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Fish assemblages and barriers in an urban stream network

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Abstract: Stream networks are vulnerable to fragmentation. Anthropogenic structures, such as dams and culverts, can isolate stream branches, potentially interrupting longitudinal gradients of fish distribution. The effect of single barriers is well documented, but the effect of multiple barriers in small streams is not as well characterized. We used a landscape approach and spatially continuous sampling across 2 y to examine the influence of anthropogenic structures on fish distributions in an urban stream network. After accounting for spatial autocorrelation, we found higher Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*) and lower Prickly Sculpin (*Cottus asper*) densities at locations up- than downstream of multiple culverts. Culverts had species- and year-specific stepwise effects that overrode fish distribution patterns attributable to environmental gradients. Prickly Sculpin exhibited strong spatial autocorrelation in both years, whereas Coho Salmon (*Oncorhynchus kisutch*) had negligible spatial autocorrelation in one year, a result indicating that spatial structure depends on species and year. Reaches did not have consistent fish densities across years and showed high temporal variability of fish or their habitats. Spatially continuous sampling captured gradients and heterogeneity in fish distributions and highlighted how anthropogenic structures alter these gradients. Our study also revealed which culverts had the strongest influences on fish densities throughout the stream network. The study design used can inform riverscape-management approaches, which are needed to conserve stream biodiversity effectively.

Key words: dendritic network, fish passage, riverscape, landscape

Landscape perspectives and approaches greatly inform our understanding of stream ecosystems (Fausch et al. 2002). Streams are a part of a larger drainage network, so understanding stream processes necessitates consideration of dynamics within and among stream branches (Fagan 2002, Fausch et al. 2002). Hierarchical classification organizes streams across scales, from microhabitat systems, such as gravel patches, to linear stream reaches that are nested within watersheds (Frissell et al. 1986). Studies that consider discrete habitats, or short stream reaches at a single scale, may miss large-scale processes that structure biological communities (Fausch et al. 2002), such as gradients in fine-sediment deposition (Smith and Kraft 2005) and temperature (Torgersen et al. 1999). Community composition is influenced by location along the stream continuum (Vannote et al. 1980), and is related to spatial indicators, such as stream order (Smith and Kraft 2005) and degree of branching (Grenouillet et al. 2004, McKay et al. 2013). Fish distributions and community composition within the network fluctuate intra-annually in response to changes in habitats associated with seasonal dynamics (Franssen et al. 2006). Interannual variability adds an additional dimension to stream dynamics because biological processes vary natu-

rally through time, even if habitat remains constant (House 1995). For example, the magnitude of natural variation (standard deviation [SD]) of annual trout abundances in North America was ½ of mean fish abundances (coefficient of variation [CV] = 0.49; Dauwalter et al. 2009). Because streams are variable through space and time, a riverscape approach, considering multiple scales and time frames, provides a more unified perspective of dynamics of stream networks than approaches at smaller spatial and temporal scales (Fausch et al. 2002, Wiens 2002, Altermatt 2013).

The dendritic network structure of streams may increase risk of fragmentation by anthropogenic barriers (Fagan 2002, Grant et al. 2007, Yeakel et al. 2014). Dispersal by fish and other aquatic organisms is restricted to habitats within the wetted stream channel (Grant et al. 2007). Thus, depending on its location, a single barrier can sever connectivity in an entire branch of a stream network. Individual barriers also can reduce or eliminate access to stream habitats needed to complete various life stages. For example, in the Willamette River (Oregon, USA), barriers caused by dams blocked access to spawning grounds, leading to declines of spring-run Chinook Salmon (*Oncorhynchus tshawytscha*; Sheer and Steel 2006). Fagan (2002) illustrated

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that random fragmentation within complex dendritic networks will lead to isolation of shorter stream segments than random fragmentation of simple linear systems. In addition, fish communities in fragmented stream sections have lower species richness and greater dissimilarity (β diversity) compared to communities connected to the rest of the network (Perkin and Gido 2012). Thus, fragmentation in streams has severe consequences for the occupancy and persistence of riverine populations (Fagan 2002).

Multiple anthropogenic barriers have overriding effects on species distributions in riverscapes (Fausch et al. 2002). The strength of barrier effects depends on location within the watershed (e.g., headwaters, main stem, estuary; McKay et al. 2013) and may be mediated by migratory tendencies of biota (Cote et al. 2009). For example, barriers closest to the ocean may have greatest effects on the distribution of anadromous fishes migrating between freshwater and marine habitat, whereas those in the center and the headwaters may have greatest effects on the distribution of resident fishes and potadromous fishes migrating within freshwater habitats (Cote et al. 2009, Rolls 2011). When multiple barriers are present in a stream network, fish dispersal and occupancy may decline, diminishing the magnitude of single barrier effects on fish distributions because absolute densities are lower (Perkin et al. 2013). Examining the biological effects of multiple barriers within a single stream network requires sampling at broad spatial scales, typically by using point surveys at various barriers across the stream network (Burford et al. 2009, Rolls 2011). However, spatially continuous sampling may provide more insight into how multiple barriers may interrupt natural changes in fish communities along the river continuum (Fausch et al. 2002).

To examine spatial and temporal patterns of fish assemblages in a small urban stream network, we used a continuous riverscape approach, following recommendations by Fausch et al. (2002). We examined fish densities and community metrics continuously along a small urban-stream network with multiple culverts in British Columbia, Canada. Urban streams are particularly susceptible to the presence of multiple barriers, particularly resulting from culvert crossings under roads (Elmore and Kaushal 2008). Our goal was to identify how culverts influenced fish densities across the stream network relative to other environmental variables over 2 y. We hypothesized that culverts would be associated with stepwise changes in upstream fish densities, indicating the presence of fragmentation, whereas environmental variables would influence fish densities in a linear manner reflecting a changing environment along the river continuum. We also hypothesized that culvert effects would be stronger than effects of environmental variables, indicating that stream fragmentation can override fine-scale biological patterns driven by the environment. Sampled stream reaches were in close proximity and, therefore, not independent, so we quantified the strength of spatial struc-

turing (autocorrelation) of fish densities and incorporated this autocorrelation into the analysis.

METHODS

Study site and sampling

We carried out our study in Suter Brook (lat 49°16' 52.2264"N, long 122°50'5.6220"W), a small urban stream network in Port Moody, British Columbia, Canada, during summer low flows on 22–24 August 2012, and 23–24 July 2013 (Fig. 1). Suter Brook originates in 2 small tributaries in a residential area. These tributaries converge into a main stem that flows through a riparian-buffer zone and enters the Burrard Inlet, a coastal fjord. Despite its urban setting, Suter Brook provides habitat for resident species and is used for spawning and rearing at different times of year by migratory fishes, such as Coho Salmon (*Oncorhynchus kisutch*), and Chum Salmon (*Oncorhynchus keta*). At the time of our sampling, Coho Salmon juveniles were rearing in the stream. The average annual discharge for Suter Brook is 0.07 m³/s (Fraser River Action Plan 1999), and on 23 July 2013, the discharge was 0.04 m³/s as measured across 6 cells using the midsection method (Gore 2006). The mean wetted width was 2.05 ± 0.68 m (SD) in 2012 and 2.07 ± 0.79 m in 2013. The headwaters and lower main stem were overgrown, meandering, and filled with woody debris, whereas mid-mainstem sections were channelized. Riparian vegetation along the stream length was dominated by red alder (*Alnus rubra*), black cottonwood (*Populus trichocarpa*), western hemlock (*Tsuga heterophylla*), and salmonberry (*Rubus spectabilis*). The stream passes through 2 culverts on the main stem, and 1 culvert on each of the 2 tributaries (Table S1).

We sampled fish and habitat characteristics along the fish-bearing and accessible length of stream. Starting upstream of tidal influence, we sampled fish in an upstream direction for 1017 and 1013 m of stream length in 2012 and 2013, respectively. To ensure that sampling reaches were consistent across years, we measured reaches in relation to static markers (e.g., large wood, culverts, bridges) and sampled in ~20-m increments (20.1 ± 3.2 m). Each 20-m sampling unit (reach) represented approximately the same section of stream in both years. We used single-pass electrofishing with a Smith–Root LR-24 Electrofisher (Smith–Root, Vancouver, Washington) without blocknets, as catchability in small streams is high (Bohlin et al. 1989). Single-pass electrofishing, rather than multiple-pass approaches, was required by permitting authorities to minimize effects on this ecosystem. Assistance with fish capture was provided by 1 crew member with a dip net (4.7-mm mesh). We kept fish from different reaches separately in dark, aerated 19-L buckets and released them near their capture location.

For each 20-m reach, we measured fish density for each species (no./m²; Prickly Sculpin [*Cottus asper*], Coastrange

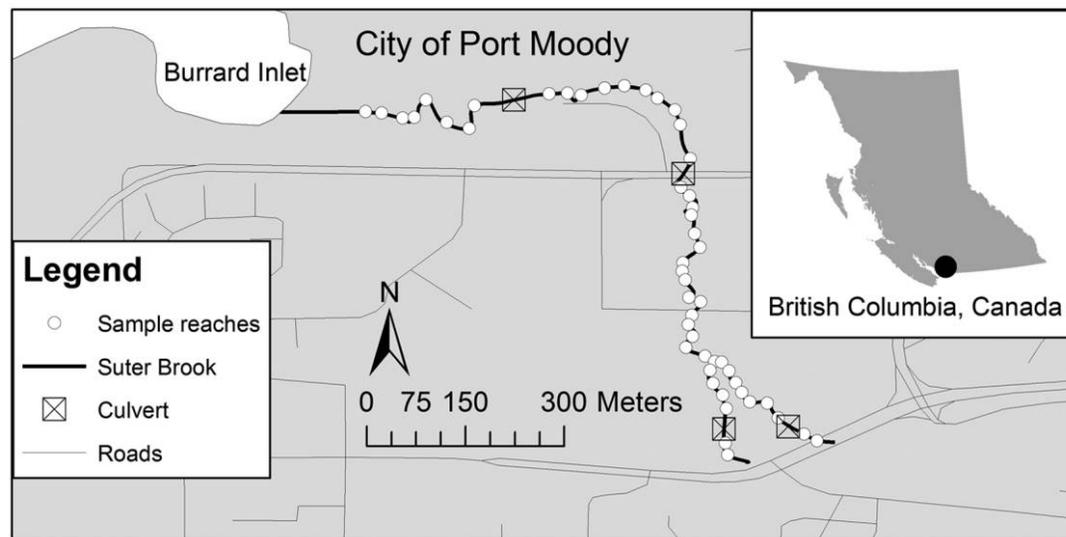


Figure 1. Map of Suter Brook and the 50 sampling reaches. The stream flows northwest into the Burrard Inlet. The most downstream culvert crosses under a pedestrian path, and the 2nd culvert crosses under Murray Street, whereas the culverts on the tributaries cross under a railroad (west tributary) and under construction rubble (east tributary). The sample reaches are marked based on coordinates obtained from the field, whereas the approximate flow path was traced to fit through the reaches.

Sculpin [*Cottus aleuticus*], Coho Salmon, Coastal Cutthroat Trout [*Oncorhynchus clarki clarki*], aggregate density (no./m²), and Simpson's Diversity Index (Simpson's diversity; $1 - D$, the probability that 2 individuals randomly selected from a reach will belong to different species). At the most downstream location of each 20-m reach, we measured wetted width, mean water depth using 3 point measurements (at 25, 50, and 75% of cross-sectional width), canopy cover (%) using a spherical densitometer, gradient (%) with an Abney hand level, and the median sediment size of haphazardly selected rocks ($n = 20/\text{reach}$) measured across the axis perpendicular to the longest axis.

Statistical analyses

Influence of culverts and environmental variables on fish abundance patterns We used an information-theoretic approach to examine the relative influence of culverts and environmental variables on fish distributions. Specifically, we assessed how fish densities within the stream network were related to cumulative culvert presence, longitudinal stream distance, and 4 other habitat variables (mean depth, median sediment size, gradient, and canopy cover; Table 1). We used generalized least squares, a type of linear regression that allows incorporation of spatial structure in model residuals (see *Spatial structuring of fish species* below). We built global models (i.e., full models including all explanatory variables) for each of the 6 fish responses, with separate models for each of the 2 years. The 6 explanatory variables accommodated multiple hypotheses that could explain fish response patterns and avoided overlooking potentially im-

portant variables. We calculated longitudinal stream distance (ocean distance) as the stream network distance from the most downstream location in the study (just above the stream outlet) to the start of a given reach. Ocean distance represents gradients in abiotic conditions that naturally occur along rivers (Vannote et al. 1980, Jackson et al. 2001). Potential effects of culverts are shown relative to mean effect of the adjacent downstream culvert. We did not count stream length in culverts toward the stream network distance (Cote et al. 2009).

We used model selection and model averaging to explore the effect of culverts on fish densities and diversity relative to ocean distance and environmental variables (Burnham and Anderson 2002). We standardized our continuous predictor variables to mean = 0 and SD = 1 so that coefficient estimates could be compared across variables measured in different units (Schielzeth 2010). We tested all combinations of models fit with maximum likelihood and ranked them by Akaike's Information Criterion for small sample size (AICc) score using the *dredge* function in package *MuMIn* (Bartoń 2013) in R (version 2.15.3; R Project for Statistical Computing, Vienna, Austria). Because the weight of the best model for all responses was <0.90, we implemented a model-averaging approach (Burnham and Anderson 2002). To estimate variable effect size and direction we computed model-averaged standardized coefficients based on the weighted average of models (Burnham and Anderson 2002, Grueber et al. 2011). We report coefficients in conjunction with their associated unconditional confidence intervals (CIs), and mean weighted variable importance (w), which is the summed Akaike weight

Table 1. Variables included in global generalized least squares model. SD = standard deviation.

Covariate (units)	Covariate type	Mean	SD	Range	Specific hypothesis	Reference
Stream gradient (%)	Continuous	2.0	1.4	0.0–6.0	Sculpin <i>Cottus</i> spp. prefer low gradients. Coastal Cutthroat Trout (<i>Oncorhynchus clarki clarki</i>) are found in high-gradient headwater tributaries.	Hawkins et al. 1983, Buehrens et al. 2013
Mean depth (cm)	Continuous	10.7	6.4	2.3–23.7	Coastal Cutthroat Trout have a strong preference for depth >25 cm. Young-of-year Coastal Cutthroat Trout prefer shallower habitat.	Heggenes et al. 1991, Rosenfeld et al. 2000
Canopy cover (%)	Continuous	77.9	16.4	7.3–98.0	Canopy cover affects invertebrate (food) distribution and foraging opportunities.	Heggenes et al. 1991, Hetrick et al. 1998
Cumulative number downstream culverts (<i>n</i>)	Ordered factor	–	–	0–3	Barriers near river outlets have greatest effects on connectivity of diadromous fishes, whereas barriers further upstream have greatest effects on connectivity of potadromous fishes.	Cote et al. 2009
Sediment size (mm)	Continuous	20.9	36.1	2.0–256.0	Fish select habitat with various substrate size. <i>Cottus</i> spp. prefer finer sediments.	Hawkins et al. 1983, Heggenes et al. 1991, Soulsby et al. 2001
Ocean distance (m)	Continuous	–	269.4	1.0–870.0	Smooth transitions in abiotic factors structure communities across longitudinal marine–freshwater gradients.	Jackson et al. 2001, de la Hoz Franco and Budy 2005, Buisson et al. 2008

of all models with the given variable. Variable importance $w = 1$ signifies that the variable was in all top models.

Spatial structuring of fish species Spatial autocorrelation occurs when sampling points and their associated data are either clustered together in space (positive autocorrelation) or dispersed (negative autocorrelation). If not accounted for, patterns may be incorrectly attributed to an environmental variable when the relationship is actually driven by proximity to sampling points with similar data (Keitt et al. 2002, Kühn 2006). To account for potential autocorrelation in fish distribution patterns, each of the global models contained a spatial correlation structure specified by an exponential variogram function (Cressie 1993). An exponential variogram function specifies that points separated by a given distance have a correlation structure defined by an exponential equation (Zhao et al. 2009). We

tested several other types of variogram functions (i.e., spherical, linear, Gaussian), but they yielded higher (indicating worse model fit) or similar AICc values ($\leq 4 \Delta AICc$ points). We fit variogram models based on a 50×50 matrix that described the network distances among each of the 50 reaches. We did not include a nugget effect because of our small sampling intervals (i.e., every 20 m; Cressie 1993). In some cases, spatial autocorrelation can be accounted for with environmental variables that explain variation in species distribution (Diniz-Filho et al. 2003). Although we had several environmental variables in the global model, for consistency, we included a formal exponential variogram structure in all 12 of our global models (6 response variables for 2 years).

We explicitly tested for the presence and magnitude of autocorrelation in our fish responses and habitat variables using Moran's *I* test, based on a matrix of inverse stream network distances (Dormann et al. 2007) made with the

igraph package (Csárdi and Nepusz 2006) in R. We visualized spatial autocorrelation by plotting Moran's I as a function of stream network separation distance by using SAM (version 4.0; Rangel et al. 2010). We used the default number of classes with equal numbers of pairs in each bin and tested significance with 999 permutations (Trautwein et al. 2012). Values of the Moran's I are bound between -1 and $+1$, where -1 signifies complete dispersion, $+1$ signifies perfect correlation, and 0 signifies random structure. The point at which Moran's I becomes negative for the first time represents the extent of positive spatial autocorrelation.

We quantified the spatial variability of fish densities among stream reaches for each of our 2 years of data. We calculated the CV for each of our fish responses by dividing the SD by the mean. Higher values of CV indicate relatively higher spatial variability in the stream network. Lower values of CV indicate relatively lower spatial variability in the stream network.

Temporal variability of species and habitats We quantified differences in densities and habitats between years with paired t -tests with unequal variance and a Bonferroni correction (α/n , where $n = 8$ and $\alpha = 0.05$) to account for multiple

comparisons. That is, data were compared between reaches that represented the same 20-m stream segments in both years. For habitat metrics, we examined the temporal differences in mean canopy cover and mean depth, but not gradient and median sediment size. The latter variables were measured once in 2012 and were not expected to change over the course of 1 year. We also examined whether reaches retained the same fish densities and diversity through time by calculating Spearman's rank correlation coefficients (ρ) for densities in paired reaches. That is, correlations represented the relationship between responses measured in the same 20-m stream reaches in 2 study years and allowed us to assess the degree to which habitats maintained similar densities across years.

RESULTS

We captured fish in 99 of 100 total reaches (50 reaches \times 2 years; Figs 2, S1) for a total of 585 and 284 fish in 2012 and 2013, respectively. Fish densities declined between 2012 and 2013 across all species except Coastal Cutthroat Trout (Table 2). In 2012, overall species composition was 40% juvenile Coho Salmon, 31% Coastal Cutthroat Trout, 14% Prickly Sculpin, and 12% Coastrange Sculpin. In con-

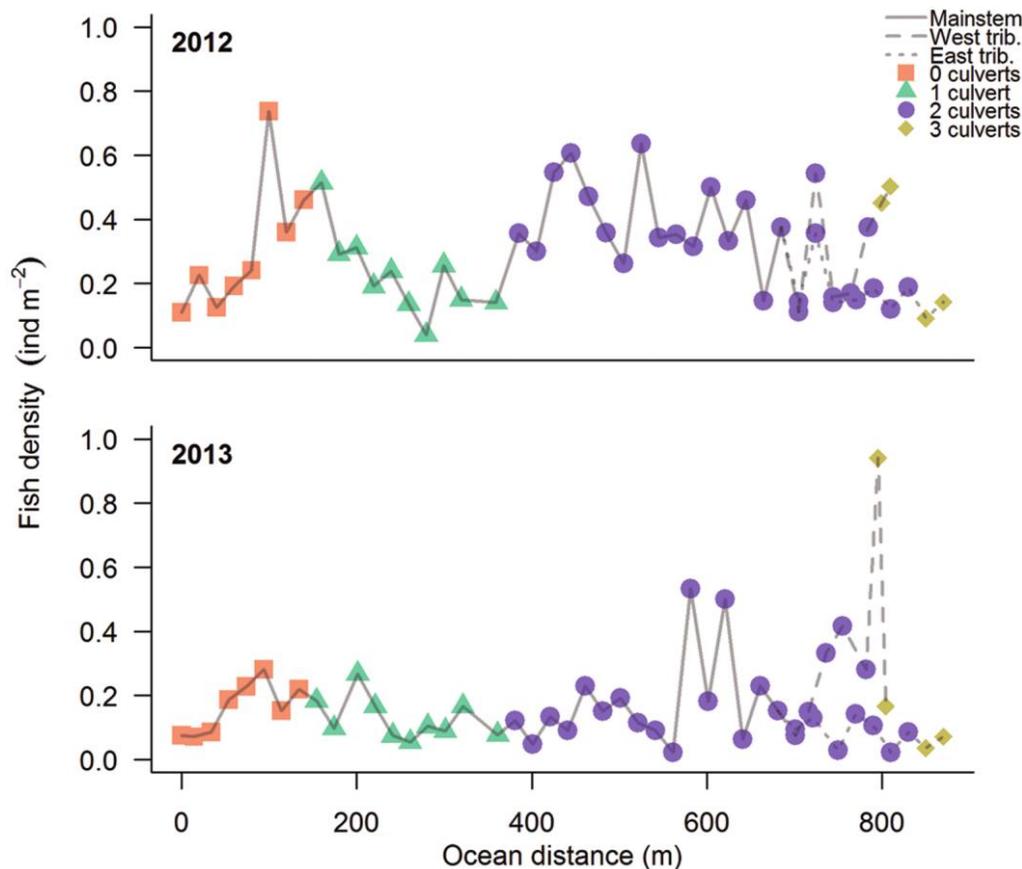


Figure 2. Total fish densities in relation to distance from the ocean for 2012 and 2013 (top and bottom, respectively). Points are connected by light gray lines and split at ~ 700 m, the junction of 2 tributaries. The stream flow moves right to left on the graphs.

Table 2. Results from paired *t*-tests examining the difference between 2013 and 2012 fish responses (densities and Simpson's diversity) and habitat responses. Fish responses are presented as densities (individuals/m²), except for Simpson's diversity (1 - D). Habitat responses are canopy cover (%) and mean channel depth (cm). * indicates significance after Bonferroni correction. In one reach, Simpson's diversity could not be measured because no fish were caught. Therefore, the row of data was removed, and sample size decreased by one. df = degrees of freedom.

Response	Difference	<i>t</i>	df	<i>p</i>
Fish				
Total fish	-0.13	-4.54	49	<0.0001*
Simpson's diversity	-0.19	-5.26	48	<0.0001*
Coho Salmon	-0.11	-7.70	49	<0.0001*
Coastal Cutthroat Trout	0.01	0.30	49	0.7655
Prickly Sculpin	-0.01	-2.86	49	0.0062
Coastrange Sculpin	-0.01	-2.41	49	0.0195
Habitat				
Canopy cover	10.61	7.79	49	<0.0001*
Mean depth	0.88	0.86	49	0.3957

trast, during 2013, the species composition was 6, 54, 18, and 16%, for juvenile Coho Salmon, Coastal Cutthroat Trout, Prickly Sculpin, and Coastrange Sculpin, respectively. In addition, over both years we caught 9 Threespine Stickleback (*Gasterosteus aculeatus*) and 4 larval lamprey (probably Pacific Lamprey [*Entosphenus tridentatus*]; McPhail and Carveth 1994). Sampled reach area did not vary between years (2012: 41.6 ± 15.0 m², 2013: 41.4 ± 15.8 m²), but mean species richness within each reach was considerably higher in 2012 (2.5 ± 1.1 species) compared to 2013 (1.5 ± 1.1 species).

Influence of culverts and environmental variables on fish abundance patterns

AICc model selection resulted in 5 to 23 models within the 4 ΔAICc group, depending on response variable and year (Tables S2, S3). Top-ranked models (those within 4 ΔAICc) had weights ranging from 0.12 to 0.45 (mean = 0.26 ± 0.10). Thus, top models existed based on ΔAICc values, but they did not meet the criterion of *w* > 0.90, which would indicate support for a single model for a given response. Across some fish responses, ocean distance and cumulative culvert number had strong support as explanatory variables (mean weighted variable importance [importance] > 0.9; Table 3). For each fish response below, we highlight the predictor variables in the top-ranked group. In addition, the importance and effect size of ocean distance and cumulative culvert number varied by year as described below. Unless otherwise noted, environmental variables did not have a strong effect on fish responses.

Total fish densities Top-ranked models were mostly made up of environmental predictor variables, and some contained ocean distance and cumulative culvert number

variables (Tables S2, S3). In 2012 and 2013, the top-ranked models included intercept-only models. Ocean distance did not influence total fish densities in 2012 ($\beta = -0.090$, CI = -0.281–0.101) and 2013 ($\beta = 0.016$, CI = -0.031–0.062; Fig. 3A) and had low importance in both years (2012: *w* = 0.25, 2013: *w* = 0.16; Table 3). In 2012, the 2nd culvert was associated with an increase in fish density upstream (culvert 2: $\beta = 0.329$, CI = 0.119–0.538), but no culvert effect was detected in 2013. Cumulative culvert number had low importance in both years (2012: *w* = 0.14, 2013: *w* = 0.04).

Simpsons diversity Top-ranked models in 2012 included predictor variables for cumulative culvert number, ocean distance, and environmental variables (Table S2). Top-ranked models in 2013 included ocean distance and environmental variables, but not cumulative culvert number (Table S3). In both years, ocean distance had a negative influence on Simpson's diversity (2012: $\beta = -0.117$, CI = -0.237–0.003; 2013: $\beta = -0.171$, CI = -0.249 to -0.093; Fig. 3B). Ocean distance importance increased from *w* = 0.60 in 2012 to *w* = 1.00 in 2013 (Table 3). The cumulative culvert number had a strong negative effect on Simpson's diversity in 2012 at the 3rd culvert ($\beta = -0.368$, CI = -0.571 to -0.165, *w* = 1.00).

Coho Salmon density Top-ranked models in 2012 included ocean distance, cumulative culvert number, and environmental predictor variables (Table S2). In 2013, cumulative culvert number was absent and the intercept-only model was present among top-ranked models (Table S3). Ocean distance did not influence Coho Salmon densities in 2012 ($\beta = -0.035$, CI = -0.132–0.063) and 2013 ($\beta = -0.001$, CI = -0.007–0.004; Fig. 3C). The importance of ocean distance declined from 2012 to 2013 (*w* = 0.43 and

Table 3. Importance of variables in the set of top models $\leq 4 \Delta AICc$ (Akaike's Information Criterion for small sample sizes) points for each fish response by year. Responses are presented as densities (individuals/m²), except for Simpson's diversity (1 - D). Importance is the summed Akaike weight of all models containing the given variable. NA indicates the variable was not in the top-ranked model set.

Year	Response	Variable importance					
		Cumulative culverts (m)	Ocean distance (m)	Canopy cover (%)	Gradient (%)	Sediment size (mm)	Depth (m)
2012	Total fish density	0.14	0.25	0.18	0.57	0.12	0.12
	Simpson's diversity	1.00	0.60	0.13	0.13	0.13	0.13
	Coho Salmon	0.47	0.43	0.20	0.89	0.20	0.24
	Coastal Cutthroat Trout	0.95	0.29	0.23	0.34	0.46	0.10
	Prickly Sculpin	0.21	1.00	0.09	0.27	0.09	0.15
	Coastrange Sculpin	0.04	0.65	0.13	0.13	0.17	0.12
2013	Total fish density	0.04	0.16	0.16	0.15	0.09	0.71
	Simpson's diversity	NA	1.00	0.13	0.13	0.13	0.15
	Coho Salmon	NA	0.15	0.13	0.46	0.14	0.16
	Coastal Cutthroat Trout	0.45	0.55	0.24	0.10	0.10	0.77
	Prickly Sculpin	1.00	0.11	0.22	0.09	0.10	0.19
	Coastrange Sculpin	0.02	0.91	0.42	0.76	0.66	0.19

0.15, respectively; Table 3). In 2012, higher Coho Salmon densities were found upstream of the 2nd culvert ($\beta = 0.134$, CI = 0.003–0.266, $w = 0.47$), but in 2013, cumulative culvert number did not rank within the 4 $\Delta AICc$ model set. Stream gradient was negatively associated with Coho Salmon density in 2012 ($\beta = -0.034$, CI = -0.063 to -0.006, $w = 0.89$).

Coastal Cutthroat Trout densities For both years, top-ranked models included ocean distance, cumulative culvert number, and environmental predictor variables (Tables S2, S3). Coastal Cutthroat Trout density was not associated with ocean distance in 2012 ($\beta = -0.025$, CI = -0.034–0.004) and 2013 ($\beta = 0.051$, CI = -0.009–0.112; Fig. 3D). Ocean distance importance increased from $w = 0.29$ in 2012 to $w = 0.55$ in 2013 (Table 3). Cumulative culvert number positively affected Coastal Cutthroat Trout density at the 3rd culvert in 2012 ($\beta = 0.136$, CI = 0.037–0.235) and 2013 ($\beta = 0.183$, CI = 0.024–0.344). Cumulative culvert number importance decreased from $w = 0.95$ in 2012 to $w = 0.45$ in 2013.

Prickly Sculpin densities For both years, top-ranked models included ocean distance, cumulative culvert number, and environmental predictor variables (Tables S2, S3). In 2012, all top-ranked models included a variable for ocean distance, whereas in 2013, all top-ranked models included a variable for cumulative culvert number. Ocean distance had a negative effect on Prickly Sculpin in 2012 ($\beta = -0.038$, CI = -0.058 to -0.018), but not 2013 ($\beta = -0.006$, CI = -0.028–0.016; Fig. 3E). For Prickly Sculpin,

ocean distance importance decreased from $w = 1.00$ in 2012 to $w = 0.11$ in 2013 (Table 3). The 2nd culvert positively affected Prickly Sculpin density in 2012 ($\beta = 0.044$, CI = 0.006–0.083). In 2013, the 1st culvert had a negative effect on Prickly Sculpin density ($\beta = -0.057$, CI = -0.087 to -0.026). Cumulative culvert number importance increased from $w = 0.21$ in 2012 to $w = 1.00$ in 2013.

Coastrange Sculpin density For both years, models in the top-ranked group included ocean distance, cumulative culvert number, and environmental predictor variables, and the intercept-model was a top-ranked model in 2012 (Tables S2, S3). Ocean distance had a negative influence on Coastrange Sculpin densities in 2012 ($\beta = -0.021$, CI = -0.040 to -0.003) and 2013 ($\beta = -0.015$, CI = -0.024 to -0.004, Fig. 3F). The importance of ocean distance was $w = 0.65$ and $w = 0.91$ in 2012 and 2013, respectively (Table 3). In 2012, cumulative culvert number had no effect, whereas in 2013, the 1st culvert had a negative effect on upstream density ($\beta = -0.036$, CI = -0.065 to -0.007). Importance of cumulative culvert number was low (2012: $w = 0.04$, 2013: $w = 0.02$), indicating the high degree of uncertainty surrounding estimates of model coefficients for the effect of culverts. Stream gradient had a weak but positive association with Coastrange Sculpin in 2013 ($\beta = 0.008$, CI = 0.0002–0.015, $w = 0.76$).

Spatial structuring of fish species

Moran's I correlograms showed that all fish responses had significant positive autocorrelation at small separation

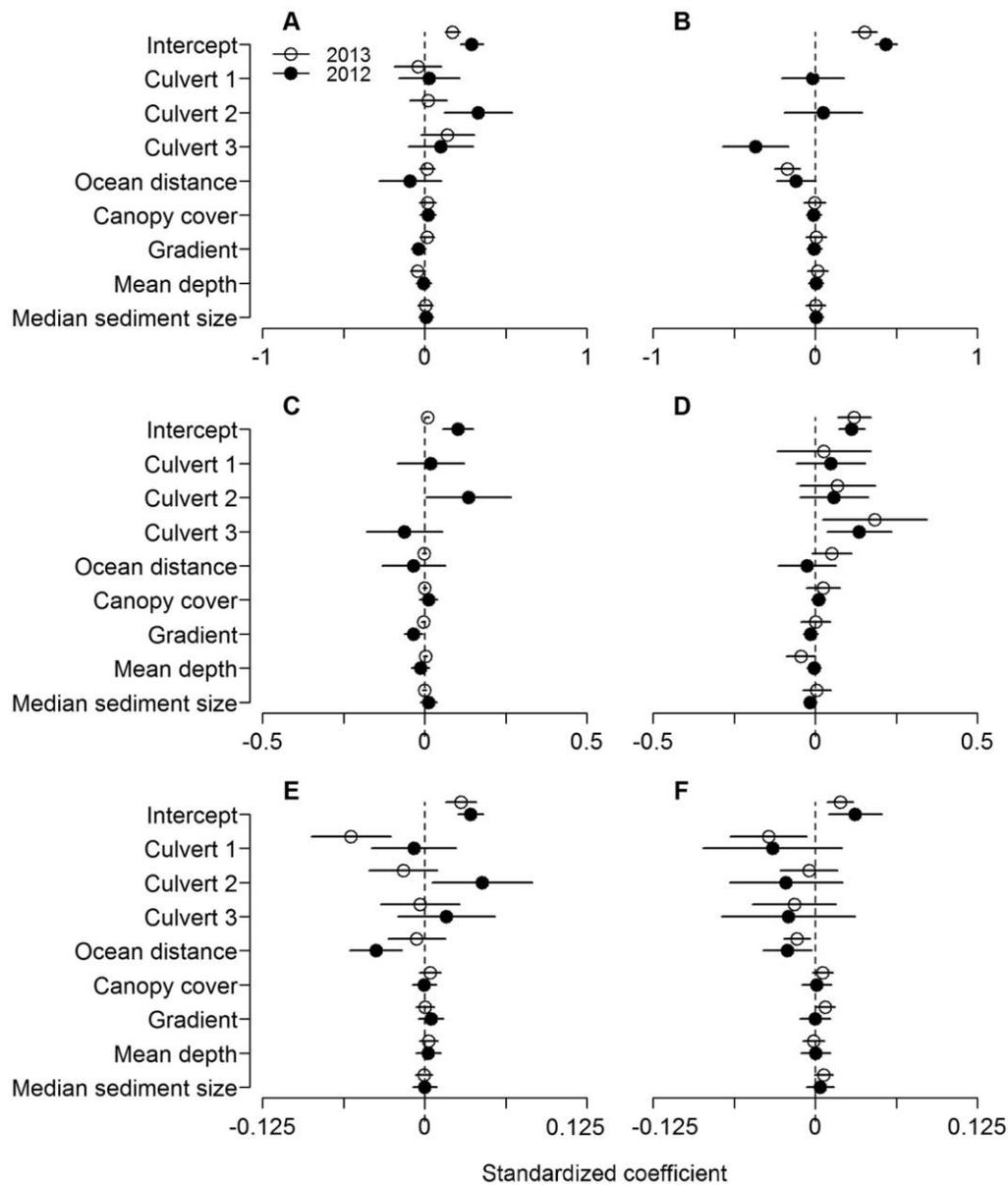


Figure 3. Standardized model average coefficients (95% CI) for generalized least squares models examining the relative effect of culvert and habitat variables on total fish density (A) and diversity (B), and density of Coho Salmon (C), Coastal Cutthroat Trout (D), Prickly Sculpin (E), and Coastrange Sculpin (F).

distances, except Coho Salmon in 2013 (Fig. 4A–F). In other words, fish density data (except 2013 Coho Salmon) were more similar when reaches were close together. Prickly Sculpin density had the overall strongest autocorrelation at small separation distances (both years), which gradually transitioned to a strong negative autocorrelation as indicated by the negative trend in Moran’s *I* with increasing separation distance. Simpson’s diversity, Coastal Cutthroat Trout, and Coastrange Sculpin density also transitioned from positive to negative autocorrelation as separation distance increased. Coastrange Sculpin transitioned to a significant

negative value of Moran’s *I* at ~600 m separation distance in both years, whereas the remaining responses did so at ~500 m. Total fish density and Coho Salmon density had the smallest degree of autocorrelation, as visualized by the narrow range of positive Moran’s *I* and values of ~0 across other separation distances. Correlograms for habitat variables showed less autocorrelation than in fish responses (Fig. 5A–D). Mean reach depth (2012) and canopy cover (2013) were positively autocorrelated at small separation distances and became randomly structured at larger separation distances. Gradient and sediment size were not auto-

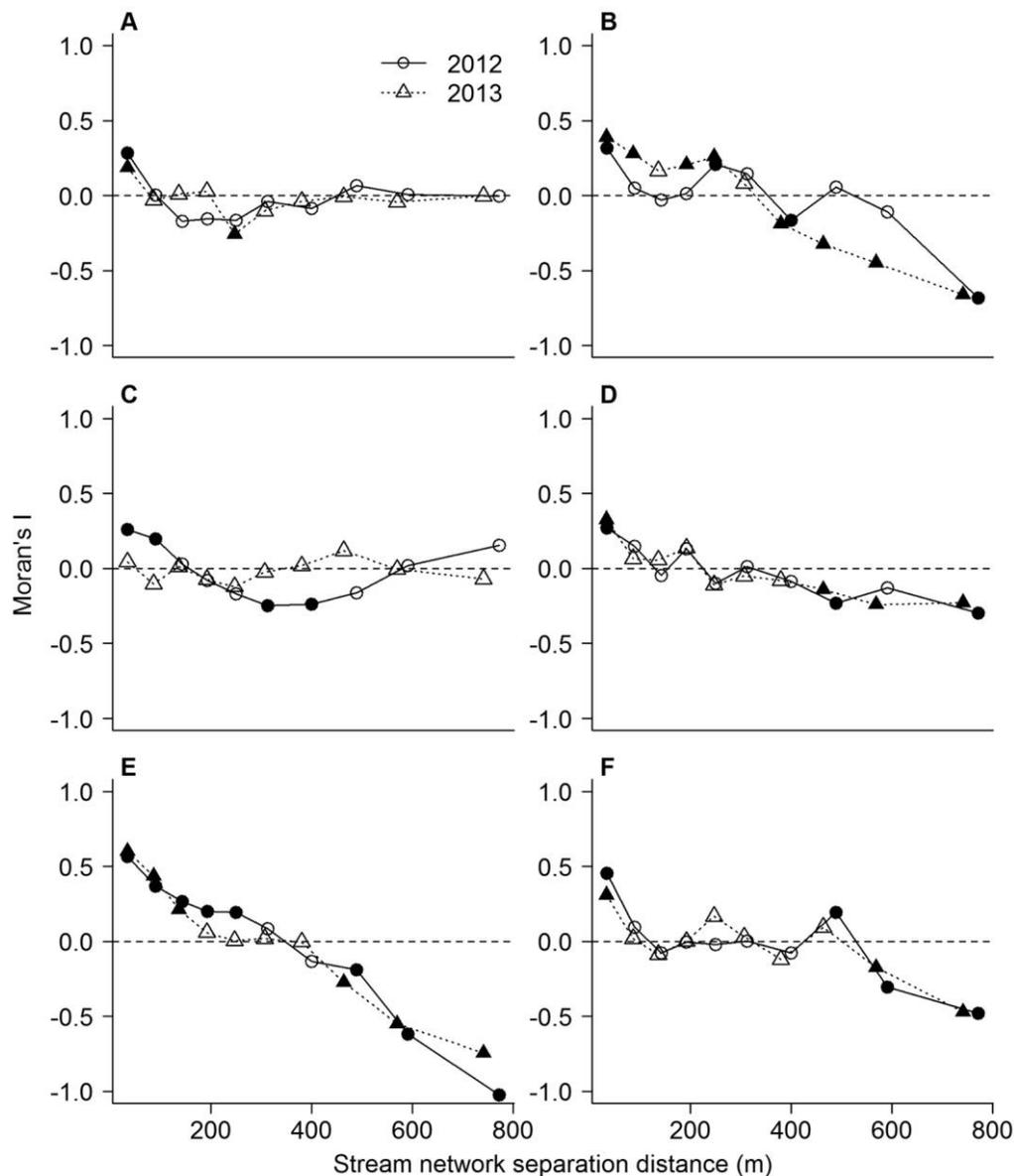


Figure 4. Spatial correlograms of Moran's I for total fish density (A) and diversity (B), and density of Coho Salmon (C), Coastal Cutthroat Trout (D), Prickly Sculpin (E), and Coastrange Sculpin (F) across various stream separation distances within the stream network. Filled symbols indicate significance at $p < 0.05$. Open symbols indicate nonsignificance. Moran's I values of -1 signify complete dispersion, $+1$ signifies perfect correlation, and 0 signifies random structure of fish metrics. The distance at which the Moran's I first becomes negative in the correlogram is the average distance at which the spatial autocorrelation no longer exists.

correlated at any distance, highlighting the fine-scale variation in these physical variables.

CVs were higher for individual species densities than for total fish density (Table 4), indicating that combined fish density was less variable across space than density of individual species. CVs showed some increases in 2013 compared to 2012, possibly because mean density decreased overall (Table 2). Between 2012 and 2013, respectively, Prickly Sculpin CV increased from 1.26 to 1.69, Coastrange Sculpin CV increased from 1.52 to 1.53, Coho Salmon CV

increased from 0.83 to 2.26, and Coastal Cutthroat Trout CV increased from 0.88 to 1.44.

Temporal variability of species and habitats

Mean Coho Salmon density, total fish density, and Simpson's diversity decreased from 2012 to 2013, whereas Coastal Cutthroat Trout, Prickly Sculpin, and Coastrange Sculpin densities did not change significantly across years (Table 2). Mean reach canopy cover increased by 10.6% ($t = 7.79$, $p < 0.0001$), but mean depth of reaches did not

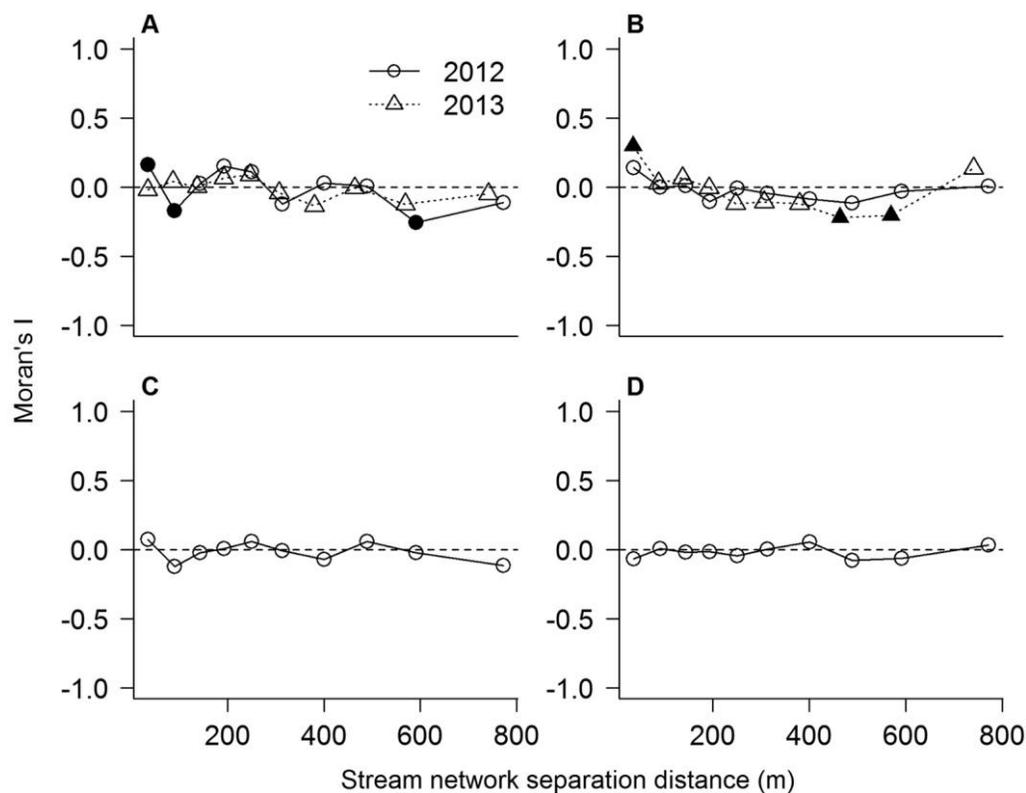


Figure 5. Spatial correlograms of Moran's I for mean reach depth (A), canopy cover (B), stream gradient (C), and sediment particle size (D) across various stream separation distances within the stream network. Filled symbols indicate significance at $p < 0.05$. Open symbols indicate nonsignificance. Moran's I values of -1 signify complete dispersion, $+1$ signifies perfect correlation, and 0 signifies random structure of fish metrics. The distance at which the Moran's I first becomes negative in the correlogram is the average distance at which the spatial autocorrelation no longer exists.

change ($t = 0.86$, $p = 0.396$). Fish densities and diversity measured in the same 20-m reaches were not tightly correlated between years. Spearman's rank correlation coefficients ranged from $\rho = 0.41$ to $\rho = 0.67$ for total fish density, Simpson's diversity, Coastal Cutthroat Trout density, Prickly Sculpin density, and Coastrange Sculpin density (Fig. 6A, B, D–F). Coho Salmon density was not correlated between years ($\rho = -0.10$; Fig. 6C).

DISCUSSION

Influence of culverts and environmental variables on fish abundance patterns

Previous theoretical work indicated that effects of barriers near stream outlets may carry through to the rest of the stream network (McKay et al. 2013). Our data provides evidence of the network-wide effect of a single downstream culvert. Prickly Sculpin density was clustered low in the stream network, and their density decreased in a stepwise manner upstream of the 1st culvert in 2013. The most downstream culvert had a negative effect on Coastrange Sculpin in the same year. These data suggest that

Table 4. Spatial coefficients of variation (CV) for fish and habitat responses. CV was calculated by dividing the standard deviation of fish density by mean fish density in reaches of a given year. Fish responses are presented as densities (individuals/m²), except for Simpson's diversity ($1 - D$).

Response	CV	
	2012	2013
Fish		
Total fish density	0.55	0.92
Simpson's diversity	0.39	0.91
Coho Salmon	0.83	2.26
Coastal Cutthroat Trout	0.88	1.44
Prickly Sculpin	1.26	1.69
Coastrange Sculpin	1.52	1.53
Habitat		
Canopy cover (%)	0.21	0.12
Mean depth (cm)	0.60	0.56
Median sediment size (mm)	1.72	–
Gradient (%)	0.71	–

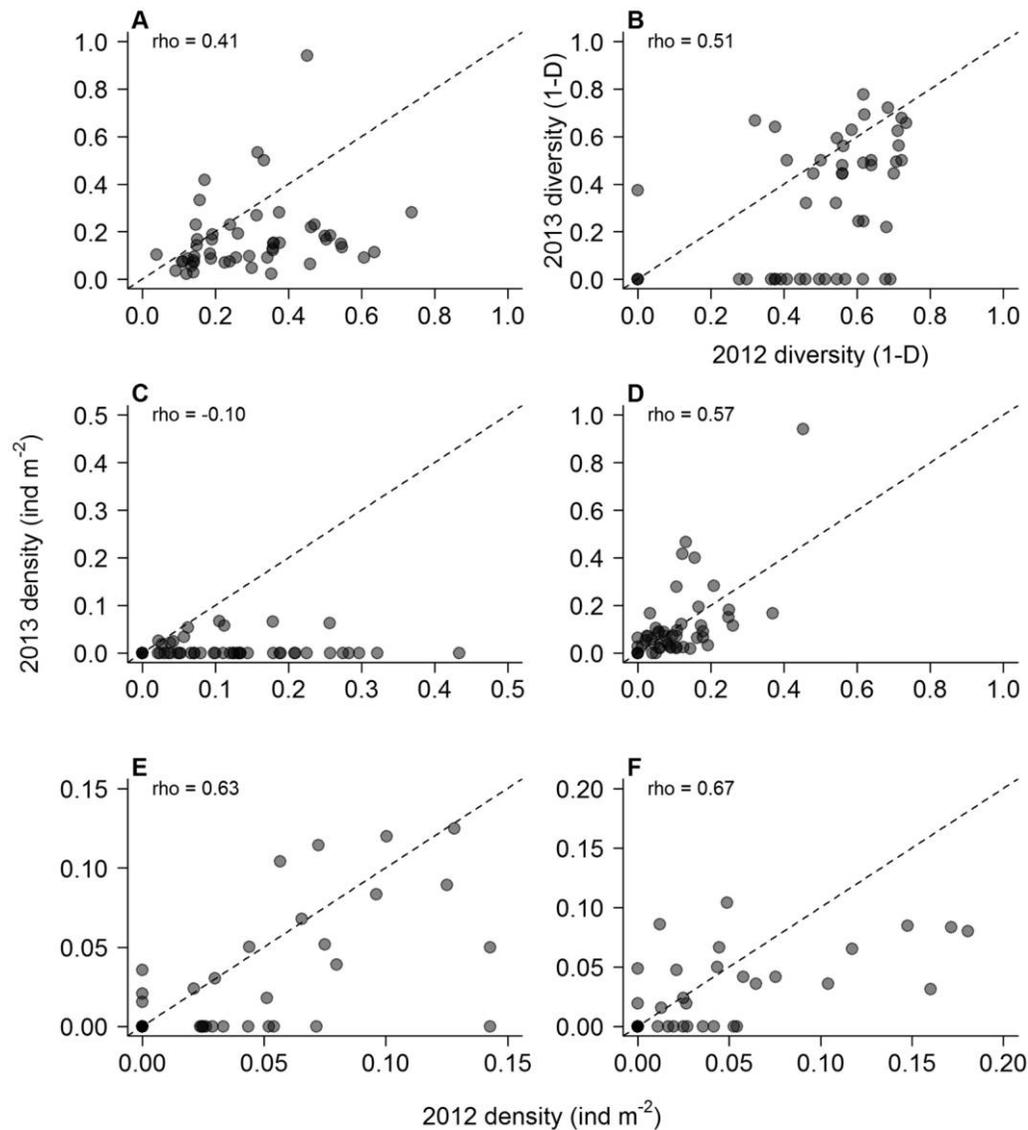


Figure 6. Scatterplots of 2012 vs 2013 raw values for total fish density (A) and diversity (B), and density of Coho Salmon (C), Coastal Cutthroat Trout (D), Prickly Sculpin (E), and Coastrange Sculpin (F). Spearman's rank correlation is given by ρ , and the dotted line is the 1:1 line. A slight transparency was applied to points so overlap can be visualized. Ind = individuals.

culverts near the outlet are particularly important to consider when prioritizing barriers for restoration (Cote et al. 2009). Maintenance of even limited passage through culverts near outlets ensures that a stream does not become fully disconnected (McKay et al. 2013). Furthermore, maintaining connectivity in central parts of stream networks also is important for biodiversity (Carrara et al. 2014). The 2nd culvert in the center of our network influenced fish responses in 2012, and the direction of effect was positive (total fish density, Prickly Sculpin density, and Coho Salmon density). This pattern may be explained by the possibility that the 2nd barrier decreased downstream movement, leading to higher fish density in some years. In tributaries, where habitat size is smaller and downstream culverts already have

filtered out components of the fish community, the magnitude of potential culvert effects was expected to be smaller because the absolute fish densities were expected to be lower (Perkin et al. 2013). However, when the tributary culverts had a detectable effect on the fish community (Coastal Cutthroat Trout densities in 2012 and 2013, and Simpson's diversity in 2012), the effect was stronger than that of the other culverts in the same year. Almost all fish upstream of culverts on tributaries were Coastal Cutthroat Trout, and their densities were high, particularly in the West tributary. The culvert on the West tributary was the only perched culvert in our study. Thus, it might have been excluding upstream movement of other species or isolating Cutthroat Trout upstream. By examining each culvert in

Suter Brook, we showed that culverts in different locations in the stream network have effects in either positive or negative directions that apparently are mediated by species-specific responses.

Spatially continuous sampling enables simultaneous examination of variables that act on different spatial scales. Continuous sampling across these scales was possible because the study stream was relatively small, but such sampling may not always be feasible. Another consideration was that locations with greater ocean distance were more likely than locations with smaller ocean distance to have a larger number of downstream culverts. Our choice to include both variables in full models, despite their relatedness, was based on the distinction that they represented 2 different processes for fish communities (Smith et al. 2009). We were able to distinguish the effects of both variables for our responses because changes in fish distribution related to ocean distance would appear as gradual and smooth gradients (Jackson et al. 2001), whereas changes driven by number of downstream culverts would be marked by discrete shifts (Mariano et al. 2012). In some instances, ocean distance and cumulative number of culverts were present together in top models. Removal of ocean distance from models would have led to overestimation of the influence of culverts (Smith et al. 2009), thus, the coefficient estimates we calculated are conservative. We did not detect many strong effects of environmental variables, so we think it likely that the effects of environmental variables occurred at spatial scales smaller than we measured, such as at pool/riffle or microhabitat levels with <20-m resolution (Frissell et al. 1986). Our sampling and statistical approach offers an important example of how to investigate natural and anthropogenic drivers of fish communities in stream networks.

Spatial structuring of fish species

Spatial autocorrelation warrants investigation in ecological studies to identify and account for potential biases in results (Diniz-Filho et al. 2003). As expected, reaches separated by smaller distances were more similar to each other than distant reaches for almost all fish responses. In the 1 instance where no spatial autocorrelation was detected (2013 Coho Salmon density data), the CV was high (>2), signifying high variability throughout the stream network, probably because density was low. Total fish density and diversity were positively autocorrelated only at very short separation distances (<~100 m). At greater separation distances, total density data became heterogeneous. This result is consistent with our observation that total fish density was more stable (lower CV) than individual species density, indicating higher spatial stability for the aggregate fish community. By testing for, and incorporating, autocorrelation structure in our analyses with spatially continuous data, we ensured that patterns were not incor-

rectly attributed to explanatory variables when they were driven by spatial proximity.

Temporal variability of species and habitats

The effects of culverts varied through the 2 y of study, suggesting potential changes in permeability and passage success. For example, the cumulative culvert factor dropped out of top model sets for 2013 Simpson's diversity and Coho Salmon density. We did not observe differences in depth or wetted width among our reaches that would indicate that changes in flow, seasonality, and preceding flow events may have influenced effects of culvert. In some instances, runoff events related to storms may raise the flow such that culverts are no longer perched, which may improve passage success (Norman et al. 2009). However, precipitation records for the 3 wk preceding our field sampling did not show evidence of large precipitation events that may have affected flow (2.9 mm in 2012 vs 0 mm in 2013; Environment Canada 2013). Another possibility is that the quality of habitat may have changed between years. For example, canopy cover, which is associated with fish food availability, increased 10.6% in 2013. The summer low-flow period between July and August is a high-stress period for fish (Thomas et al. 1986), so changes in an unmeasured habitat variable may have exacerbated stress and initiated a shift in fish distributions. Thus, our results support the possibility that culvert permeability may change between years depending on subtle flow conditions (Bouska and Paukert 2010).

Even when habitat remains consistent, fish populations can vary interannually (Platts and Nelson 1988, Pess et al. 2002). Therefore, it might not be surprising that Coho Salmon decreased substantially between the 2 sampling years. This pattern cannot be attributed to the supplementation of juveniles with hatchery outplanting because Suter Brook has not had hatchery supplementation of Coho Salmon in ~20 y (R. Foster, Mossom Creek Hatchery, personal communication). Coastal Cutthroat Trout density did not significantly change between years, even though annual Coastal Cutthroat Trout abundances can fluctuate naturally within a range that is greater than mean abundances (Platts and Nelson 1988).

Toward understanding river networks through space and time

The distribution of fish habitats in rivers is temporally variable (Stanford et al. 2005). Processes that occur in the short term, such as flood and high-flow events may move sediments by erosion and deposition, changing habitat structure and distribution (Stanford et al. 2005). This concept, called the shifting habitat mosaic, describes the dynamic nature of riverine habitats (Stanford et al. 2005). Our results support the concept that streams have a shifting mosaic

of fish habitat. Reaches with high densities in 2012 were only moderately likely to have high densities in 2013, as evidenced by moderate correlation coefficients. For Coho Salmon especially, correlation between years was negligible, probably in part, because densities dropped significantly in 2013. Our results are similar to findings that suggest habitats with similar morphology can have variable abundances of Coastal Cutthroat Trout over space (Torgersen et al. 2004), whereas we highlight that this variation also occurs over time.

Conclusion

The body of research on stream networks and how barriers structure fish communities is growing, and modeling approaches are used often (e.g., Fagan 2002, McKay et al. 2013, Perkin et al. 2013; but see Rolls 2011, Perkin and Guido 2012). Together, theoretical studies, such as these, have shown that branching riverine networks respond to barriers in a manner different from linear and 2-dimensional landscapes (Fagan 2002). For example, randomly placed barriers in riverine landscapes create smaller patch sizes with greater variance than in linear landscapes (Fagan 2002). If the barrier is placed low in the network, the effect can be detected throughout the branches upstream (McKay et al. 2013). When barriers create small fragments (such as those often found in headwaters), and their permeability is low, they may have severe consequences for the persistence of communities (Perkin et al. 2013).

Our empirical study supported some of the predictions of these modeling studies. For example, we found an effect at the 1st barrier that carried into the rest of the stream network and that the small habitat patches created by culverts in tributaries had the lowest diversity. However, we also found context dependency, with the direction of responses to culverts depending on the species, culvert location in the stream network, and year. Reconciling theory with the complexity of stream fish dynamics remains a challenge. We think that the continuous whole-stream network approach we took offers promise for illuminating riverscape dynamics and providing insights for applied issues. Understanding these relationships has important management applications, such as evaluation of barriers to prioritize restoration and guiding fish monitoring.

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