat	m	ODFW AQI	Calculated

*Instream variables chosen for analysis using principal components analysis.

ArcView 3.2 (ESRI, 1999) extension, Shortest Network Paths Version 1.1 (Remington, 1999) (Figure 4). The distance to 'adequate' spawning; distance to 'adequate' summer refuge; and distance to 'adequate' winter rearing comprise the connectivity variables (Table 2).

Analysis

Variable selection

Key instream habitat variables were identified by considering results of principal components analysis (PCA – using a correlation cross-products matrix)

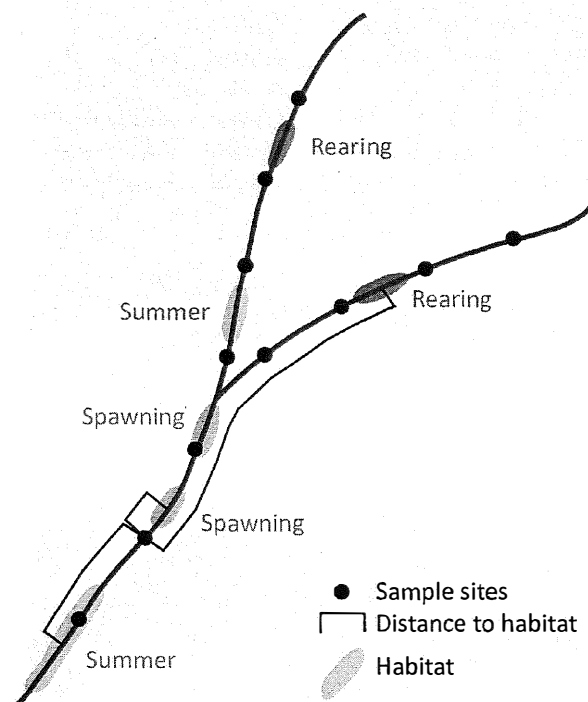


Figure 4. Network distances calculated from juvenile coho salmon snorkel sites to the closest available seasonal habitat.

(PC-ORD software, McCune and Mefford, 2011) for each year of data. Only variables that were important in the eigenvectors of the first three PCA axes in any year were retained for further analysis. Selected instream habitat variables were then tested for correlation. All available network variables were used in the analysis.

Variation among sites

To explore the first objective, comparing the effectiveness of instream habitat and network variables to explain variation in the density of juvenile coho salmon among sites, data were analysed annually from 1998 to 2002.

Juvenile coho salmon density was modelled at each snorkel site with the instream and network datasets independently and together using local-mean non-parametric multiplicative regression (LM-NPMR) (Hyperniche software, McCune and Mefford, 2009). This method accommodates non-linear relationships and is constrained by fewer assumptions than parametric methods (McCune, 2011). Hyperniche software uses a leave-one-out cross-validation model selection technique to guard against model overfitting. Models were compared based on a cross-validated R^2 value and model fit in graphs of residuals and estimated values. The LM-NPMR used in this analysis incorporates a Gaussian local mean to describe the shape of the model at the mean of each point (McCune, 2011).

Differences across and within sub-basins

The second objective was to explore whether densities of juvenile coho salmon differ among sub-basins, differ within sub-basins among years, or exhibit inter-annual trends. The mean log density of juvenile coho salmon in pools was compared using analysis of variance (ANOVA) (SAS, 2003) to assess the effects of sub-basin, year, and the interaction of year and sub-basin. Juvenile coho density was log transformed to meet parametric assumptions for ANOVA. The Bonferroni adjustment was used for all multiple comparisons. Means and differences were back-transformed to medians and ratios, respectively, for interpretation. The distance from each site to the stream mouth was included in the ANOVA to control for autocorrelation (evaluated with Durbin–Watson test). Because all sub-basins were surveyed in 2001 and 2002, the ratio of mean juvenile density was generated to compare whether sub-basins performed similarly over this time-step.

Discrimination among sub-basins

The third objective was to compare the effectiveness of instream habitat and stream network variables to distinguish among groups of sub-basins. Trends within sub-basins detected using ANOVA, and comparisons of means, indicated two potential groups of sub-basins, one with increasing and the other with decreasing median juvenile coho salmon density between 2001 and 2002. Differentiation between these two groups was performed using two discriminant analyses (DA) (SAS, 2008); one with just the network dataset, and the other with just the reduced habitat dataset (Table 2). Canonical functions were developed using stepwise procedures with a tolerance level of 0.001, partial F tests of $P=0.15$, and the Wilks' Lambda statistic as the selection criterion. Within-group variances of explanatory variables were similar and no outliers were detected in scatter and box plots of the canonical functions.

RESULTS

Variable reduction: instream habitat dataset

PCA results for instream habitat variables differed among years (Appendix 2). The dominant variable that was identified on each of the first three PCA axes in any of the 4 years was retained. The first three PCA axes were used because they explained nearly half of the variation in the dataset. Dominant variables were identified as those with the largest weight per eigenvector. The selected variables were slope, % sand, % gravel, % boulder, % cobble, % bedrock, number of pieces of wood, and number of key pieces of wood (Table 2). Selected variables were tested for correlation and none were correlated at a significant level (> 0.60).

Comparing instream habitat and network variables to explain variation among sites

None of the best fitting models identified in the LM-NPMR analysis contained more than three variables. Network variables consistently explained a greater percentage of variation in juvenile coho salmon density at the site scale than instream habitat variables (Table 3). The model identified from a combination of network and instream variables contained only network variables in 1999 and 2001 but contained both instream and network variables in 1998 and 2002, although instream variables explained little variation (Table 3).

Table 3. Local-mean non-parametric multiplicative regression model results for 1998, 1999, 2001 and 2002 for sites in Oregon's mid-coast region. The dependent variable is juvenile coho density

Year	Variable set	R ²	Variable 1	Variable 2	Variable 3
1998	Network variables	0.42	Basin area	Maximum gradient downstream	Distance to spawning habitat
	Instream variables	0.18	Slope	% Gravel	Number of pieces of wood
	Instream and network variables	0.43	% Gravel	Maximum gradient downstream	Distance to spawning habitat
1999	Network variables	0.42	Maximum gradient downstream	Distance to spawning habitat	Distance to summer pools
	Instream variables	0.33	% Sand	Number of key pieces of wood	
	Instream and network variables	0.42	Maximum gradient downstream	Distance to spawning habitat	Distance to summer pools
2001	Network variables	0.33	Basin area	Maximum gradient downstream	Distance to summer pools
	Instream variables	0.11	% Sand	Number of key pieces of wood	
	Instream and network variables	0.33	Basin area	Maximum gradient downstream	Distance to summer pools
2002	Network variables	0.38	Basin area	Maximum gradient downstream	Distance to summer pools
	Instream variables	0.12	% Sand	Number of pieces of wood	
	Instream and network variables	0.40	% Cobble	Basin area	Distance to summer pools

Differences across and within sub-basins

Analysis of variance (ANOVA) results indicated that mean log density of juvenile coho salmon among years was different in different sub-basins ($F_{13,1966} = 18.8$ $P < 0.0001$) when downstream distance was included in the model (Table 4(a)). The Durbin Watson test value of 1.038 indicates control of spatial autocorrelation within the dataset. Bonferroni-adjusted comparisons among years within sub-basins indicated significant differences among years within each sub-basin (Table 4(b)). Ratios of mean density of juvenile coho salmon between 2001 and 2002 were calculated as: Cedar Creek = 0.63; Upper Drift Creek = 1.03; Five

Rivers = 1.98; Rock Creek = 0.50; Sams Creek = 0.96; S.F. Alsea = 1.77; Sunshine Creek = 1.50. Ratios greater than 1.0 indicate that densities in 2002 were higher than in 2001; ratios less than 1.0 indicate a decrease in density over this time step.

Comparing instream habitat and network variables to discriminate among sub-basins

Between 2001 and 2002, the mean juvenile coho salmon density appeared to increase in some sub-basins but decrease in others. The ratio of mean juvenile density was greater than 1.0, indicating increasing densities between 2001 and 2002 for Upper Drift Creek, Five Rivers, South Fork Alsea, and Sunshine Creek. In contrast, the ratio of mean juvenile density was less than 1.0, indicating decreasing densities between 2001 and 2002 for Cedar, Rock, and Sams Creeks. Groupings of increase and decrease were based strictly on the calculated ratio, even though Upper Drift Creek and Sams Creek had ratios close to 1.0.

Two stepwise discriminant analyses (DA) were conducted to evaluate whether instream habitat or network variables could distinguish between the juvenile density-increasing and density-decreasing sub-basins. The DA identified a significant linear combination of variables in each dataset that distinguished between these sub-basin groups (Table 5). The squared canonical correlation for the network dataset (45%) exceeded that for the instream habitat dataset (6%), indicating that network variables distinguished the two groups better than instream habitat variables. In the DA with the network variables, sub-basins with decreasing density of juvenile coho are positively

Table 4. ANOVA results examining mean log of juvenile coho density and sub-basins on the mid-coast of Oregon over time. Downdist is a variable used in this analysis to control for spatial autocorrelation and is a calculation of the distance from the snorkel site to the sub-basin mouth

(a) Log juvenile coho density ~ year + sub-basin + year*sub-basin + downdist

Effect	df	F Value	Pr > F
Year	3	35.82	< 0.0001
Sub-basin	6	13.2	< 0.0001
Year*sub-basin	13	18.8	< 0.0001
Downdist	1	15.15	0.0001

(b) Test of whether mean log juvenile coho density within individual sub-basins differed over available years

Sub-basin	df	F value	Pr > F
Cedar	2	18.05	< 0.0001
Five Rivers	2	6.85	0.0011
Rock	3	54.08	< 0.0001
Sams	2	6.46	0.0016
S.F. Alsea	2	26.39	< 0.0001
Sunshine	3	21.96	< 0.0001
Upper Drift	2	35.99	< 0.0001

Table 5. Discriminant analysis results for instream and network datasets used to differentiate between groups of sub-basins with increasing or decreasing juvenile density between 2001 and 2002

	Discriminating variables	Wilks' Lambda partial F-ratio P > F	Total canonical structure coefficient	Standardized canonical coefficients	Percentage squared canonical correlation
<i>Network</i>	Max. gradient downstream	0.0001	-0.3758	-0.2528	45
	Distance to spawning habitat	0.0001	0.9225	1.4398	
	Stream order	0.0001	0.0253	-0.2298	
	Distance to winter habitat	0.0001	0.5841	-0.2569	
	Basin area	0.0001	0.1238	0.3133	
<i>Habitat</i>	% Sand	0.0001	-0.6122	-0.3368	6
	% Bedrock	0.0001	0.1249	0.0767	
	% Boulder	0.0001	0.8770	0.7374	
	key pieces of wood	0.0001	0.4513	0.3695	

related to longer distances to spawning and winter habitat. This is supported by simple graphs displaying juvenile density and the proximity of seasonal habitat (Figure 5). In the DA using instream habitat variables, sub-basins with decreasing density of juvenile coho are positively related to high % boulder in stream substrate.

DISCUSSION

Traditional instream habitat datasets were compared with network variables in their effectiveness at explaining spatial and temporal patterns in the density of juvenile coho salmon on the mid-coast of Oregon. The two categories of instream habitat and

network variables that were explored are not meant to be mutually exclusive. Rather, these complement one another, with each type of metric contributing to the story about juvenile coho salmon habitat use and needs over time across spatial scales. Also, the important habitat metrics that described the proximity between high-quality seasonal habitats depend on mapped instream habitat surveys to construct network relationships within the stream system. In this way, network variables that represent habitat connectivity within the stream system actually expand the utility of traditional field survey data.

The loss of complex and diverse instream habitat is a well-documented element of the decline in salmonids throughout the Pacific North-west USA

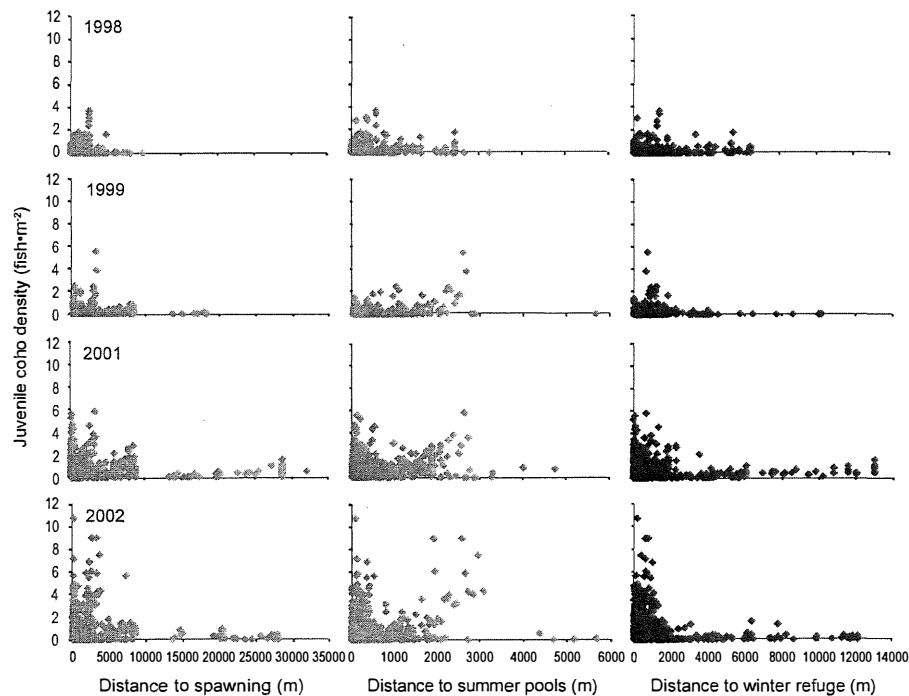


Figure 5. Distance to critical seasonal habitats from a snorkelled pool against the density of juvenile coho salmon in the pool.

(Lichatowich, 1999). Habitat restoration is a core component of population recovery planning for imperilled salmonids (Beechie *et al.*, 1994) with millions of dollars spent annually on habitat restoration programmes in the Pacific North-west alone. Restoration aimed at increasing the capacity of streams to support population resilience and recovery through habitat diversity has been described (Ebersole *et al.*, 1997; Bisson *et al.*, 2009) but not generally practised. Rather, instream restoration that targets specific life-history stages (Tippary *et al.*, 2010) or geomorphic criteria (Bond and Lake, 2003; Budy and Schaller, 2007) is more common. Quantifying whether habitat restoration programmes provide salmonid population-level improvements in targeted species is difficult. Challenges arise from various factors, not least of which is inter-annual variability in ocean conditions that affect marine survival and freshwater returns of anadromous salmonids. Reviews of the effectiveness of instream habitat enhancement projects often refer to changes in geomorphic criteria that may (Van Zyll De Jong *et al.*, 1997; Tippary *et al.*, 2010) or may not (Frissell and Nawa, 1992; Kondolf *et al.*, 1996; Burnett *et al.*, 2008) produce enduring changes in channel morphology. Simple techniques are needed that allow practitioners to translate comprehensive, integrated, river-scale recovery plans for aquatic species at risk into practical restoration projects or specific management prescriptions. Our work addresses this knowledge gap and illustrates the importance of habitat proximity and quality at site and sub-basin scales.

Juvenile coho salmon density might have been expected to increase or decrease synchronously between years across sub-basins as each sub-basin responded to the same set of environmental conditions such as precipitation and temperature. Indeed, juvenile density appeared to increase relatively consistently among sub-basins except between 2001 and 2002 (Table 5). The lack of consistency among sub-basins between 2001 and 2002 is intriguing. Network variables were more effective than instream variables at distinguishing between groups of sub-basins with increasing or decreasing densities of juvenile coho salmon between 2001 and 2002. Our results suggest that in some years, juvenile density is higher in sub-basins with close proximity among important seasonal habitats.

Different sets of habitats or entirely different sub-basins may be most hospitable for juvenile coho salmon at different times (Reeves *et al.*, 1995; Quinn

and Peterson, 1996) as populations respond to dynamic stream conditions including geomorphic and climatic drivers. We suspect that in response to a large-scale environmental driver in 2002, fewer juvenile coho salmon survived in sub-basins where seasonal habitats were further apart than closer together. One possible environmental driver is stream flow during emergence. Flow levels can affect juvenile abundance in other stream fishes (Schlosser, 1985). For salmonids, higher stream flows can scour redds (Montgomery *et al.*, 1999), reducing survival to emergence. Also, high stream flow can impede movement of juvenile coho salmon, which are less adapted to high velocity environments than other salmonids (Bisson *et al.*, 1988). Therefore, moving from spawning beds to summer rearing pools could be more difficult under high-flow conditions in sub-basins with long distances between seasonal habitats. Precipitation and stream-flow records necessary to test this hypothesis were not available for individual sub-basins. However, basin-scale hydrographs indicate that stream discharge during egg incubation and early juvenile rearing was higher for 2002 than 2001 in both the Siletz and Alsea river basins (Figure 6). Among-sub-basin variation in adult returns is another possible explanation that may or may not be related to large-scale environmental drivers. Fewer spawning adults returning to some of the sub-basins would have produced fewer progeny to be counted the following summer. Estimates of spawning run sizes for the entire Siletz or Alsea basins are available; however, detailed estimates at

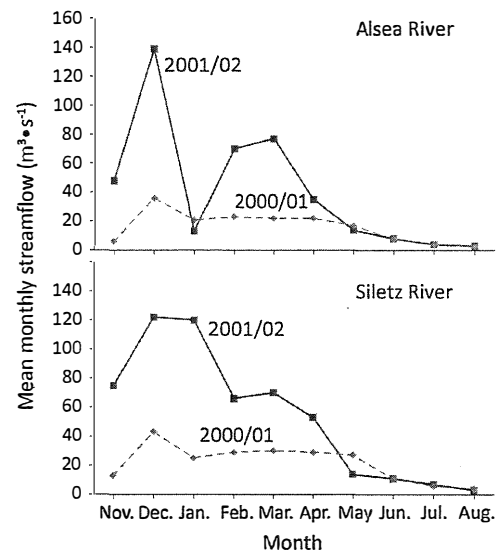


Figure 6. Hydrograph of the Siletz and Alsea rivers during the time when juvenile salmon would be within the gravel, through emergence.

the sub-basin scale that track spawner occupancy patterns are not available. Research that examines adult spawner counts, stream flow, and precipitation at a sub-basin scale will be necessary to tease apart the effect of stream hydrographs as well as size and distribution of spawning runs on juvenile coho salmon density and survival.

Modelling results show that juvenile coho salmon density changed among years within sub-basins, but stream habitat characteristics over a 2–4-year time period are relatively constant. Although the overall explanatory power of models using the instream habitat or network variables datasets individually or together was low, network variables were consistently useful in each year. We interpret this to mean that while juvenile density may change across years, the fish tend to occupy the same types of habitats over time (Bell, 2001; Bell *et al.*, 2001). In addition, we noted that only sub-basins near seasonal habitats contained high densities of juvenile coho. This observation is supported by Kocik and Ferreri (1998), who found that the productivity for Atlantic salmon (*Salmo salar*) depends on the proximity of the array of habitats necessary for freshwater spawning and rearing. Stream network metrics have also proved useful in modelling stream temperature (Gardner *et al.*, 2003) and for detecting spatial patterns in stream networks (Torgersen *et al.*, 2004, 2008; Ganio *et al.*, 2005; Som, 2009). It is possible that the explanatory power of the network metrics might be increased further if a comparative measure of the quality of the seasonal habitat could have been included. Further refinement of stream survey procedures that would allow for the comparative quantification of habitat quality would be informative in the assessment of network-scale relationships among habitats.

The ability to move among habitats is critical for survival of native aquatic organisms (Hanski and Gilpin, 1991; Gresswell *et al.*, 2006). Habitats may be isolated from one another because of stream network configuration or changing environmental conditions (e.g. floods, droughts, and debris flows). Also, some habitats may be more common than others. For example, anthropogenic changes in the disturbance regimes and geomorphology of rivers in the Pacific Northwest are credited with reducing slow-water refuge habitat for juveniles, thereby limiting juvenile survivorship in the winter (Nickelson *et al.*, 1992). Individuals may be isolated from one another, or from habitats

needed to survive. Isolation for individuals in either of these instances may be related to the physical configuration of the stream network (Fagan, 2002) and to the level of mobility of the individual, which varies by species and by life-history stage (Schlosser, 1991). We found that instream habitat variables interpreted in the context of the stream network identified proximity to seasonal habitats as a possible explanation for patterns at site and sub-basin scales for juvenile coho salmon. Quantifying habitat availability and proximity as a means of understanding patterns of density is a concept relevant to other native aquatic species as well. Isolation of individuals due to habitat configuration, beyond physical barriers to movement, may provide insight to managers tasked with the recovery of species that move long distances, such as salmon, but may be even more relevant for species that have more limited mobility, such as salamanders. Management strategies that fail to consider the relative positions of habitat in a stream network ignore a critical element of the riverscape. Management strategies that consider the spatial distribution of habitats and habitat connectivity in different sub-basins are more consistent with complex environmental conditions in which native aquatic species evolved and continue to persist.

Other variables that may also be important in explaining the variation in juvenile density but were not captured in this analysis include movement barriers (complete and partial), microhabitat variables, intra- and inter-specific interactions, food availability, and predation. Natural and human barriers to movement are an important element of habitat fragmentation (Cote *et al.*, 2009) that could not be included in this analysis. Unfortunately, accurate maps of barriers were unavailable in the area of study. The importance of documenting barriers in basins is gaining recognition by conservation groups and public land managers alike, and barrier inventories are currently under way in basins throughout the western USA. Inclusion of barrier information can only improve the utility of network metrics in describing habitat connectivity. The low explanatory power of the models (especially using the instream habitat variables) could result from the ability of juveniles to exploit a wide variety of pool habitats, as is consistent with the diversity of their behaviours (Nielsen, 1992). The spatial arrangement or topology of stream habitats has been shown to be helpful in assessments of habitat

quality in other species (Jones *et al.*, 2003). In this analysis, topology appears to explain density patterns of juvenile coho salmon at least as well as instream habitat variables.

Restoration of the capacity (Ebersole *et al.*, 1997) of streams to support salmon populations may be enhanced by including habitat connectivity with habitat quantity in targeted restoration projects that increase habitat diversity and accessibility for each life-history stage. Analysis that incorporates multiple spatial scales and entire stream networks is time consuming, but offers the opportunity to tailor restoration plans and population viability assessments to stream conditions. Habitat fragmentation and lack of connectivity caused by permanent human alterations of the stream system (i.e. dams) is recognized as part of the instream habitat restoration rubric (Hart *et al.*, 2002). Including connectivity among seasonal habitats does not require a change in restoration philosophy, rather an expansion of the context of habitat beyond individual habitat units or reaches of stream to include the larger context of connectivity within the stream network. In this study, the proximity between seasonal habitats appears to be an important factor in differentiating between sub-basins with increasing or decreasing densities of juvenile coho salmon from 2001 to 2002. If a sub-basin is deficient in summer refuge habitat, but has adequate quantities of spawning gravels, such an assessment will help to identify the type, amount, and location of habitat restoration that may benefit fish the most in that stream system. This may be particularly relevant when considering the location and availability of habitats already rare or limiting to population persistence, such as over-winter refuge habitat for juvenile salmonids (Nickelson *et al.*, 1992). Considering the availability, diversity, and connectivity of habitats in a stream system necessary to support all life-history stages of coho salmon offers a holistic approach that is overlooked in current habitat restoration and protection programmes that often plan projects opportunistically rather than strategically.

Integrating metrics that represent network connectivity and position into analysis at multiple spatial scales includes an important dimension of the environment in which coho salmon evolved, and juvenile fish survive. The riverscape in which coho salmon must endure includes a diversity of habitats with varied productivity and connectivity among years and environmental conditions. Ultimately, the

persistence of coho salmon, and all aquatic species, depends on access to multiple, diverse, and connected habitat. Salmon evolved the ability to exploit the diversity of habitats and environmental conditions that naturally occur in the Pacific Northwest. This adaptability is how they have coped with the frequent disturbances and the inconsistent spawning and rearing conditions that are present around the Pacific Rim. Management strategies that consider the spatial distribution of habitats within the stream network will be better suited to the complex environmental conditions in which coho salmon evolved and continue to persist.

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APPENDIX 1

ODFW Aquatic Inventory and Analysis Project: Habitat Benchmarks

Pools		Undesirable	Desirable
	Pool area (% total stream area)	<10	>35
	Pool frequency (channel widths between pools)	>20	5–8
	Residual pool depth (m)		
	Small streams (<7 m width)	<0.2	>0.5
	Medium streams (≥7 m and <15 m width)		
	Low gradient (slope <3%)	<0.3	>0.6
	High gradient (slope >3%)	<0.5	>1.0
	Large streams (≥15 m width)	<0.8	>1.5
	Complex pools (pools w/ LWD pieces ≥3)/km	<1.0	>2.5
Riffles			
	Width/depth ratio (active channel based)		
	East side	>30	<10
	West side	>30	<15
	Gravel (% area)	<15	≥35
	Silt-sand-organics (% area)		
	Volcanic parent material	>15	<8
	Sedimentary parent material	>20	<10
	Channel gradient <1.5%	>25	<12
Shade (reach average, %)			
	Stream width <12 m		
	West side	<60	>70
	North-east	<50	>60
	Central-south-east	<40	>50
	Stream width >12 m		
	West side	<50	>60
	North-east	<40	>50
	Central-south-east	<30	>40
Large woody debris* (15 cm × 3 m minimum piece size)			
	Pieces/100 m stream length	<10	>20
	Volume/100 m stream length	<20	>30
	'Key' pieces (>60 cm dia. and ≥10 m long)/100 m	<1	>3
Riparian conifers (30 m from both side channels)			
	Number >20 in dbh/1000 ft stream length	<150	>300
	Number >35 in dbh/1000 ft stream length	<75	>200

*Values for streams in forested basins

Citation: Foster SC, Stein CH, Jones KK. 2001. *A Guide to Interpreting Stream Survey Reports*. Bowers PA (ed). Oregon Department of Fish and Wildlife, Information Reports 2001–06, Portland, OR

APPENDIX 2

Principal components analysis results for sites on the mid-coast of Oregon in 1998, 1999, 2001, and 2002 used in variable reduction for the instream habitat dataset.

Year	Axis	Eigenvalue	Percentage of variance	Cumulative percentage of variance	Dominant variables in eigenvector
1998	1	2.586	19.894	19.894	% boulder
	2	2.002	15.397	35.290	% gravel
	3	1.466	11.274	46.564	Slope
1999	1	3.138	24.139	24.139	% cobble
	2	1.778	13.678	37.817	% gravel
	3	1.445	11.115	48.932	Number of key pieces of wood
2001	1	3.084	23.726	23.726	% sand
	2	1.747	13.440	37.166	% bedrock
	3	1.575	12.116	49.282	% gravel
2002	1	2.973	22.870	22.870	% sand
	2	1.698	13.065	35.934	Number of pieces of wood
	3	1.614	12.414	48.348	% gravel

