Fish Assemblages and Potential Barriers in Urban Streams

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Ethics Statement

Abstract

Urbanization and associated infrastructures may fragment habitats, particularly within streams. This thesis examines the impacts of culverts on fish assemblages near Vancouver, Canada. I compared fish communities across 26 streams with and without culverts. Densities of cutthroat trout (*Oncorhynchus clarkii*) increased whereas coastrange sculpin (*Cottus aleuticus*) and prickly sculpin (*C. asper*) densities decreased, on both sides, relative to unculverted reference streams. I also found that simple retrofits for improving culvert passage may increase fish diversity over decadal timescales. I then examined the effects of four culverts within one urban watershed and show that successive culverts had a cumulative effect on fish distributions, particularly for prickly sculpin and cutthroat trout (negative and positive, respectively). Overall, this thesis demonstrates that culverts may drive changes in fish communities through species-specific impacts that are consistent both within and across watersheds. Understanding biotic responses to stream fragmentation can inform urban watershed restoration and conservation efforts.

Keywords: barrier; connectivity; culvert retrofit; fish passage; road crossing; river restoration

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Chapter 1.

Introduction

Traditionally, ecologists have sought to explain patterns and variations in natural systems. Pristine ecosystems such as meandering rivers, expansive tundras, and lush wild forests, provided backdrops for studies that avoided confounding effects of human impacts. However, in the face of global changes such as human population increase and climate change, our impacts on natural ecosystems are becoming pervasive, to the point where it is hard to find areas that have not been impacted by human activity. Therein, the role of an ecologist has expanded over the past half a century to include study of direct and indirect effects of anthropogenic impacts on natural ecosystems (Grimm et al. 2000).

Some of the most extensively modified environments are in cities. By 2050 the global human population is expected to reach 9.3 billion from 7.0 billion in 2011, and urban areas are expected to absorb this population growth (UNPD 2011). Ecosystems in urbanized regions are disproportionately important as hot spots for biodiversity and endemic species as cities often occur in productive and diverse coastal lowland regions. For example, heavily urbanized areas (> 30% urban land cover) represent only 0.3% of global land cover, but are home to 12% of world's terrestrial vertebrate species (McDonald et al. 2008). Although urban areas currently cover only 1-2% of terrestrial ecosystems (Grimm et al. 2000, Mcdonald et al. 2008), their range is increasing, as they sprawl outwards (Batty 2008). City expansion may appear chaotic, but cities of all sizes grow in fractal patterns and predictable rates, as a result of intense competition for space (Batty 2008). These changes in land use drive "urban-syndromes" that characterize urban climate, soils, streams, wildlife and plants (Pickett et al. 2011). One common example, known as the urban heat island effect, describes how city-generated heat traps atmospheric pollutants (Alberti 2005) and may increase urban temperatures by up to 3°C relative to surrounding suburbs (Pickett et al. 2011). Understanding how urbanization influences ecological functioning is an increasingly important field as cities expand.

Urbanization can also alter watershed function. This occurs because natural interactions between land and surface runoff are restricted by several urban features (Walsh et al. 2005). First, reduced riparian vegetation and impermeable surfaces (e.g. roads, buildings) cause water to flow into streams more efficiently, rather than being absorbed and released by soils and vegetation (Pickett et al. 2011). Stream storm flows increase at faster rates than in natural systems (Paul and Meyer 2001), causing nutrients to be flushed out of the system (Filoso and Palmer 2011). Even relatively low levels of urban land cover (10-20%) may increase stream runoff two-fold (Arnold and Gibbons 1996, White and Greer 2006). Second, urban storm flows carrying high loads of fine sediments washed off roads and buildings, can combine with high flows and cause erosion and widening of stream channels (Paul and Meyer 2001). Residential and commercial areas close to streams can be protected from flooding and erosion by armored banks or channels, reducing natural habitat features such as undercut banks. Finally, networks of storm sewers, culverts, and channels are superimposed on stream networks to remove surface water and drain it directly into watercourses through pipes (Paul and Meyer 2001). Thus, watersheds in urban areas can sometimes be invisible, buried underground, with city dwellers unaware of their existence (Elmore and Kaushal 2008).

When streams are encased in pipes, ecological connectivity may be lost. Connectivity in rivers refers to the multidirectional flow of energy, matter and organisms between landscape components (Ward et al. 2002). These flows occur not only in longitudinal (upstream to downstream) direction, but also in lateral directions (via floodplains) and vertical directions (through hyporheic zones). Ward et al. (1999) suggested that connectivity in rivers can also be described as movement of materials across ecotones, or transition zones between habitats. These transitions can occur across multiple scales and refer to links between land and water; tributaries and mainstems; and surface water and ground water (Ward et al. 1999). Structures such as culverts, dams, and flood gates are constructed to protect urban property but can alter the natural flow of water, materials, and organisms. Thus, anthropogenic structures can sever or reduce efficiency of connections between habitats.

Reduction of connectivity can have various impacts on fish communities. By impeding access to habitats, anthropogenic structures can lead to isolation of resident species (Burford et al. 2009), exclusion of migratory species (Sheer and Steel 2006), and reduction of species abundances by limiting habitat size (Nilsson et al. 2005). Sometimes connectivity is partially lost, meaning that only some species, individuals, or life stages are able to transition between habitats. The severity of connectivity loss can depend on factors at the individual barrier (e.g. perch height, slope) (Bouska and Paukert 2010) and on factors at the landscape level (e.g. location in watershed) (Cote et al. 2009). Both individual-level and watershed-level factors must be considered for quantifying connectivity and prioritizing conservation strategies (Fausch et al. 2002).

To date, quantifying connectivity loss has been largely targeted at large barriers (e.g. dams; Nilsson et al. 2005, Hatry et al. 2011) leading to restoration projects on large rivers (Service 2011, Brenkman et al. 2012). However, small scale barriers on headwaters and small streams are much more abundant, and often invisible because they divert streams underground (Januchowski-Hartley et al. 2013). For example, more than 20% of urban streams in Baltimore, M.D. are out of sight, encased within underground culverts (Elmore and Kaushal 2008). The potentially pervasive impacts of barriers on small streams remain understudied and poorly understood (Januchowski-Hartley et al. 2013).

In this thesis, I examine fish communities and their potential fragmentation in urban streams in Metro Vancouver, British Columbia, Canada. First, I use a broad spatial comparative approach and examine the impacts of culverts across watersheds in multiple municipalities (Chapter 2). I also examine the effect of installing baffles in culverts as a potential rehabilitative measure for connectivity (Chapter 2). Second, I focus on impacts of culverts within one watershed, Suter Brook, Port Moody, to examine their cumulative effects on connectivity of fish communities. I undertake a watershed-based approach towards my studies, examining how the potential cumulative effects of culverts on the distribution of fishes in a watershed (Chapter 3).

In Chapter 2, I explore the impacts of culverts on urban fish communities, and the effects of baffles, a culvert rehabilitative technique (Figure 1-1). I begin by examining the effect of culverts compared to unculverted reference streams and show that fish communities on both sides of culverts have fewer coastrange sculpin (*Cottus aleuticus*) and prickly sculpin (*Cottus asper*) and more coastal cutthroat trout (*Oncorhychus clarkii*), than unculverted reference streams. Next, I examine the effect of baffles on fish communities, compared to culverts without baffles. Baffles are panels or blocks fitted inside a culvert that create resting areas for fish while swimming through. Although baffles are increasingly common, their effectiveness as a tool for rehabilitation has had little study outside of Australia (Macdonald and Davies 2007, Franklin and Bartels 2012). I show that mean densities are not statistically different between culverts with and without baffles. However, the age of baffles across my study sites varied, and I found that older baffles have higher species richness on both sides. This chapter suggests that culverts have species-specific impacts on fish abundances and distributions. Addressing impacts of individual culverts provides important local information that can be used to prioritize restoration efforts.

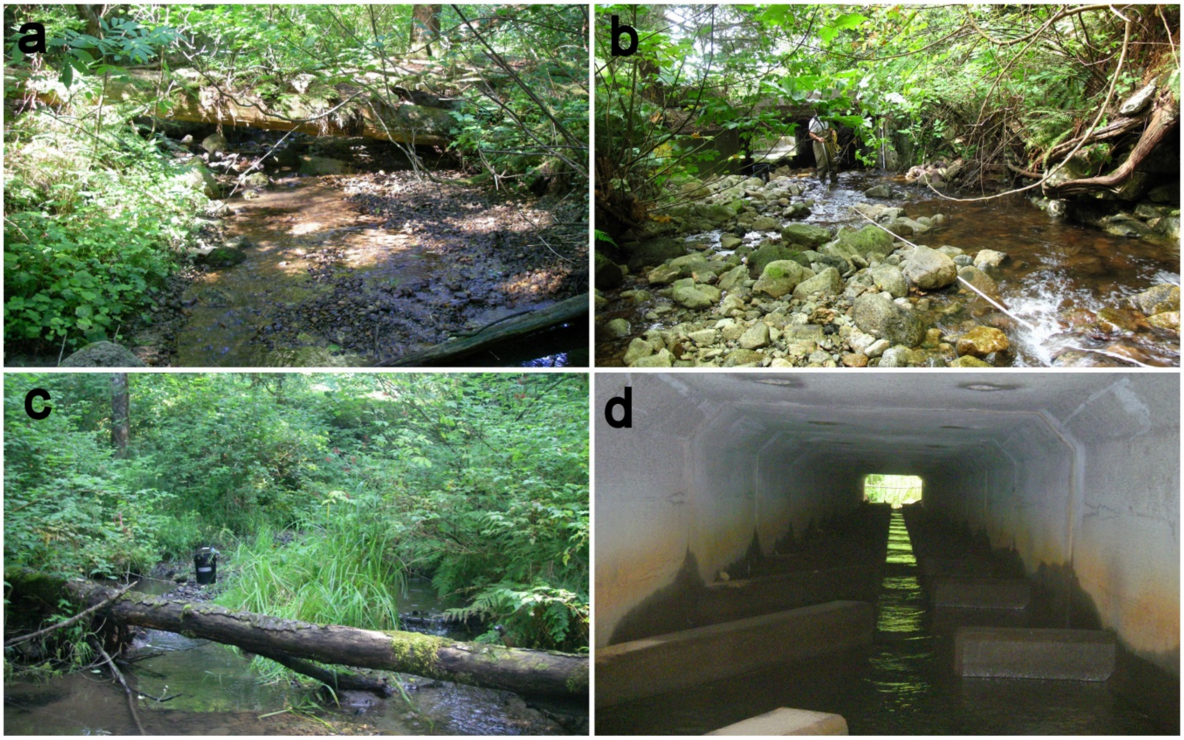

Figure 1-1. **Typical stream sites in Chapter 2. (a) Watkins Creek, "reference site", (b) Nelson Creek, "baffled-culvert site", (c) Dunlop Creek, "non-baffled site", (d) Baffles inside a culvert at Suter Brook.**

Urban areas are frequently culverted multiple times along stream lengths; therefore impacts do not occur in isolation. There is an average of one road culvert per 2 km of road in the Great Lakes region of Canada and the U.S.A. (Januchowski-Hartley et al. 2013). The cumulative impacts of culverts in urban watersheds remain unclear in the literature. In Chapter 3, I examine cumulative impacts of culverts on urban fish communities within Suter Brook, a small stream in Port Moody, British Columbia. Using insights from Chapter 2, I designed a spatially continuous sampling scheme along the length of the entire stream, including two tributaries. I sampled over 1,000 m of stream length, in each of 2 summer field seasons, in this small watershed that has 4 culverts. I found that culverts cumulatively impacted fish densities in both positive and negative directions. Specifically, prickly sculpin densities decreased at the first culvert in the second year of sampling, whereas cutthroat trout increased in densities, but only upstream of the third culvert. Meanwhile, other species such as coastrange sculpin densities were structured along a gradient, decreasing as distance from the ocean increased. These different responses of different fish species lead to relatively consistent total fish densities across the watershed. Finally, this study also quantified spatial and temporal variability in urban fish population densities. My Chapter 3 concludes that culverts can interrupt natural gradients in fish communities, and suggests that population monitoring programs consider natural variability through space and time to understand population distributions.

In Chapter 4, I synthesize my findings in a broad context and consider how they can inform management, future research directions, and survival of streams in cities.

Chapter 2.

Urban fish assemblages, culverts, and potential rehabilitation with baffles

2.1. Abstract

Watershed connectivity is important to the persistence of fish communities, yet human impacts can sever connections. For example, there are millions of culverts on streams in North America, which may impede fish movements in both directions. In some streams baffles are installed to mitigate impediments, but evaluation of their effectiveness is rare. We examined species abundance and fish communities in streams (n = 26) with unmodified (non-baffled) culverts, baffled culverts, and un-culverted reference streams in Metro Vancouver, B.C., Canada. We used mixed effects models to compare differences between- and within-streams (upstream vs. downstream) and to test whether within-stream patterns depended on stream type. When compared to reference stream types, non-baffled culvert stream types were negatively associated with coastrange sculpin *Cottus aleuticus* and prickly sculpin *C. asper* densities, and positively associated with cutthroat trout *Oncorhynchus clarkii* and rainbow trout *O. mykiss* densities. Upstream and downstream differences did not depend on the stream type. When compared to non-baffled culverts, streams with baffles did not have statistically different species- or community-level responses. We tested if communities change with time since baffling and found that species richness increased with age of baffles. These data suggest that culverts may drive stream-scale changes in fish communities, but restoration of these effects with baffles may occur over decadal time frames.

2.2. Introduction

One of the major anthropogenic alterations of rivers and streams is through structures that alter patterns of connectivity. Major dams have been built on more than 50% of the world's large rivers (Nilsson et al. 2005). Extensive work on these large dams has found that they fundamentally change river systems, homogenizing hydrology (Poff et al. 2007), restricting sediment transport (Ligon et al. 1995), facilitating invasive species (Johnson et al. 2008), and filtering out native species (Mims and Olden 2013). However, there is growing appreciation that small structures such as culvert road crossings may also act as impediments. For example, Januchowski-Hartley et al. (2013) report that culverts and road crossings are 38 times more abundant than dams throughout the Great Lakes basin (Canada and U.S.A.) and on average only 36% of road crossings are fully passable to fish. No global- or national-scale documentation of culverts exists (Hatry et al. 2011), likely because they are so numerous. In particular, culverts are disproportionately more likely to be used on urban streams (Elmore and Kaushal 2008) and thus have potentially wide-ranging and extensive impacts on urban watershed connectivity (Cooney and Kwak 2013, Januchowski-Hartley et al. 2013). Small streams, such as those that frequently have culverts, play an important role in watershed functioning by providing habitat to various life stages of fish species (Moore and Richardson 2003), therefore their connection to the rest of the watershed is critical.

Culverts can alter both abiotic and biotic connectivity in small streams. By impeding flows, culverts may prevent passage of sediments and wood which accumulate upstream of the culvert leading to clogging and widening of the upstream channel (Wheeler et al. 2005). Additionally, fine sediments may deposit inside and downstream of the culvert, which may impede fish passage (Wellman et al. 2000, Wheeler et al. 2005). Fine sediment deposition detrimentally affects habitat quality for fishes and invertebrates, which may have consequences for species distribution patterns (Hawkins et al. 1983, Heggenes et al. 1991). Furthermore, culverts may reduce stream nutrient inputs by limiting access to spawning salmon whose carcasses would have been deposited upstream (Roni et al. 2002, Gibson et al. 2005). Aquatic species vary in their responses to culverts (Warren Jr and Pardew 1998) and this variety is only recently becoming understood. For instance, aquatic insects, such as caddisflies, can become obstructed in upstream flight, achieving 250% higher abundances directly downstream than upstream of culverts (Blakely et al. 2006). A recent study by Nislow et al. (2011) in West Virginia showed that some common fish species decreased markedly upstream of culverts (e.g. mountain redbelly dace (*Phoxinus oreas*), blacknose dace (*Rhinichthys atratulus*), and creek chub (*Semotilus atromaculatus*)), whereas there was little effect on another common species, brook trout (*Salvelinus fontinalis*), likely due to its strong swimming and leaping abilities. Conversely, increases in abundance upstream of culverts have been observed for mottled sculpin (*Cottus bairdi*; Nislow et al. 2011) and juvenile coho (*Oncorhynchus kisutch*; Davis and Davis 2011), likely due to isolation and aversion to culverts. Understanding the ecological consequences of these culverts and their impacts on fish community connectivity remains a critical research need (Cooney and Kwak 2013).

A variety of measures are used to improve fish passage through culverts (Wild et al. 2011, David and Hamer 2012), such as the addition of baffles. Baffles are retrofitted panels or other structures inside culverts that create heterogeneous flow conditions that help fish swim through them. The costs of baffles depend on culvert size, slope and length, but they are typically 1,000 – 8,000 USD, or on average 12.5% of the cost of culvert (Hansen et al. 2009). These costs are considerably lower than the median 30,000 USD estimated cost of removing fish impediments or building alternative pathways (Bernhardt et al. 2005). Thus, baffles are economically appealing for stream rehabilitation projects with limited funding (O’Hanley and Tomberlin 2005, O’Hanley 2011). One baffle design—spoiler baffles, which comprises arrangements of blocks on the culvert bottom—has been found to improve passage success for *Galaxias* spp. in Australia (Macdonald and Davies 2007, Franklin and Bartels 2012, Feurich et al. 2012). Another design, weir baffles, and associated variants, divides the culvert into cells. Weir baffles are simpler and thus recommended for fish passage by the Washington Department of Fish and Wildlife (Ead et al. 2002, Bates et al. 2003, Hotchkiss and Frei 2007). However, field studies on fish composition in relation to weir baffles, and their utility through time, are lacking. The efficacy of many rehabilitation actions, such as those involving weir baffles, remains unclear (Bernhardt et al. 2005, Moore and Moore 2013).

The goal of our study was to investigate how culverts and their rehabilitation alter urban stream fish assemblages. Given that historic data are lacking on fish assemblage before and after culvert construction or their rehabilitation, we used a comparative approach. Specifically, we compared species and communities both across, and within, urban streams impacted by culverts without baffles, culverts with baffles, and reference streams without culverts in Metro Vancouver, British Columbia, Canada. Hereafter, these three treatments are referred to as “stream type”. We considered timescales of fish assemblage change by including sites with baffles of various ages. We sought first, to determine the impact of culverts on fish species and communities, and second, to determine if baffles mitigate potential impacts of culverts. We created the following hypotheses that are framed in terms of our analyses: 1) The stream type would impact species densities and communities. Specifically stream types with culverts would support lower fish densities and lower community metrics, providing evidence of stream-wide habitat alteration due to culverts. Reduced fish densities in culverted streams could also be explained by a metapopulation effect, in which smaller habitat fragments increase risk of stream-wide extirpation (Hanski et al. 1995). 2) The effect of stream type would interact with position to impact species densities and communities. Specifically, upstream habitats within culverted streams (and not reference streams), would have relatively fewer fish, providing evidence of movement impediments and fragmentation within culverted streams. 3) Stream-wide and within-stream fish densities and community metrics in baffle stream types would more closely resemble reference stream types over time since rehabilitation, indicating recovery of fish communities. Considering both spatial and temporal patterns is important for evaluating rehabilitation outcomes (Suding 2011), thus our study addresses both research needs to examine the impacts of culverts on fish communities and, for the first time, their mitigation with weir baffles.

2.3. Methods

2.3.1. Study sites

In British Columbia, there are an estimated 370,000 culverts, 76,000 of which are on fish-bearing streams (Forest Practices Board, 2009). We selected 27 streams in the Lower Fraser River region in the greater Vancouver urban area, British Columbia, Canada (Appendix A-1) for our study. This region has a population of 2.3 million people (Metro Vancouver 2013) and is used for spawning, rearing, and migration by five species of Pacific salmon (coho (*O. kisutch*)*,* chum (*O. keta*), pink (*O. gorbuscha*), chinook (*O. tshawytscha*), and sockeye (*O. nerka*)). Our study took place from July 6-August 20, 2012, in the summer low flow season. All streams were fish-bearing streams located in urban parks, residential areas, or commercial areas with mean gradient of 2.7% ± 1.7 standard deviation (SD).

We used a spatial comparison with replication across and within streams to examine relationships between fish communities, culverts and baffles. At the stream level, we evaluated fish community composition in streams: with non-baffled culverts (n=7, this and the following refers to the number of streams), with baffled culverts (n=13), and reference (unculverted) streams (n=6). Thus, we examined three treatments (non-baffled, baffled, and reference) replicated at the stream level. All stream types were in similar urban areas. Reference stream types did not have culverts within or downstream of the study site, except Watkins and Partington Creeks which had one culvert arrangement downstream of sampling. However, the culvert arrangements on Watkins and Partington Creeks apparently do not pose a fish passage impediment (Michalak 2004) because they are made of multiple ~3 meter diameter open arch structures in parallel that maintain channel width and contain natural substrates. Impacts of non-baffled culverts were examined relative to the reference stream type, which represents more natural patterns of connectivity (Wortley et al. 2013). Impacts of the baffled stream type (representing a rehabilitated system) were examined relative to the non-baffled culvert stream type. Within each stream, we sampled five consecutive 20-m reaches upstream, and five consecutive 20-m reaches downstream of culverts. We used 10 consecutive 20-m reaches in reference stream types as a comparison of potential natural gradients in fish assemblages. Upstream and downstream location is hereafter referred to as “stream position”. The specific 20-m reach is hereafter referred to as “stream reach”. Thus, there were 5 stream reaches within each position, and two positions per stream type.

We collected various habitat and culvert measurements in each stream to examine variation among our study sites (Appendix A-2). At each 20-m reach we measured wetted width, mean water depth using three point measurements (at 25%, 50%, and 75% of cross-sectional width), and percent canopy cover with a spherical densitometer (Appendix A-1). In each upstream and downstream position per stream we measured gradient near culvert (%) with an Abney hand level and the median sediments size of haphazardly selected rocks (n=100) measured across the axis perpendicular to the longest axis. When a culvert was present we noted shape, construction materials, and physical dimensions related to fish passage: width (or diameter), culvert length, culvert gradient, and perch height (Table 2-1). We calculated a stream width:culvert width ratio by dividing the width of stream upstream of the culvert by width of the culvert at widest point. We also used Google Earth to count the number of potential culverts downstream of the sample site. To analyze timescales of rehabilitation we gathered information from municipalities on the year baffles were installed (range: 1976- 2010, Table 2-1).

2.3.2. Fish sampling

We used single pass electrofishing to quantify fish assemblages. Our streams had a mean wetted width of 3.04 m ± 1.49 SD. Thus, we sampled a total of 100 m (5 x 20 m) in both stream positions – approximately equivalent to the 30-40 stream widths recommended to capture community diversity by single pass electrofishing (Sály et al. 2009). We used a Smith Root LR24 Electrofisher assisted by one dipnetter with a 4.7 mm mesh dipnet. We did not use block nets because fish catchability tends to be high in small, shallow streams (Bohlin et al. 1989). We recorded electrofishing effort in seconds per 20-m reach (Appendix A-1). Upon capture, we lightly anaesthetised fish (clove oil; 40 mg/L), identified the species, and collected measurements of length (fork length: *Oncorhynchus* spp., total length: all other species) to the nearest 1 mm and mass to the nearest 0.01 g. We recorded rainbow trout (*O. mykiss*) and cutthroat trout (*O. clarkii*) less than 70 mm long as generic "trout" because of uncertainty distinguishing between species (Pollard et al. 1997). We kept fish from different reaches separate in dark, aerated 19-L buckets for processing and released them into their reach origin. In one creek, Byrne Creek, only three fish were caught, 2 cutthroat trout and 1 goldfish (*Carassius auratus auratus*), therefore we excluded the stream from analyses reducing our sample size to n = 26 streams.

Table 2-1. **Culvert characteristics. CO = concrete, CS = corrugated steel, DS = downstream, OFF = offset weir, WEIR= weir and Alberta fishweir**

Stream	Shape	Length (m)	Slope (%)	Perch height (m)	Culvert material	Culverts DS	Const-riction ratio	Baffles present	Baffle spacing (m)	Baffle pattern	Baffle material	Baffles added (year)
Dunlop	Box	18.4	0.5	0	CO	1	0.64	N				
Eagle	Pipe	18.7	1.0	0	CO	4	0.64	N				
Elgin	Pipe	27.3	2.0	0	CS	0	0.36	N				
Jacobson	Pipe	33.5	2.0	0.18	CO	1	0.42	N				
Scott	Box	24.0	0.5	0	CO	5	0.73	N				
Siegel	Pipe	38.9	4.0	0	CS	1	0.71	N				
Maple	Box	19.5	0.0	0	CO	0	1.24	N				
Mossom	Pipe	39.0	2.5	0.20	CS	0	0.47	Y	2.44	WEIR	Wood	1976
Suter Brook	Box	50.6	1.0	0	CO	0	0.88	Y	3.37	OFF	CO	1995
Brothers	Box	31.2	4.5	0	CO	0	0.6	Y	2.08	OFF	Wood	1997
Hadden	Box	109	3.0	0.18	CO	0	0.78	Y	2.42	OFF	CO	1997
Nelson	Box	76.7	2.5	0	CO	0	1.32	Y	2.74	OFF	CO	1999
Chantrell	Box	22.8	4.0	0	CO	0	0.62	Y	2.28	OFF	CO	2003
Stoney (i)	Pipe	57.4	2.0	0	CO	1	0.42	Y	4.78	WEIR	Wood	2004
Yorkson	Pipe	92.0	3.0	0.27	CS	4	0.98	Y	5.75	WEIR	Wood	2004
Beecher	Pipe	30.5	3.0	0	CO	2	0.35	Y	1.79	WEIR	Wood	2005
McLennan	Pipe	58.0	1.5	0.37	CO	2	0.74	Y	6.44	WEIR	Metal	2007
Serpentine	Box	10.8	2.0	0	CO	4	1.33	Y	2.16	WEIR	CO	2007
Fergus	Pipe	76.0	4.0	0.62	CS	3	0.45	Y	5.85	WEIR	Wood	2010
Stoney (ii)	Box	39.7	4.0	0.27	CO	4	1.3	Y	3.61	OFF	CO	2010

2.3.3. Statistical Analysis

We assessed individual species and fish community variability among and within stream types. We examined the response of coho, trout and sculpin densities, and three community level responses (total density (number m^{-2}), biomass (g m^{-2}), richness) within and among stream types. We examined juvenile coho salmon, cutthroat trout, rainbow trout, prickly sculpin *Cottus asper* and coastrange sculpin *C. aleuticus* at the species level because they were the most abundant species (see Results). We grouped together "trout" (cutthroat trout and rainbow trout) and "sculpin" (coastrange sculpin and prickly sculpin) because of their broadly similar life histories and because they gave qualitatively similar results separately (not shown).We used mixed-effects models for all analyses because of the nested nature of our data with reaches replicated within stream positions, nested within streams. We visually examined residual plots to confirm the assumption of homoscedasticity in variance. Because our models had relatively few explanatory variables, we retained the fixed effects tested in our models, regardless of statistical significance, and did not reduce models to the "best" model; instead we present estimated parameters from full models as conservative estimates of effects (Bolker et al. 2009). We assigned an α value of 0.05 as statistical significance for tests. We performed all analyses in R (version 2.15.3; R Core Team 2013) with the packages glmmADMB (Skaug et al. 2013) and nlme (Pinheiro et al. 2013).

Physical variables

Physical environment can drive patterns in fish distributions, thus we conducted a two part analysis using physical variables. First, we tested whether physical habitat conditions intrinsically differed by stream type and position (Appendices A-2, A-3). Second, we tested whether fish metrics were a function of physical variables, regardless of stream type (Appendix A-4). We used the following habitat variables that are commonly associated with fish distribution: canopy cover (%; e.g. Hetrick et al. 1998), mean depth (cm; e.g. Heggenes et al. 1991), wet width (m; e.g. Rosenfeld et al. 2000) and median sediment size (mm; e.g. Hawkins et al. 1983). We used generalized linear mixed models (GLMM) to examine the effects of physical variables canopy cover (%), mean depth (cm), and sediment size (mm) on fish species and community structure across all stream types lumped together (Appendix A-4). We specified Poisson error structure for richness data, and negative binomial error structure for species counts which were overdispersed and contained many zeros (Browne et al. 2009). Biomass data were log transformed, enabling the use of simpler linear mixed models with normal error structure. All models included a reach area offset term (log m^2; except species richness model) to account for different areas sampled in reaches and we present count data as densities (O'Hara and Kotze 2010). Offset terms model count data variance without explicitly estimating a parameter for the sampling interval, in our case the area covariate. Additionally, to account for random effects of each individual stream, each model included a random intercept term for stream.

Species and community level responses

To test whether culverts and baffles influenced fish, we assessed fish species and community responses among stream types and positions. For species counts (coho, trout and sculpin counts) we used GLMM; and for community responses we used a combination of GLMM (total fish counts, richness) and LME (biomass) (Appendix A-5). We modelled each fish metric as a function of stream type, stream position, an interaction of stream type and position, a random intercept for stream type, reach area (log m^2) offset, and median sediment size (Appendices A-3, A-4). We fit a simpler model without specifying the interaction between stream type and position for sculpin data because data were too sparse and models did not converge with the full model. A significant effect of stream type would suggest statistical differences in a response metric between culverts vs. baffled culverts vs. reference streams after accounting for within stream type variability with the random intercept (i.e., stream-scale impacts of culverts). A significant stream position effect would suggest differences in a response metric upstream compared to downstream. A significant interaction term between stream type and stream position would indicate that differences between upstream and downstream patterns of response metrics depend on stream type (i.e., within-stream impacts of culverts).

Fine scale spatial and temporal effects

We performed a post-hoc analysis to assess if the distance from baffled culverts affected community biomass, and trout size near baffled culverts. We performed separate GLMMs for each of the three stream types by analyzing total biomass as a function of reach-distance from culvert (categorical: 10 bins of 20-m), an offset term for reach area, and a random intercept covariate for streams. We performed the three analyses separately, rather than making one model that included a stream type factor, to simplify interpretation of the model output (Appendices A-6, A-7). We focused on total biomass because we were interested in whether areas near scoured outlet pools had higher fish biomass (Wellman et al. 2000).

Finally, we explored how baffle age related to species richness. We used GLMM with richness as the response (Poisson distribution) and fixed effects of baffle age (years), position (upstream or downstream), and a random intercept for stream-level effects.

2.4. Results

We caught 3,581 fish comprising eight species in the 26 streams. We sampled 652 m^2 per stream ± 249 SD and caught 4.3 ± 1.2 SD species per stream on average. Juvenile coho salmon was the most abundant species, comprising 51% of fish captured, followed by trout at 29% (15% trout <70mm, 10% cutthroat trout > 70 mm, 4% rainbow trout >70 mm), coastrange sculpin (15%), and prickly sculpin (4%). The remaining 1% was composed of 16 longnose dace *Rhinichthys cataractae*, 62 threespine stickleback *Gasterosteus aculeatus*, and 15 larval lamprey, likely Pacific lamprey *Lampetra tridentata* (McPhail and Carveth 1994).

2.4.1. Physical variables

There were several differences in physical variables between and within stream types (Appendix A-3). However, median sediment size was the only variable related to our various fish metrics (Appendix A-4). Higher median sediment size was negatively associated with coho density (GLMM: $\beta = -0.014$, standard error (SE) = 0.004, $z = -3.65$, $P = 0.0003$) and species richness (GLMM: $\beta = -0.004$, SE = 0.001, $z = -3.54$, $P = 0.0004$). Conversely, higher median sediment size was positively associated with sculpin density (GLMM: $\beta = 0.036$, SE = 0.014, $z = 2.53$, $P = 0.011$).

2.4.2. *Species and community level responses*

The effect of culverts was species dependent after accounting for differences in sediment sizes. Coho densities were highly variable and not significantly associated with stream type or position (Figure 2-1; Appendix A-5), contrary to our predictions. The stream type X position interaction term was not significant either.

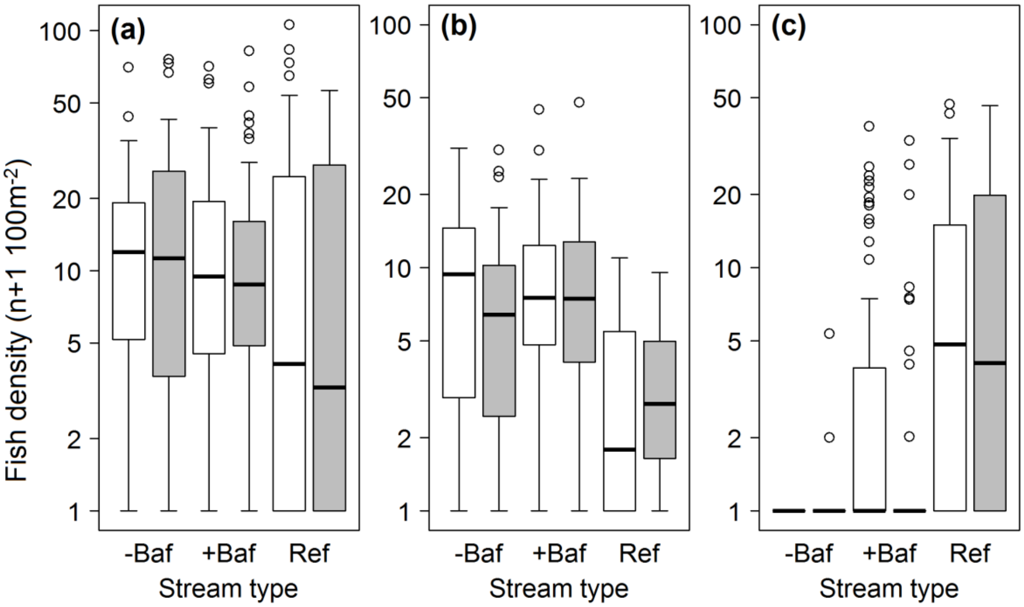

Figure 2-1. Boxplots showing individual species density on a logged y-axis for (a) coho, (b) trout, (c) sculpin, across stream types (no baffles, baffles, reference).

Note. White bars represent data from downstream positions, grey bars represent data from upstream positions. Thick horizontal lines represent medians, and whiskers extend to 1.5 times the interquantile range. Points outside of this range are shown with open circles. Unlike Figure 2-2, natural log response ratios are not shown so that magnitude of values between stream types can be visualized.

We were surprised to find that trout densities were on average 68% lower in reference stream types than in non-baffled culvert stream types (GLMM: $\beta = -1.14$, SE = 0.44, z = -2.62, *P* = 0.009; Figure 2-1). There was no difference between trout densities between stream types with baffled and non-baffled culverts (GLMM: $\beta = 0.25$, SE = 0.33, z = 0.75, *P* = 0.456; Figure 2-1), and no significant effect of stream position on trout densities (GLMM: $\beta = -0.13$, SE = 0.18, z = -0.69, *P* = 0.491; Figure 2-1). Differences in trout densities were present at the stream type level, but not within stream positions, therefore there was no stream type X position interaction. Thus, trout were more abundant in stream types with culverts, and their densities did not predictably change relative to position of reaches, or presence of baffles (Appendix A-5).

Sculpin densities were strongly negatively associated with culverts on the stream-scale. There were on average 90 times more sculpin in reference sites compared to non-baffled culvert sites (GLMM: $\beta = 4.50$, SE = 2.22, $z = 2.03$, $P = 0.043$; Figure 2-1) and no statistical difference between baffled and non-baffled stream types (GLMM: $\beta = 1.56$, SE = 1.91, $z = 0.82$, $P = 0.415$; Figure 2-1). Upstream positions had on average 44% less sculpin, regardless of stream type (GLMM: $\beta = -0.57$, SE = 0.18, $z = -3.19$, $P = 0.001$; Figure 2-1). Thus, sculpin were much more abundant in reference stream types, and across all stream types their densities systematically decreased in upstream vs. downstream positions (Appendix A-5). The interaction between stream type and position was not tested due to limited data (see Methods).

Community metrics were not significantly influenced by culverts. When controlling for sediment sizes, stream type did not significantly influence total density (number m^{-2}), biomass (g m^{-2}), or richness contrary to our predictions (Figure 2-2; Appendix A-5). There were no significant effects of stream position, and no significant interaction between stream type and position, on the community response variables.

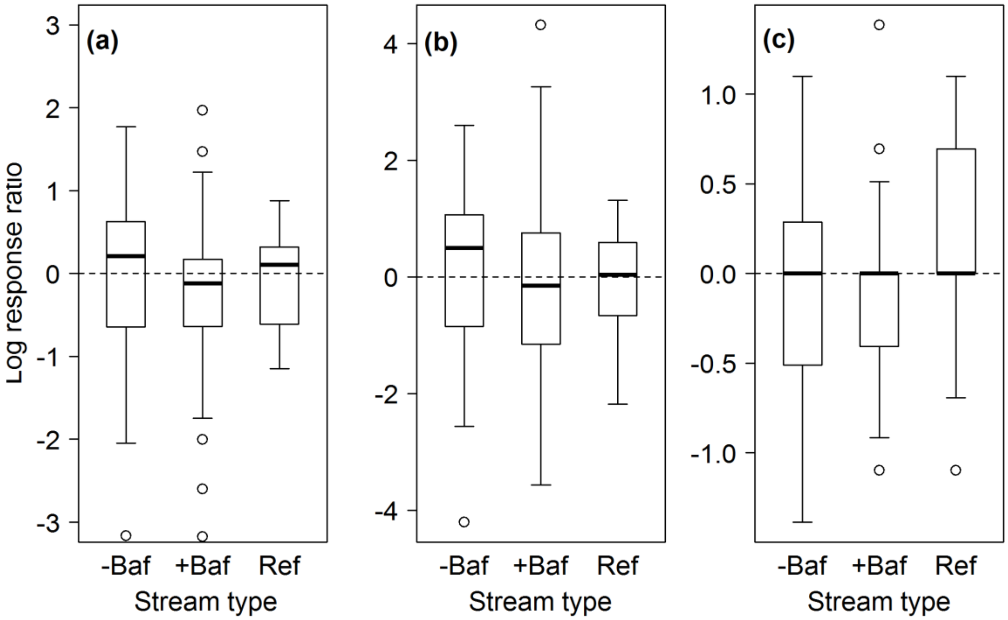

Figure 2-2. Community response data showing natural log response ratio for (a) total fish m^{-2}, (b) total biomass m^{-2}, and (c) species richness per reach by stream types.

Note. Each bar represents the response between paired positions (upstream and downstream) in the same stream. Values greater than zero indicate there are more fish, higher biomass, or increased richness upstream vs. downstream. Thick horizontal lines represent medians. Points outside whiskers are outside 1.5 times the interquartile range).

2.4.3. Fine scale spatial and temporal effects

We found evidence of fine scale spatial variation of fish in association with culverts. In stream types with baffled culverts, the first 20-m downstream of baffled culverts had, on average, 1.9 times the total fish biomass (g m^{-2}) compared to the other reaches (GLMM: β = 0.66, SE = 0.33, z = 2.04, *P* = 0.042; Figure 2-3; Appendix A-6). This was driven by large-bodied cutthroat trout, which were on average 46 mm larger (fork length) in the first 20-m downstream of a baffled culvert type (LME: β = 46.17, SE = 13.20, z = 3.50, *P* <0.001; Figure 2-3; Appendix A-7).

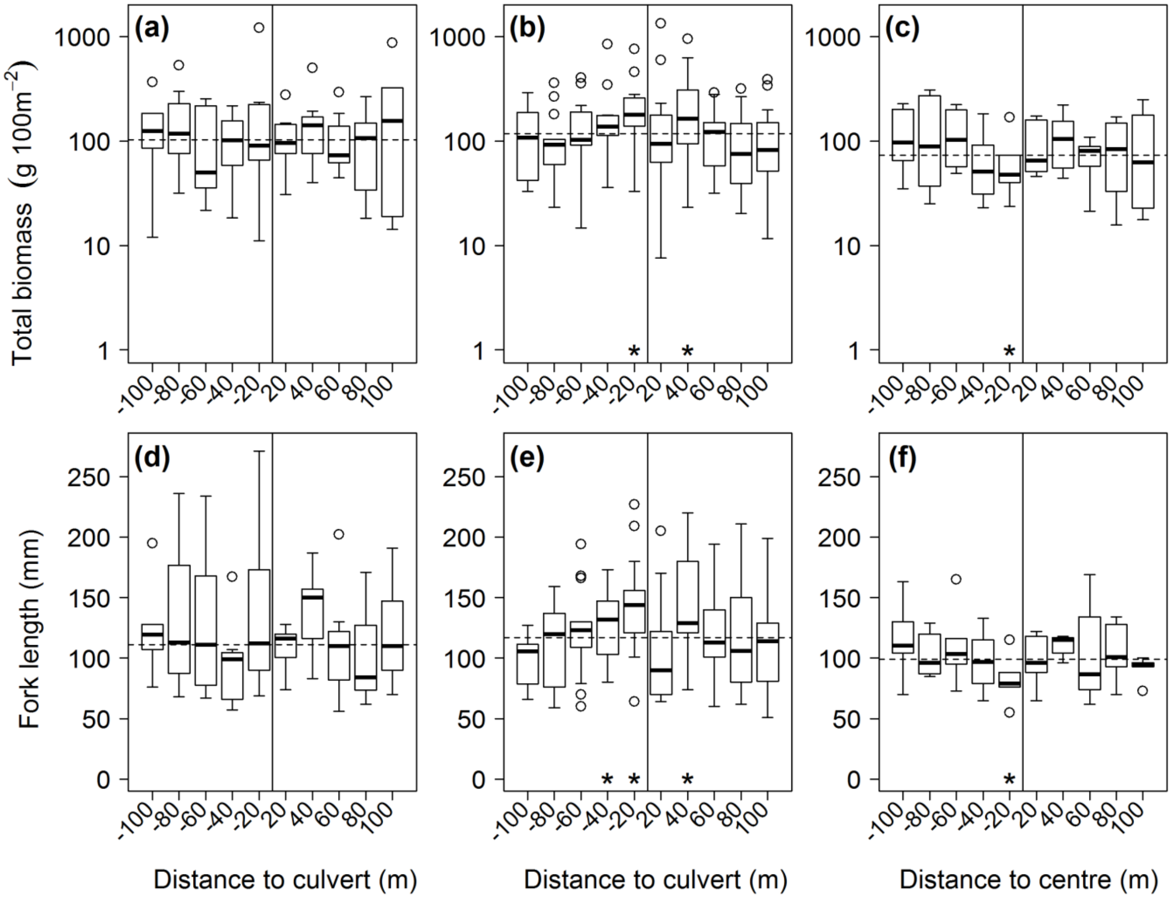

Figure 2-3. **Top panels: total biomass 100m^{-2} by reach position, (a) in reference streams, (b) streams with baffles, (c) streams with no baffles. Bottom: maximum fork length of rainbow or cutthroat trout, (d) in reference streams, (e) streams with baffles, (f) streams with no baffles.**

Note. The dotted midline signifies aggregate median for all reaches in the given stream type, and thin vertical line signifies the midpoint between upstream and downstream positions; flow moves right to left. Asterisks signify significance at *P* <0.05. Note the logged y-axis.

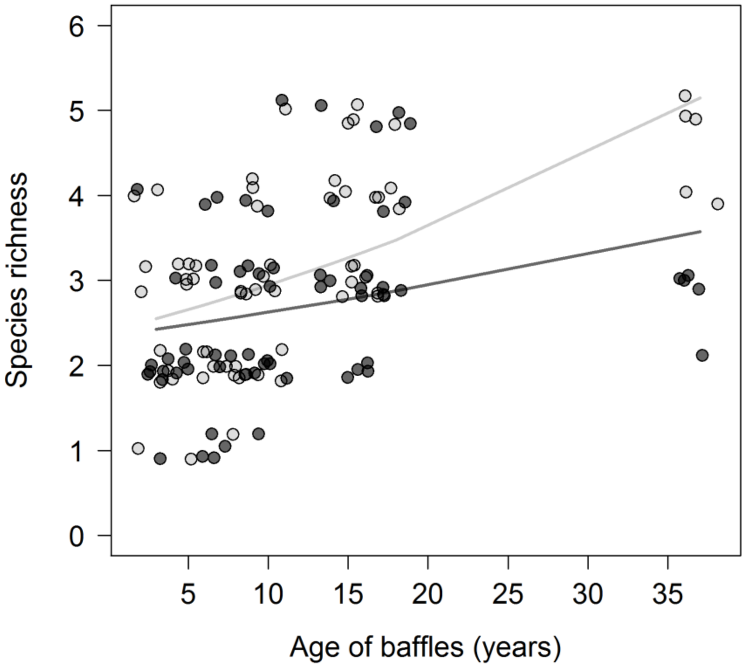

Figure 2-4. Species richness versus age of baffles, for reaches below (light gray) and above (dark gray) baffled culverts.

Note. Lines did not differ significantly and represent mean increase in species richness vs. time as predicted by a generalized linear mixed effects model that accounts for random intercept effect of stream. A slight jitter was added to the points to avoid overlap.

There was a significant increase in species richness with older baffles, as predicted (Figure 2-4). Species richness increases on average 2% for each year baffles are present (GLMM: β = 0.021, SE = 0.008, z = 2.69, *P* = 0.007). Stream position did not significantly affect the positive relationship between baffle age and species richness (Figure 2-4).

2.5. Discussion

Culverts accommodate flows under road crossings, but may fragment aquatic populations. In this study we examined how culverts and their rehabilitation alter fish communities in urban streams. After statistically accounting for habitat differences, we found that the presence of culverts was associated with higher stream-wide densities of trout, and lower stream-wide densities of sculpin in comparison to reference sites. We found that upstream vs. downstream differences in species densities and communities did not depend on the stream type. The presence of baffles did not influence species densities, but was, however, associated with increases in species richness over time.

Our study stream types had some differences in physical habitat, most notably in sediment sizes, which influenced fish metrics. Sediment size had a negative influence on total fish densities, species richness and coho salmon density, but a positive influence on sculpin density. Because sediment size is an important predictor of fish distribution for fish commonly caught in our study, e.g. sculpin and trout (Hawkins et al. 1983, Heggenes et al. 1991), it is possible that culverts have an indirect effect on fish assemblages through changes in the geomorphology of the impacted system. We quantitatively controlled for variation in sediment sizes in our study, and still found that culverts were significantly associated with species composition of urban streams.

Species densities varied in response to culverts at the stream-wide level for cutthroat trout and rainbow trout. Thus, contrary to our hypothesis, we found no interaction between stream type and position, and therefore no evidence of fragmentation expressed as lower trout densities upstream of culverts. Trout density was on average 68% lower in reference stream types compared to non-baffled culvert stream types (Figure 2-1). The positive association between culverts and trout density results are similar to MacPherson et al. 2012, who attributed high rainbow trout densities in culverted streams to strong swimming abilities, ability to self-sustain populations on upstream sides, and potential release from competition and predation from burbot (*Lota lota*), a voracious but weak-swimming predator that was impacted by culverts in their system. Our culverted stream types (baffled and non-baffled) both appeared to exclude sculpin to some degree, which could similarly offer trout a release from inter-specific competition and predation (of eggs and juvenile trout). In contrast, others have found strong decreases between downstream to upstream densities of brook trout and westslope cutthroat trout (*O. clarkii lewisi*; Burford et al. 2009, Pépino et al. 2012). Declines occurred with combinations of culvert slope >3% and perch >0.61 m (Pépino et al. 2012), or >4.5% slope and >0.2 m perch (Burford et al. 2009). Most of our study sites had combinations of lower values for slope and perch (Table 2-1), therefore it is possible our study culverts were permeable to trout and did not influence densities. Additionally, there was no significant difference in trout densities between non-baffled and baffled stream types.

Coastrange sculpin and prickly sculpin species densities were on average 90 times higher in reference stream types than in non-baffled culvert stream types. Thus, we found evidence that culverts may decrease sculpin populations on stream-scales, but we were not able to assess within-stream impacts of culverts due to a lack of model convergence. Similar to our findings, MacPherson et al. 2012 found that 6 out of 51 (12%) of their culvert sites did not have spoonhead sculpin (*C. ricei*), while 22 out of 32 (69%) of bridge-reference sites did have them. In our study, sculpin densities declined on average by 43% upstream relative to downstream, however this was true across all stream types (Figure 2-1). MacPherson et al. (2012), who found that spoonhead sculpin (*C. ricei*) proportions upstream of culverts were lower than expected based on comparisons with bridge-reference sites, and they partially attributed to culvert perch heights. Our results are also in contrast to Nislow et al. (2011), who found increases in mottled sculpin upstream of culverts (Nislow et al. 2011), which they attributed to low movement rates. We found no significant difference in sculpin density patterns between non-baffled and baffled streams types. Thus, in short, culverts apparently affected species densities by increasing the density of trout and reducing the density of sculpin on both sides of culverts, but baffles did not mitigate these apparent effects of culverts on sculpins (Figure 2-1). We note that it is possible that stream type covaried with an unknown and unmeasured physical characteristic, but we quantitatively examined a suite of physical characteristics and accounted for the significant variable (sediment) in order to minimize the chance that a covariate drove the observed stream-scale patterns.

While culverts are known to restrict distribution of migratory salmonids (Davis and Davis 2011), surprisingly we found that coho salmon juveniles were distributed across all stream types and stream positions. The longitudinal distribution of fry could reflect the spatial distribution of spawners, thus signifying that culverts did not impede adult spawners from moving upstream of culverts (Pépino et al. 2012). Additionally, patterns of coho distribution may have been influenced by hatchery coho releases in study creeks. Releases of hatchery coho took place upstream of some culverts, but it was difficult to gather rigorous data on releases. Programs to mark some hatchery salmon with adipose fin clips exist, but we did not encounter any marked coho salmon despite the apparent presence of hatchery inputs. Further, coho juveniles may congregate in reaches directly upstream of culverts in avoidance of downstream migration through culverts (Davis and Davis 2011), likely due to aversion of fast downstream flow conditions created at culvert inlets (Kemp et al. 2005, 2008). Coho passage through baffled and non-baffled culverts in both directions warrants further study with consideration of hatchery releases.

We observed significant effects of baffles at fine spatial scales. By examining gradients in fish distribution among our 20-m reaches we found that overall fish biomass was higher in the first 20-m reach immediately downstream of baffled culverts relative to other reaches within the same streams (Figure 2-3*b*), which was driven in part by large-bodied cutthroat trout and rainbow trout (Figure 2-3*e*). Our results are in line with previous findings that brook trout densities increase downstream of culverts, especially if the culvert permeability is low (Pépino et al. 2012). Deep pools with low to-mid velocity can be created downstream of culverts due to scouring (Wellman et al. 2000), which may generate preferable trout habitat (Heggenes et al. 1991).

A key aspect of examining stream rehabilitation is to track changes across time (Kondolf 1995). We found fish species richness was higher in sites with older baffles. Specifically, all reaches with only one species were found in sites with recent baffles (<10 years), while reaches with older baffles had upwards of 2 or more species. It was intriguing that this pattern of increasing richness with increasing time since rehabilitation occurred on a stream-scale (i.e., downstream of culverts as well). This suggests that the time since rehabilitation plays a role in the community structure, and that rehabilitation of culverts may lead to stream-wide increases in diversity, perhaps mediated by large-scale changes in habitat or slow recolonization rates (Kondolf 1995). It is also possible that rehabilitation took place on the most species-rich systems first.

The utility of baffles to rehabilitate streams with culverts remains unclear. We found species richness increased through time since baffle construction. However, there were no significant species- or community- level responses to baffles as a factor. The lack of significant stream type X position interactions also weakened our ability to examine the impacts of culvert rehabilitation. Managers in British Columbia do not recommend baffles for new culvert installations because of the complex biological and engineering input for designs, and high ongoing maintenance costs to prevent debris clogs (B.C. Ministry of Forests, Lands and Natural Resource Operations, B.C. Ministry of Environment, Fisheries and Oceans Canada, 2012). Yet, because baffles can be retrofitted into existing culverts they remain an attractive restoration option. To date, this is the first published field study that we are aware of that examined the effectiveness of baffles as a restoration measure, especially weir baffles. As such, managers and restoration practitioners are left with inadequate information to decide if retrofitting culverts with baffles require further consideration as a restoration option. Because of their ongoing use, it is important to consider and assess initial costs and maintenance costs given that fish diversity benefits might be realized only over long time periods.

We note that while our surveys provide information on fish communities on either side of the crossing structure, they do not provide information on actual passage through the culvert. Our method was applied to a broad suite of sites to make general observations about fish community impacts on a large scale. Our aim was to capture general patterns over the greater Metro Vancouver region, thus we surveyed culverts in various cities, all of which use different designs and installation practices.

Although culverts are built on relatively small streams, their high prevalence can potentially impede fish access to large areas of potential habitat (Cote et al. 2009, Kemp and O'Hanley 2010, Perkin et al. 2013). Our data suggest that culverts drive shifts in fish communities, and that rehabilitation efforts may restore communities over long time periods. Our study contributes to the call for research on impacts of in-stream structures and the methods used to reconnect small streams (Roni et al. 2008).

Chapter 3.

Fish assemblages and barriers in an urban stream network

3.1. Abstract

Stream networks can be vulnerable to fragmentation. Anthropogenic structures such as dams and culverts can simplify stream networks by isolating branches of watersheds, potentially interrupting natural gradients in fish communities. Though the impact of a single barrier is well documented, the impact of multiple barriers in small streams is not as well characterized. Using a landscape approach and spatially continuous sampling across two years, we examined the influence of anthropogenic structures on fish distributions in an urban watershed. After accounting for spatial autocorrelation, we found spatial location in the watershed and presence of culverts can positively influence cutthroat trout densities (*Oncorhynchus clarkii*) and negatively influence prickly sculpin densities (*Cottus asper*). Differential responses of different species buffered total fish densities, which were relatively consistent throughout the watershed. Prickly sculpin exhibited strong spatial autocorrelation in both years, whereas coho salmon (*Oncorhynchus kisutch*) had negligible spatial autocorrelation in one year, indicating spatial structure depends on species and year. Finally, habitats in the same location did not have consistent fish densities across years, illustrating high temporal variability of fish or their habitats. Spatially continuous sampling captured natural gradients and heterogeneity in fish distributions and highlighted the added effects of anthropogenic structures. Our study revealed which culverts had the strongest influences on fish densities throughout the watershed, and can inform riverscape management approaches needed to effectively conserve stream biodiversity.

3.2. Introduction

Landscape perspectives and approaches could greatly inform our understanding of stream ecosystems (Fausch et al. 2002). Understanding stream processes necessitates considering 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 deposition of fine sediments (Smith and Kraft 2005) and increases in temperature (Torgersen et al. 1999). The biological structure of communities is influenced by spatial location along the stream continuum (Vannote et al. 1980), relating to spatial indicators such as stream order (Smith and Kraft 2005), and degree of branching (Grenouillet et al. 2004, McKay et al. 2013). Inter-annual variability adds an additional dimension to stream dynamics, because biological processes vary naturally through time, even if habitat remains constant (House 1995). For example, a review of trout population dynamics, showed that the magnitude of natural variation (standard deviation) of annual fish abundances was half of mean fish abundances (coefficient of variation = 0.49: Dauwalter et al. 2009). Because streams are variable through space and time, a “riverscape approach”, considering multiple scales and timeframes, provides a more unified perspective of dynamics of stream networks (Fausch et al. 2002, Altermatt 2013).

The dendritic network structure of streams may render them particularly vulnerable to fragmentation by anthropogenic barriers (Fagan et al. 2002, Campbell Grant et al. 2007). Fish and other aquatic organisms are generally restricted to a watershed (Campell Grant et al. 2007), thus, a single barrier can sever connection with an entire branch of a stream network. Indeed, Fagan (2002) illustrated that random fragmentation in complex dendritic networks was more likely to lead to shorter stream segments than random fragmentation of simple linear systems. Fish communities in fragmented stream sections have lower species richness and greater dissimilarity compared to communities connected to the rest of the network (Perkin and Gido 2012). In some instances individual barriers can decrease access to stream habitats needed to complete various life stages. For example, in the Willamette River (Oregon, U.S.A), barriers caused by dams have blocked access to spawning grounds and led to declines of spring-run Chinook salmon (*Oncorhynchus tshawytscha*) (Sheer and Steel 2006). Thus, anthropogenic barrier pose substantial threats to freshwater biodiversity.

Multiple anthropogenic barriers can have overriding effects on natural gradients and heterogeneity in riverscapes (Fausch et al. 2002). The strength of barrier impacts can depend on location within the watershed (e.g. headwaters, mainstem, estuary; McKay et al. 2013) mediated by the life history of biota (Cote et al. 2009). That is, barriers located closest to the ocean may have greatest impacts on the distribution on migratory species, (e.g. salmon swimming upstream to spawning habitat) while those in the headwaters may have greatest impacts on the distribution of resident fishes (Cote et al. 2009, Rolls 2011). When barriers are successive, fish dispersal and occupancy may decline, diminishing the magnitude of barrier impacts on fish communities because absolute densities are lower (Perkin et al. 2013). The study of multiple barriers across watersheds necessitates sampling at large spatial scales, typically by employing point surveys spread across the watershed (Rolls 2011, McKay et al. 2013). However, due to the continuous nature of river processes, point surveys may not capture variability in fish distributions across watersheds (Fausch et al. 2002). Thus, there is a need to examine gradients and connectivity in fish distribution in relation to multiple barriers using spatially continuous sampling.

Here we used a continuous “riverscape” approach, following recommendations of Fausch et al. (2002), to examine spatial and temporal patterns of fish assemblages in a small urban watershed. We examined fish densities and community metrics continuously along a small urban stream network with multiple culverts in British Columbia, Canada. Urban watersheds are particularly susceptible to the presence of multiple barriers within watersheds, particularly due to culvert crossings under roads (Elmore and Kaushal 2008). Our goal was to determine how culverts influenced fish densities across the stream network relative to other environmental variables. We hypothesized that culverts would be associated with stepwise changes in upstream fish densities and community metrics, indicating the presence of fragmentation; while environmental variables would influence fish densities and community metrics along a gradient reflecting a changing environment along the river continuum. We also hypothesized that culverts’ effects would be stronger than environmental variables, indicating that stream fragmentation can override fine-scale patterns driven by environment. Because sampled stream reaches were in close proximity and therefore not independent, we quantified the strength of spatial structuring (autocorrelation) of different fish species, and incorporated this autocorrelation into analysis. Finally, we hypothesized fish assemblages would fluctuate through space and time, reflecting changes in environment; therefore we examined fish distribution and abundance change over our two years of study.

3.3. Methods

3.3.1. *Study site and sampling*

We carried out our study in Suter Brook (49° 16' 52.2264'' N, 122° 50' 5.6220'' W), a small urban watershed in Port Moody, British Columbia, on 22 – 24 August 2012, and 23 – 24 July 2013 (Figure 3-1). Suter Brook originates in two small tributaries located in a residential area, and converges into a mainstem that flows through a riparian buffered zone near high-rise residences (average annual discharge = 0.07 m^3s^{-1}). The headwaters and lower mainstem are overgrown, meandering and filled with woody debris, while mid-mainstem sections are channelized. Suter Brook drains into the Burrard Inlet, a coastal fjord connected to the Strait of Georgia. Riparian vegetation along the stream length is dominated by red alder (*Alnus rubra*), black cottonwood (*Populus trichocarpa*), western hemlock (*Tsuga heterophylla*) and salmonberry (*Rubus spectabilis*). The stream passes through two culverts on the mainstem, and one culvert on each of the two tributaries (Appendix B-1). In 2013, a new construction project for a rapid transit line commenced in the headwater area of our study. Although the stream had not been directly altered at the time of our study, construction crews were present in the upper watershed delineating construction areas and flagging trees for removal.

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 sampling reaches were consistent across years, we measured reaches in relation to static markers (e.g. large wood, culverts, bridges), sampling ~20 m increments (mean ± S.D. = 20.1 ± 3.2 m). Each 20 m sampling unit, hereafter referred to as "reach", represented approximately the same section of stream in both years. We used single-pass electrofishing with a Smith Root LR24 Electrofisher, without blocknets, as catchability in small streams is high (Bohlin et al. 1989). Assistance with fish capture was provided by one crew member with a dipnet (4.7 mm mesh). We anaesthetised fish lightly (clove oil; 40 mg L^{-1}), as needed, to identify species. Fish from different reaches were kept separate in dark, aerated 19-L buckets and released near capture location

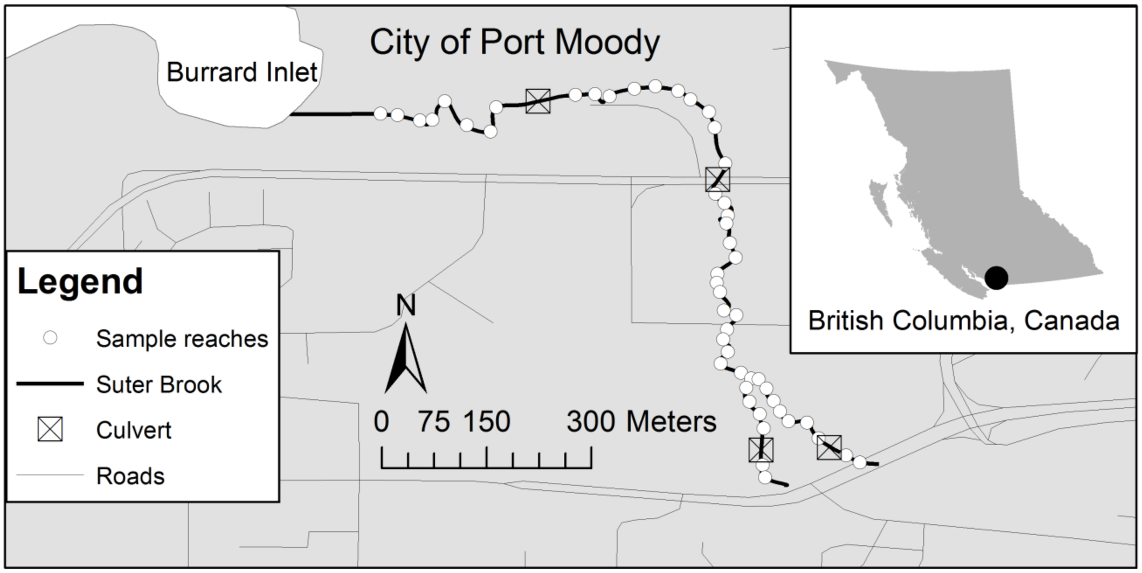

Figure 3-1. Map of Suter Brook showing the 50 sampled reaches.
Note. The stream flows northwest into the Burrard Inlet. The most downstream culvert crosses under a pedestrian path, the second culvert crosses under Murray Street, while the culverts on the tributaries cross under a railroad (West tributary) and under construction rubble (East tributary). The sample reaches are marked based on coordinates we obtained from the field, while the approximate flow path is was traced by authors to fit through the reaches.

We measured fish density for specific species (number m^{-2}; prickly sculpin (*Cottus asper*), coastrange sculpin (*Cottus aleuticus*), coho salmon (*Oncorhynchus kisutch*), cutthroat trout (*Oncorhynchus clarkii*)), aggregate density (number m^{-2}), and Simpson's diversity (1-D) per 20-m reach. At each 20-m reach we measured wetted width, mean water depth using three 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 per reach) measured across the axis perpendicular to the longest axis.

3.3.2. Statistical analyses

Patterns of fish abundance

We used an information-theoretic approach to assess how fish densities within the watershed related to cumulative culvert presence, longitudinal stream distance and four other habitat variables. We used generalized least squares, a type of linear regression that allows for incorporation of spatial structure in model residuals (see *Spatial autocorrelation* section below), to build a global model (i.e. full model) for each of the six fish responses and for each of the two years. Each global model included a variable for: cumulative number of culverts downstream of a given reach (as an ordered factor), ocean distance, mean depth, median sediment size, gradient, and canopy cover (Table 1). These six covariates were used to accommodate multiple hypotheses that could explain fish response patterns, and to avoid overlooking potentially important explanatory variables. Effects of culverts are shown relative to mean effects of the adjacent downstream culvert. Longitudinal stream distance, hereafter “ocean distance”, was measured along the network stream from the most downstream location in the study (just above the stream ocean outlet) to the start of a reach. Ocean distance represents gradients in abiotic conditions that naturally occur along rivers (Vannote et al. 1980, Jackson et al. 2001). We assumed culverts did not take up space in the stream, thus we did not count stream length in culverts towards the stream network distance (Cote et al. 2009).

We used model selection to explore the effect of culverts relative to ocean distance and aforementioned environmental variables on fish densities and diversity (Burnham and Anderson 2002). We standardized our continuous predictor variables to a mean of 0 and standard deviation of 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 AICc score using the dredge function in package MuMIn (Barton 2013) in R (R Core Team 2013, v2.15.3). 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 that were within the top 4 ΔAICc units (Burnham and Anderson 2002). We report coefficients in conjunction with their associated unconditional confidence intervals (CI), and variable importance (*w*), which is the summed Akaike weight of all models with the given variable.

Table 3-1. Variables included in global generalized least squares model

Covariate (units)	Type	Mean	S.D.	Range	Potential importance	Reference
Gradient (%)	continuous	2.0	1.4	0.0 – 6.0	Sculpin *Cottus* spp. prefer low elevations, rainbow trout *O. mykiss* present in high elevations	Hawkins et al. 1983, de la Hoz Franco and Budy 2005
Mean depth (cm)	continuous	10.7	6.4	2.3 – 23.7	Cutthroat trout have a strong preference for depth greater than 25 cm. Young of year 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 # downstream culverts (n)	ordered factor	-	-	0 – 3	Connectivity of river is most impacted by first (most downstream) barriers	Cote et al. 2009
Sediment size (mm)	continuous	20.9	36.1	2.0 – 256.0	Fish select habitat with various substrate size. *Cottus* spp. prefer finer sediments	Hawkins et al. 1983, Heggenes et al. 1991, Soulsby et al. 2001
Ocean distance (m)	continuous	17.4	269.4	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

Spatial patterns

Spatial autocorrelation occurs when sample points and their associated data are either clustered together in space (positive autocorrelation) or dispersed (negative autocorrelation). If not accounted for, patterns may incorrectly be 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 equivalent AICc values (within 2 ΔAICc points). We fit variogram models based on a 50 x 50 matrix that described the network distances between 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), and although we had several environmental variables in the global model, for consistency we still included a formal exponential variogram structure in all twelve of our global models (six fish responses for two 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 (Csari and Nepusz 2006) in R (R Core Team 2013, v2.15.3). We visualized spatial autocorrelation by plotting Moran’s I as a function of stream network separation distance by using SAM v4.0 (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.

We quantified the variability of fish densities among stream reaches for each of our two years of data. We calculated the coefficient of variation (CV) for each of our fish responses by dividing the standard deviation by the mean. Values greater than 1 signify that dispersion of data is greater than the mean, whereas values less than 1 signify that dispersion of data is less than the mean.

Temporal patterns

To quantify differences in densities between years, we used paired t-tests with unequal variance. Data was compared between reaches that represented the same 20-m stream segments over 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 one 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. Correlations represented the relationship between responses measured in the same 20-m stream reaches over two study years. They demonstrate the degree to which habitats that had high densities in the first year would also have high densities in the second year.

3.4. Results

We captured fish in 99 out 100 total sampled reaches (50 reaches X 2 years; Figure 3-2) for a total of 585 and 284 fish in 2012 and 2013, respectively. Fish densities declined significantly in the second year for all species except cutthroat trout (Table 3-2). In 2012, our catch was composed of 40% juvenile coho salmon, 31% coastal cutthroat trout, 14% prickly sculpin, and 12% coastrange sculpin. The remainder of the 2012 catch was composed of four threespine stickleback (*Gasterosteus aculeatus)*, and one larval lamprey, likely Pacific lamprey (*Lampetra tridentate;* McPhail and Carveth 1994). In 2013, our catch was composed of 6% juvenile coho salmon, 54% coastal cutthroat trout, 18% prickly sculpin, and 16% coastrange sculpin. The remainder of the 2013 catch was composed of five threespine stickleback, and three larval lamprey, likely Pacific lamprey (McPhail and Carveth 1994). In 2012, 20-m reaches were on average 41.6 m^2 ± 15.0

standard deviation (SD) with 2.5 species per reach ± 1.1 SD; while in 2013, 20-m reaches were on average 41.4 m^2 ± 15.8 SD with 1.5 species per reach ± 1.1 SD.

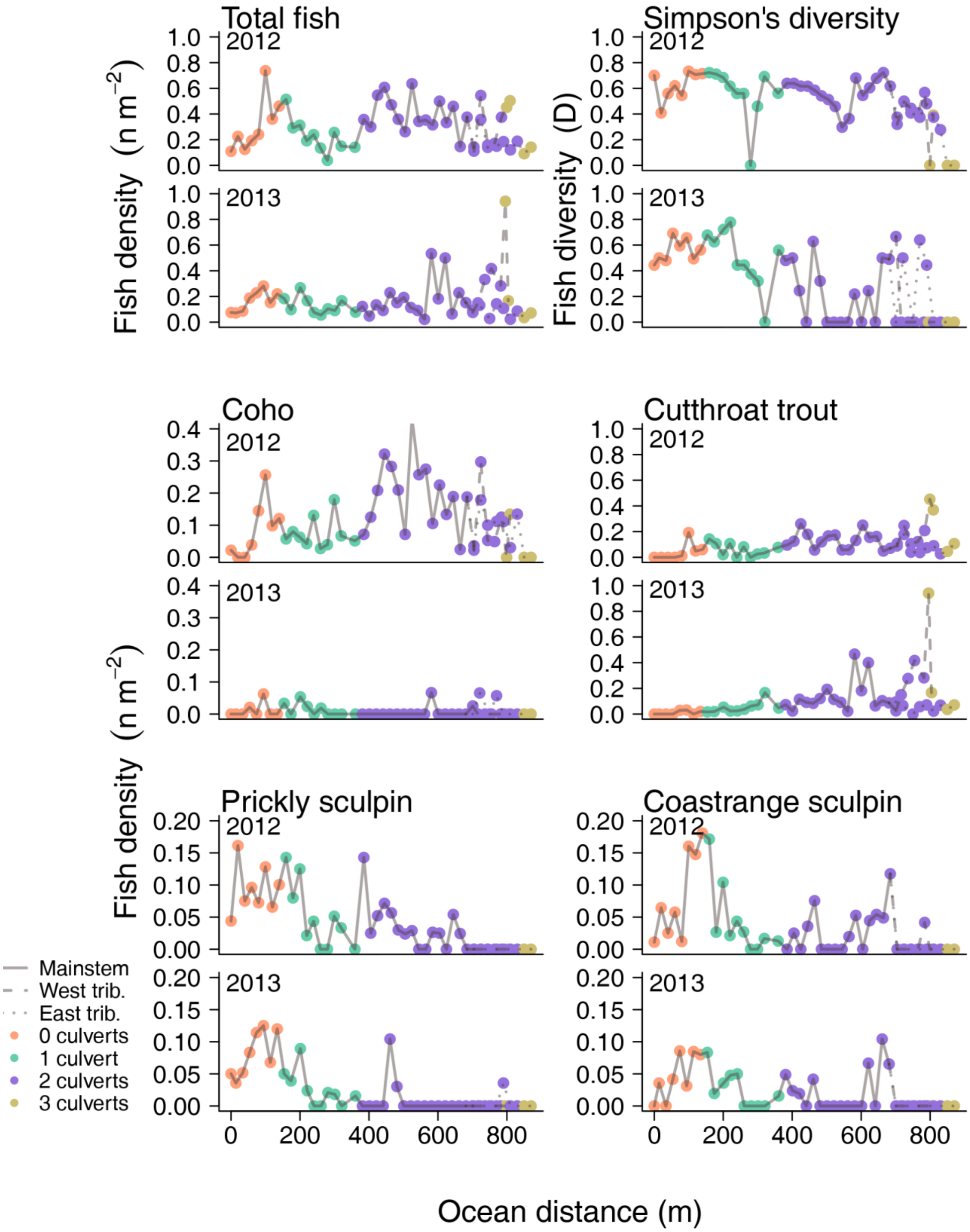

Figure 3-2. Fish densities and diversity in relation to stream distance.
Note. Points are connected by light gray lines and split at ~700 meters, the junction of two tributaries. The stream flow moves right to left on the graphs.

Table 3-2. Results from paired t-tests examining the difference between 2013 and 2012 fish metrics (densities and Simpson's diversity) and habitat metrics.

Response	Difference	t-value	DF	P
Fish				
Total fish (n m^{-2})	-0.13	-4.54	49	<0.0001
Diversity (D)	-0.19	-5.26	48	<0.0001
Coho salmon (n m^{-2})	-0.11	-7.70	49	<0.0001
Cutthroat trout (n m^{-2})	0.01	0.30	49	0.7655
Prickly sculpin (n m^{-2})	-0.01	-2.86	49	0.0062
Coast range sculpin (n m^{-2})	-0.01	-2.41	49	0.0195
Habitat				
Canopy cover (%)	10.61	7.79	49	<0.0001
Mean depth (cm)	0.88	0.86	49	0.3957

Note. DF = degrees of freedom, n = number. 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.

3.4.1. Patterns of fish abundance

AICc model selection resulted in 5 – 23 models within the top group, depending on response variable and year (Appendices B-2, B-3). Top models had average weights ranging from 0.12 – 0.45 (mean = 0.26 ± 0.10 SD), thus there was no support for a single top model for any responses (Appendices B-2, B-3). Ocean distance and cumulative culvert number were the explanatory variables with the most support (variable importance > 0.9; Table 3-3). The effect size and direction of ocean distance and cumulative culvert number depended on the response and year.

Mean total fish densities (number m^{-2}) declined from 0.289 (CI = 0.219 – 0.359) in 2012 to 0.171 (CI = 0.126 – 0.217) in 2013 (Figure 3-2; Table 3-2). Ocean distance had low variable importance (w) in 2012 and 2013 (w = 0.25 and 0.16, respectively) and did not influence total fish densities. Cumulative culvert number also had low variable importance in 2012 and 2013 (w = 0.14 and 0.04, respectively). However, in 2012 the second culvert in the watershed had a positive influence on fish densities (Culvert 2: β =

0.329, CI = 0.119 – 0.538; Figure 3-3). Environmental variables did not influence total fish densities with certainty in both years. Null models had support as possible top models in both years; their ∆AICc scores were only slightly higher than the top models (0.92 ∆AICc in 2012; 1.85 ∆AICc in 2013; Appendices B-2, B-3).

Table 3-3. **Importance of variables in top 4 ΔAICc model set for each fish response, by year. Responses are presented as densities (number m^{-2}), except for Simpson's Diversity (D).**

		Variable importance					
Year	Response	Cumulative culverts	Ocean distance	Canopy cover	Gradient	Sediment size	Depth
2012	Total fish	0.14	0.25	0.18	0.57	0.12	0.12
	Diversity	1	0.6	0.13	0.13	0.13	0.13
	Coho salmon	0.47	0.43	0.2	0.89	0.2	0.24
	Cutthroat trout	0.95	0.29	0.23	0.34	0.46	0.10
	Prickly sculpin	0.21	1	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	0.04	0.16	0.16	0.15	0.09	0.71
	Diversity	NA	1	0.13	0.13	0.13	0.15
	Coho salmon	NA	0.15	0.13	0.46	0.14	0.16
	Cutthroat trout	0.45	0.55	0.24	0.1	0.1	0.77
	Prickly sculpin	1	0.11	0.22	0.09	0.1	0.19
	Coastrange sculpin	0.02	0.91	0.42	0.76	0.66	0.19

Note. Importance is the summed Akaike weight of all models containing the given variable. When NA is indicated, the variable was not present in the top ranked model set.

Mean diversity was 0.436 (CI = 0.369 – 0.503) and 0.303 (CI = 0.227 – 0.380) in 2012 and 2013, respectively. Ocean distance variable importance increased from *w* = 0.6 in the 2012 model, to *w* = 1.0 in the 2013 model. Ocean distance had a negative influence in both 2012 (β = -0.117, CI = -0.237 – 0.003) and 2013 (β = -0.171, CI = -0.249 – -0.093). Additionally, the cumulative culvert factor had high variable importance in 2012 (*w* = 1) and had a negative effect on diversity in 2012 at the third culvert (β = -0.368, CI = -0.571 – -0.165; Appendix B2). In 2013, the cumulative culvert factor did not rank in the top 4 delta AICc models (Appendix B3). Environmental variables did not influence diversity across both years.

Mean coho salmon densities (number m^{-2}) were 0.072 (CI = 0.056 – 0.149) and 0.009 (CI = 0.003 – 0.014) in 2012 and 2013, respectively. The importance of ocean distance declined from 2012 to 2013 (*w* = 0.43 and 0.15, respectively) and ocean distance did not influence coho salmon densities. In 2012, the second culvert had a positive effect on coho densities (β = 0.134, CI = 0.003 – 0.266, *w* = 0.47); while in 2013 the cumulative culvert variable did not rank in the top delta 4 AICc model set (Figure 3-3). In 2012, gradient was weakly negatively associated with coho salmon densities (β = -0.034, CI = -0.063 – -0.006, *w* = 0.89).

Mean cutthroat trout densities (number m^{-2}) were 0.112 (CI = 0.073 – 0.152) and 0.120 (CI = 0.070 – 0.171) in 2012 and 2013, respectively. The importance of ocean distance increased from *w* = 0.29 in the 2012 model to *w* = 0.55 in the 2013 model, but did not strongly influence cutthroat trout densities across years. Cumulative culvert number variable importance decreased from *w* = 0.95 in 2012 to *w* = 0.45 in 2013. Cumulative culvert number had a positive effect on cutthroat trout densities, only at the third culverts in the watershed in 2012 (β = 0.136, CI = 0.037 – 0.235) and 2013 (β = 0.183, CI = 0.024 – 0.344). None of the environmental variables had a certain effect on cutthroat trout densities.

Mean prickly sculpin densities (number m^{-2}) were 0.035 (CI = 0.026 – 0.045) and 0.028 (CI = 0.016 – 0.040) in 2012 and 2013, respectively. Ocean distance variable importance decreased from *w* = 1 in 2012 to *w* = 0.11 in 2013. The influence of ocean distance had a negative influence on prickly sculpin in 2012 (β = -0.038, CI = -0.058 – -0.018), but not 2013. Conversely, cumulative culvert variable importance increased from *w* = 0.21 to *w* = 1 from 2012 to 2013. The second culvert had a positive effect on 2012 prickly sculpin densities (β = 0.044, CI = 0.006 – 0.083), but not in 2013. In 2013, the first culvert had a negative effect on prickly sculpin densities (β = -0.057, CI = -0.087 – -0.026). Environmental variables did not influence prickly sculpin across both years.

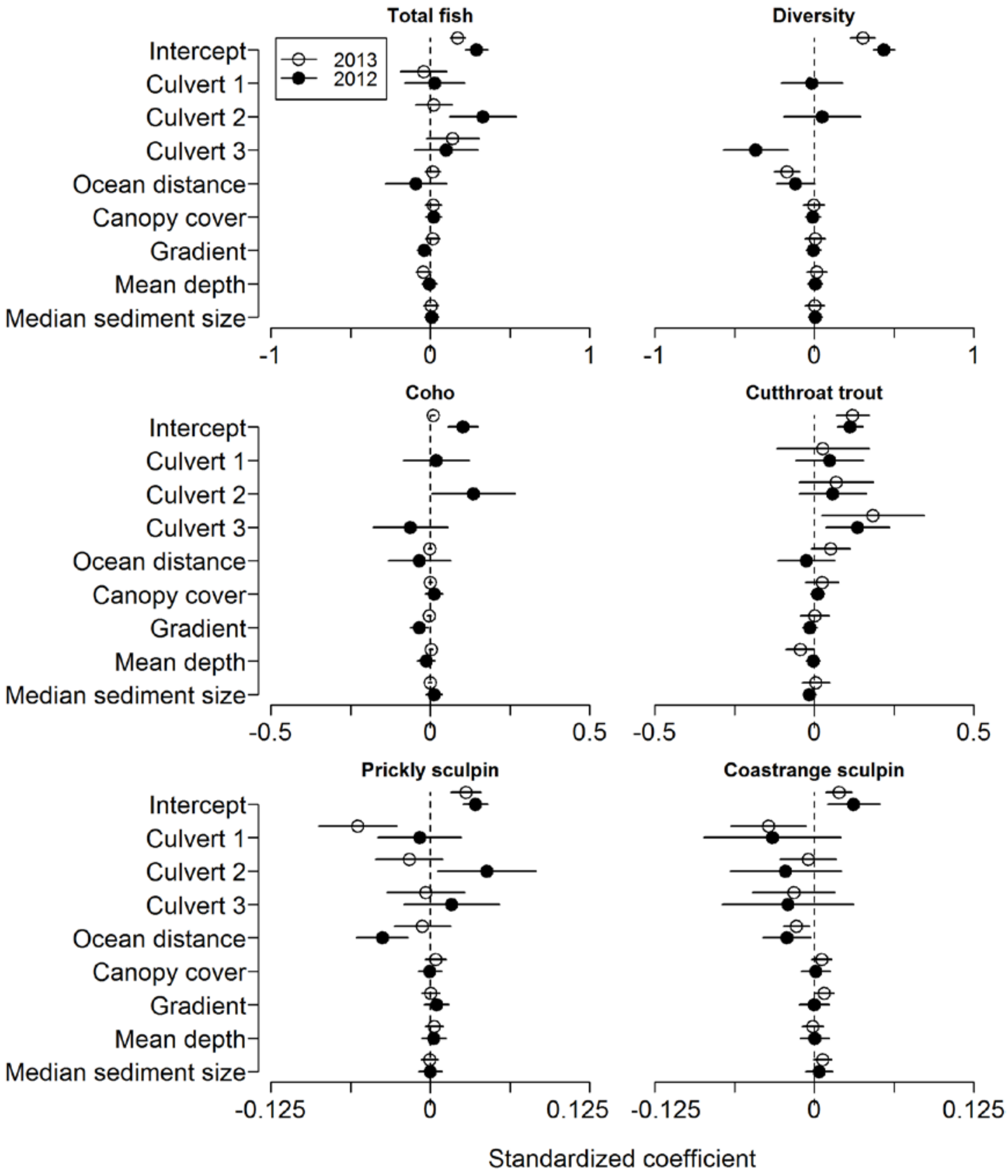

Figure 3-3. Standardized model average coefficients for generalized least squares models examining the relative effect of culvert and habitat variables on fish densities and diversity.

Note. Bars indicated 95% confidence intervals. Filled and open points represent 2012 and 2013 data, respectively.

Coastrange sculpin densities (number m^{-2}) were 0.031 (CI = 0.010 – 0.052) and 0.019 (CI = 0.009 – 0.029) in 2012 and 2013, respectively. Ocean distance had variable importance *w* = 0.65 and *w* = 0.91 in 2012 and 2013 respectively. The influence of ocean distance was negative on coastrange sculpin densities in 2012 (β = -0.021, CI = -0.040 – -0.003) and 2013 (β = -0.015, CI = -0.024 – -0.004). For cumulative culvert effects, variable importance was very low (*w* = 0.02 in 2012, and *w* = 0.04 in 2013) indicating uncertainty regarding their effect. However, in 2012 there was an additional negative effect at the first culvert (β = -0.036, CI = -0.065 – -0.007; Figure 3-3). The stream gradient environmental variable had a weak but positive influence on coastrange sculpin in 2013 (β = 0.008, CI = 0.0002 – 0.015, *w* = 0.76).

3.4.2. Spatial patterns

Moran's I correlograms revealed the degree of spatial autocorrelation for each fish response (Figure 3-4). All fish responses had significant positive autocorrelation at small separation distances, except coho salmon in 2013 (Figure 3-4). In other words, data were more similar when reaches were close together. Prickly sculpin densities 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. The point at which Moran's I becomes negative for the first time represents the extent of spatial autocorrelation. For prickly sculpin, autocorrelation disappears after ~300 m (2012) and ~200 m (2013). Cutthroat trout, coastrange sculpin and diversity also transition from positive to negative autocorrelation as separation distance increases, but to a lesser degree than prickly sculpin (Figure 3-4). Total fish densities and coho salmon densities had the smallest degree of autocorrelation, as visualized by the narrow range of positive Moran's I and values around zero across other separation distances. Correlograms for habitat variables show less autocorrelation than in fish responses (Figure 3-5). At small separation distances mean reach depth (2012) and canopy cover (2013) were positively autocorrelated, and at larger separation distances became randomly structured. Gradient and sediment size were not autocorrelated at any distances, highlighting the fine-scale variation in these physical variables.

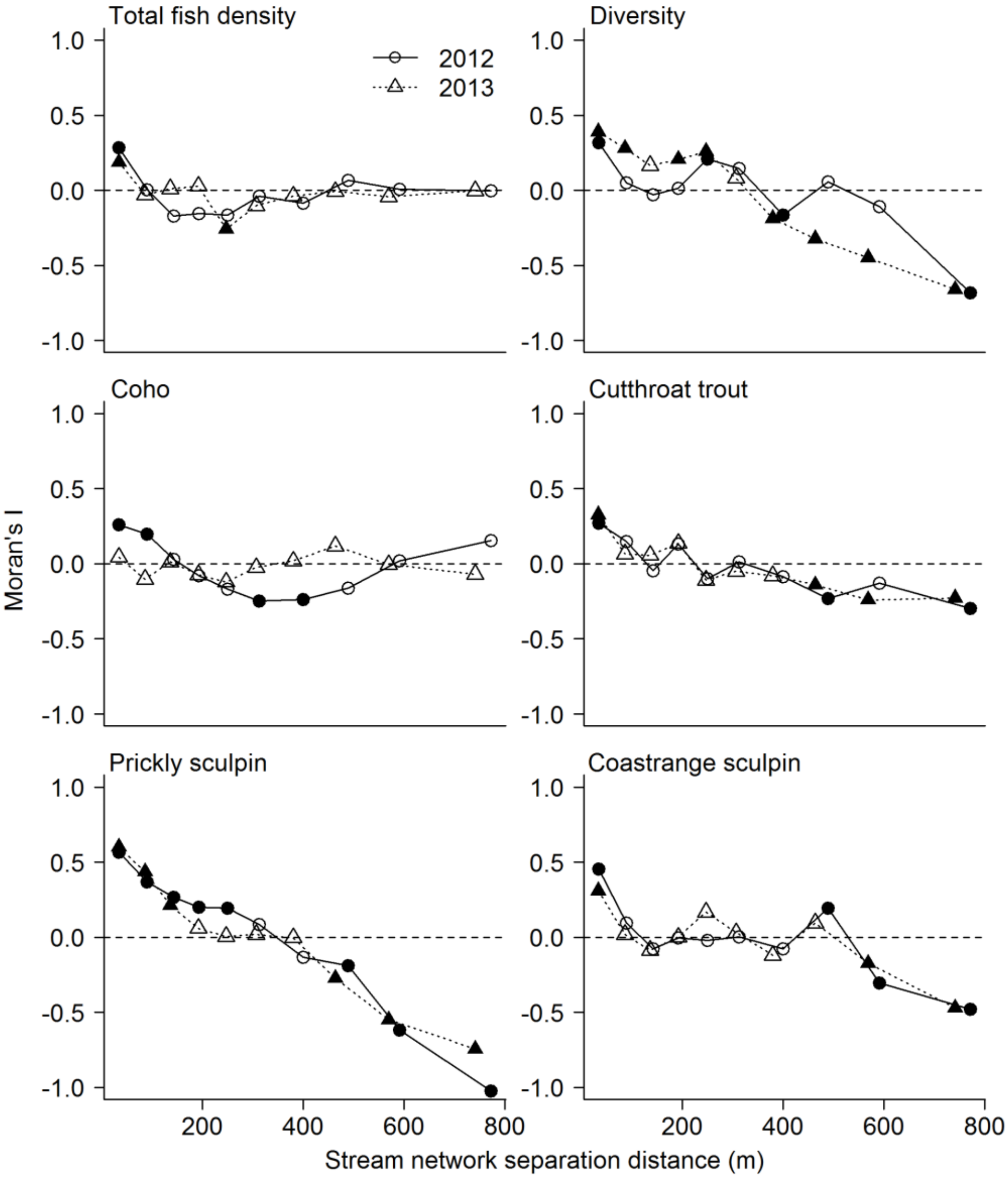

Figure 3-4. Spatial correlograms of Moran's I for fish responses across various stream separation distances.

Note. Filled symbols represent significance at $P < 0.05$; open symbols represent non-significance. 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.

Coefficients of variation (CV) were higher for individual species densities compared to total fish densities (Table 3-4). This indicates that combined fish densities are less variable across space than individual species. For all responses, CV's showed some increases in 2013 compared to 2012, possibly because mean densities decreased overall (Table 3-2). For prickly sculpin, CV was 1.26 in 2012, and 1.69 in 2013. For coastrange sculpin, CV's were 1.52 and 1.53 in 2012, and 2013, respectively. Coho salmon CV's increased from 0.83 in 2012, to 2.26 in 2013. CV's of cutthroat trout increased from 0.88 to 1.44 in 2012 and 2013, respectively. CV's greater than 1 indicate that the variation between reaches was greater than mean densities.

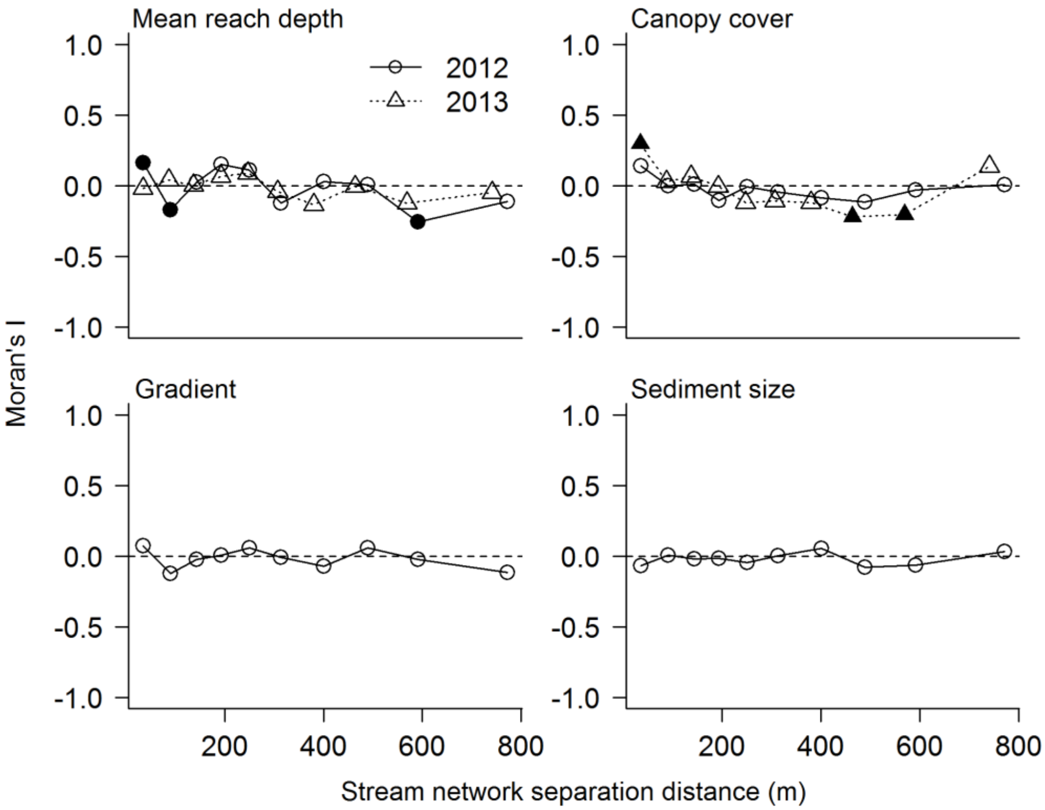

Figure 3-5. Spatial correlograms of Moran's I for habitat variables across various stream separation distances.

Note. Filled symbols represent significance at $P < 0.05$; open symbols represent non-significance. Moran's I values of -1 signify complete dispersion, +1 signifies perfect correlation, and 0 signifies random structure of habitat variables. The distance at which Moran's I first becomes negative in the correlogram is the average distance at which the spatial autocorrelation no longer exists.

Table 3-4. Spatial coefficients of variation (CV) for fish and habitat responses.

	CV	
Response	2012	2013
Fish		
Total fish	0.55	0.92
Diversity	0.39	0.91
Coho salmon	0.83	2.26
Cutthroat trout	0.88	1.44
Prickly sculpin	1.26	1.69
Coast range 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	-

Note. Fish responses are presented as densities (number m^{-2}), except for Simpson's Diversity (D). CV was calculated by dividing the standard deviation of fish density by mean fish density in reaches of a given year.

3.4.3. Temporal patterns

Mean species densities, except cutthroat trout, decreased from 2012 to 2013 (Table 3-2). Habitat changed from 2012 to 2013, as reaches increased in canopy cover by 10.6 % on average (t = 7.79, P < 0.0001). However, mean depth of reaches did not change (t = 0.86, P = 0.396). Fish densities and diversity measured within the same 20-m reaches were not tightly correlated between years. Spearman's rank correlation coefficients ranged from 0.41 to 0.67, for total fish density, diversity, cutthroat trout densities, prickly sculpin densities, and coastrange sculpin densities (Figure 3-6). Coho salmon densities between years were not correlated (ρ = -0.10; Figure 3-6).

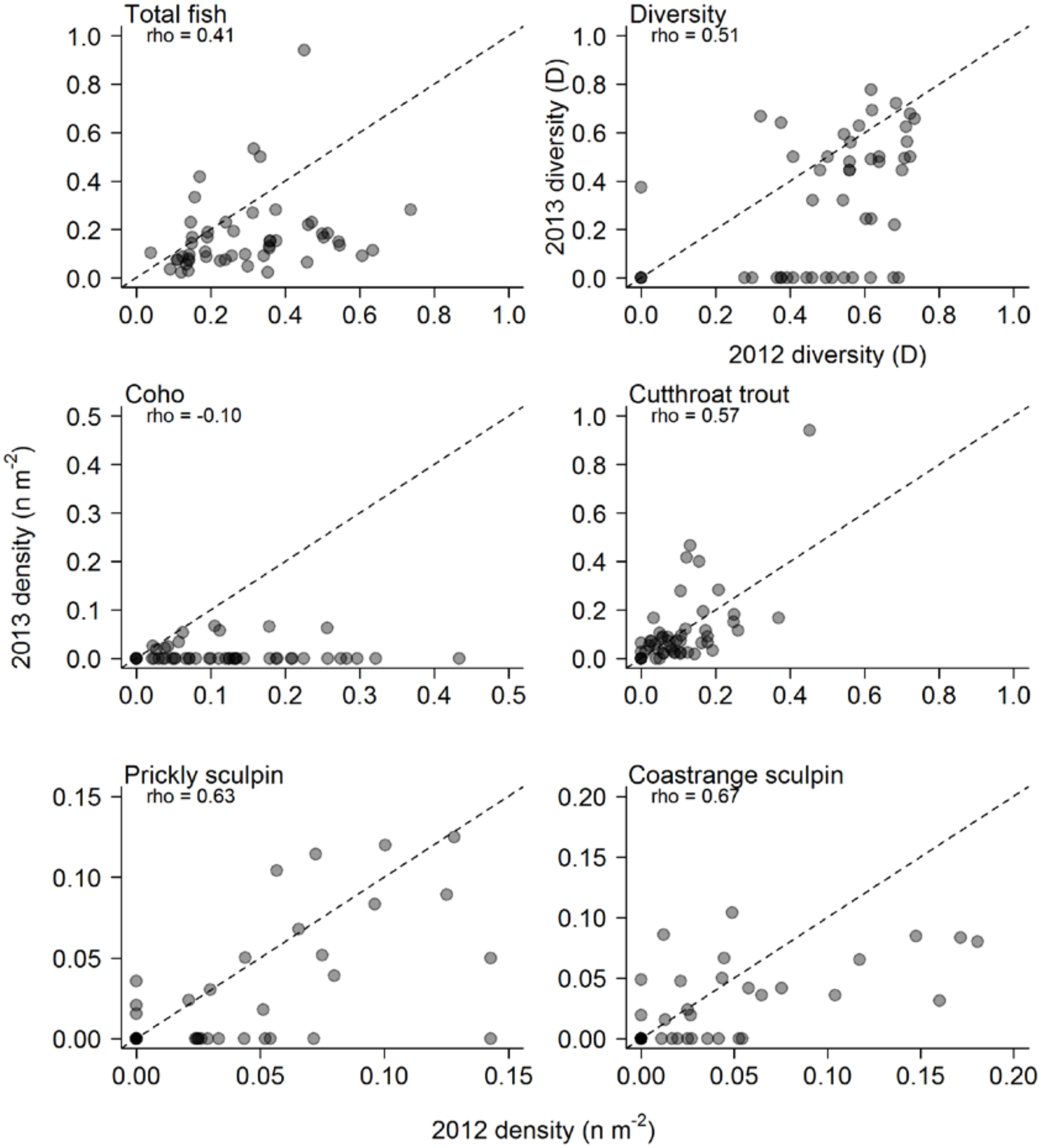

Figure 3-6. Scatter plots showing 2012 vs 2013 species densities and diversity.
Note. Spearman's rank correlation is given by rho (ρ), while the dotted line represents a 1:1 line.

3.5. Discussion

3.5.1. Patterns of fish abundance

Ocean distance and cumulative culvert number had the largest effect sizes on fish densities. The effect sizes were highly variable, and their direction depended on the fish response, culvert location, and year (Figure 3-2; Figure 3-3). Additionally, ocean distance and cumulative culvert number effects were not independent, as in some cases a gradient in fish response along the ocean distance continuum was interrupted by a culvert. For example, ocean distance negatively influenced Simpson's diversity in both years, consistent with Jackson et al. (2001) who found lower watersheds had higher diversity likely due to greater habitat size and higher stability in abiotic factors. However, in 2013 the third culvert in our study was associated with a strong, additional stepwise drop in diversity (Figure 3-3). Similarly, in 2012, prickly sculpin densities were structured negatively along ocean distance, but the second culvert was associated with a stepwise increase in upstream densities. Interestingly, in the next year, prickly sculpin densities were no longer structured along the ocean distance gradient; their densities were clustered low in the watershed and strongly dropped upstream of the first culvert. Culverts on tributaries had strong positive effects on cutthroat trout, where other species were largely absent and diversity was lowest. MacPherson et al. (2012) similarly found increases in rainbow trout (*Oncorhynchus mykiss*) densities above headwater culverts, specifically when culverts excluded predatory burbot (*Lota lota*) and subsequently released rainbow trout from predation. Surprisingly, environmental variables did not have strong effects on total fish densities, potentially because their effects occurred at smaller spatial scales.

When species respond uniquely to a variable, such as cutthroat trout and prickly sculpin in this study, the phenomenon is known as response diversity (Elmqvist et al. 2003). We showed that total fish densities were relatively consistent across the watershed, whereas densities of individual species varied spatially (Figure 3-4). This result is consistent with the observation that total fish density was more stable (lower CV) than for individual species density (Table 3-4), indicating higher spatial stability for the aggregate fish community. For example, in 2013 prickly sculpin and cutthroat trout responded to culverts in the opposite direction resulting in a more consistent aggregate density. In addition, although coastrange sculpin and prickly sculpin are functionally similar, with comparable morphology, and sympatric distributions in coastal streams (White and Harvey 1999), they also responded differently to cumulative culverts. The resultant consistent fish densities would lead to spatial stability in ecological functions, such as nutrient excretion and consumption of invertebrate prey, to take place along the stream network.

The impacts of culverts varied through time. For example, cumulative culvert factor dropped out of top model sets for 2013 diversity and coho salmon densities. Culvert permeability may change between years, depending on flow, which influences passage success (Bouska and Paukert 2010). However, we did not observe differences in depth or wetted width among our reaches to potentially indicate flow changes (Table 3-2). Flows may have been lower in 2013 owing to less precipitation in the preceding 3 weeks (0 mm in 2013, vs 2.9 mm in 2012; Environment Canada 2013), which can create water internal depths that are too shallow for passage (Bates et al. 2003).

Cumulative culvert number and ocean distance are positively related, but our model selection approach indicated differential support for these factors depending on year and response variable. Locations with greater ocean distance are further up in the watershed, and therefore are more likely to cross through road culverts. We are able to distinguish between them in some cases because fish distribution changes relating to increasing ocean distance would appear as gradual and smooth gradients (Jackson et al. 2001), whereas changes driven by number of downstream culverts would be marked as discrete shifts (Mariano et al. 2012). However, in some instances both ocean distance and cumulative culvert variables were present together in top models, making it difficult to differentiate their individual effects. Our choice to include them both in global models, despite their relatedness, was based on the distinction that they represent two different processes for fish communities (Smith et al. 2009). We treated the cumulative number of culverts as an ordered factor, to allow us to see change at each culvert relative to the effect of the previous culvert. Removal of ocean distance from models would have led to an overestimation of the influence of culverts (Smith et al. 2009), thus the coefficient estimates we presented are conservative.

3.5.2. Spatial patterns

As expected, reaches separated at smaller distances were more similar to each other than distant ones, for almost all fish responses (Figure 3-4). Coho densities in 2013 were the only case in which densities were not autocorrelated, likely because of high spatial variability indicated by CV = 2.26 (Figure 3-4; Table 3-4). Total fish densities and diversity were positively autocorrelated at only very short separation distances (< ~100 m). However, at increasing separation distances total densities became heterogeneous, likely due to buffering effects of individual species. Diversity became negatively autocorrelated at greater separation distances, which is supported by earlier results that diversity declines along the ocean distance gradient (Jackson et al. 2001).

3.5.3. Temporal patterns

Fish populations can vary inter-annually, even when habitat remains consistent (Platts and Nelson 1988, Pess et al. 2002). Therefore, it is perhaps not highly unusual that three out of four study species significantly decreased in the second year of study. Coho salmon decreased particularly dramatically; however, there may be supplementation of juveniles with hatchery outplanting in some years, thus making it difficult to ascertain whether patterns where driven by hatchery releases or variation in recruitment. The only species that did not decrease was cutthroat trout, even though annual cutthroat trout abundances can fluctuate naturally within a range that is greater than mean abundances (Platts and Nelson 1988). Several habitat factors changed over the two years and may partly explain concurrent decreases in coho salmon, prickly sculpin and coastrange sculpin in this study. Canopy cover, which is associated with fish food availability, increased 10.6 percentage points in 2013, possibly because sampling in 2013 occurred later in the summer (mid-August versus mid-July) in the previous year. More closed canopy cover could indicate less primary productivity within the stream, and potentially less invertebrate food sources for fish (Hetrick et al. 1998). Finally, recent start of construction for a new rapid transit line (Evergreen Line) may have impacted downstream fish communities in 2013. Construction of a new rail line and transit station resulted in excavations and removal of riparian vegetation upstream of the last sampling point within the watershed. Potential impacts, such as increased construction crew traffic, pollutants, or fine sediment run off, may have influenced downstream fish communities. With only two years of data it is not possible to tell whether populations have declined, or whether fluctuation is natural. Dauwalter et al. (2009) suggested that to detect population changes at one stream site, monitoring should take place over approximately 10 years.

The distribution of fish habitats in rivers is also 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, coined the shifting habitat mosaic, describes the dynamic nature of riverine habitats (Stanford et al. 2005). Our study supports 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 moderately-valued correlation coefficients (Figure 3-6). For coho salmon especially, there was negligible correlation between years, likely in part because densities significantly dropped in the second year (Table 3-2). Our results are similar to Torgersen et al. (2004) who found that habitats with similar morphology had variable abundances of cutthroat trout. Torgersen et al. (2004) specifically highlights variation in similar habitats over space, whereas we highlight that this variation can occur over time.

3.5.4. Conclusion

In this study, we used spatially continuous sampling in a stream network to determine whether culverts pose bottlenecks for fish distributions. We showed that fish densities can follow continuous gradients within an urban riverscape, and culverts can interrupt these gradients. The direction of responses to cumulative culverts depended on the species, location within the watershed, and year. We also found that more upstream culverts on tributaries influenced fish differently than those on the mainstem. Therefore, when evaluating individual culverts for fish passage, the location of the barriers in the watershed and in relation to other barriers should be considered. We also showed that habitat with high fish density in one year may not necessarily retain high densities in the next year. This result has implications for design of fish monitoring programs, particularly those implemented after restoration activities. Monitoring should sample across multiple scales and years and consider intrinsic spatial and temporal variability in fish populations rather than conducting point surveys at one time period. Understanding the stepwise effects of barriers on natural fish gradients helps identify the strongest barriers, which in turn can aid management of riverscape connectivity.

Chapter 4.

General discussion

In my thesis, I examined effects of culverts on urban fish communities across and within watersheds. First, I made upstream-downstream comparisons of fish communities at culverted sites and unimpacted reference sites in 26 streams. I also examined the effect of baffles, retrofitted panels that mitigate impediments, to determine whether they maintain connectivity along streams. Next, I evaluated cumulative culvert impacts on fish densities within one watershed. In this discussion, I briefly synthesize these findings, place my findings in the context of literature on urbanized ecosystems and restoration, and I outline thoughts on future directions for urban stream ecology.

4.1. Connectivity in urban stream ecosystems

Human settlements of all sizes concentrate around freshwater sources. Freshwaters provide humans with abundant ecosystem services, such as sources of drinking water, water for industrial and agricultural purposes, conduits for waste disposal, and locations for commercial and artisanal fisheries. Because of their utility to humans, freshwater ecosystems are influenced by a variety of stressors (Preston and Shackelford 2002), placing them among the most impacted ecosystems in the world (Malmqvist and Rundle 2002). Stressors range from invisible chemical pollutants that can cause premature mortality of organisms (Feist et al. 2011), to biological invasions of species that can wipe out native fauna (Ricciardi and MacIsaac 2011).

The focal stressor in my thesis was loss of connectivity in watersheds. I found that individual culverts influenced structure of fish communities, compared to those in unculverted reference streams. Across studies, I found remarkably consistent species-specific patterns. Cutthroat trout were positively associated with culverts, while sculpin were negatively associated with culverts in both Chapters 2 and 3. Interestingly, in Chapter 2, both cutthroat trout and sculpin densities were influenced at the stream level, suggesting that the community assemblage of streams was impacted on either side of the culvert. As sculpin were most prevalent in streams where connectivity was not disturbed, this suggests that sculpin may be good indicator species of connectivity (Carignan and Villard 2002).

Both chapters teased out these impacts of culverts from natural gradients in fish communities. For example, data from both Chapters 2 and 3 suggested that sculpin naturally decreased along ocean-headwater gradient. In Chapter 2, sculpin densities declined in upstream positions of reference streams and culverted streams alike, but absolute densities were lower in culverted streams. In Chapter 3, I found that coastrange sculpin (and 2012 prickly sculpin) densities decreased along the ocean-headwater gradient in Suter Brook. However, culverts had added effects which were species-dependent. For example, the first culvert in Suter Brook appeared to create sharp drop in prickly sculpin densities in 2013. Therefore, it appears that barriers in small streams are potentially interrupting natural gradients in fish populations. I note that while barriers in streams can occur naturally (e.g. waterfalls, debris jams), culverts and other anthropogenic structures may be accelerating these patterns across the longitudinal stream gradient.

Our sampling indicated that culvert presence did not lead to local extirpations of fish in upstream segments, which is consistent with some studies (e.g. Burford et al. 2009), but contrary to others (e.g. Eisenhour and Floyd 2013). However, one specific instance, at Mossom Creek, the culvert had clearly excluded sculpin species (Chapter 2). Mossom Creek was dominated by prickly sculpin and coastrange sculpin downstream but had none upstream. The exclusion of sculpin was likely because the culvert had a ~0.2 m perch that may have created a barrier for sculpin. One previous study of impassable culverts (defined as having perch height > 12 cm and internal water depth < 2.54 cm) found average fish abundance and species richness declined by half upstream compared to downstream (Nislow et al. 2011). Two of my study culverts had depth < 2.54 cm (Dunlop, Siegel Creeks), and six had a perch > 12 cm (Fergus, Hadden, Jacobson, McLennan, Stoney (ii), Mossom Creeks), but no culverts met both of Nislow et al.'s (2011) criteria, which could indicate potential for passability of some species. Additionally, none of my study culverts had slopes > 4.5%, which represent the threshold for upstream reductions in densities of brook trout (*Salvelinus fontinalis*) and westslope cutthroat trout (*Oncorhynchus clarkii lewisi;* Burford et al. 2009). Even though it is not clear whether study culverts were passable, I note that passable culverts may continually influence rates of movement and distributions. For example, one study reports that westslope cutthroat trout (*Oncorhyncus clarkii lewisi*) had upstream movement rates were 2.45 times lower through culverts than natural reaches (Burford et al. 2009).

Figure 4-1. Two juvenile coho salmon captured in Stoney Creek, Burnaby. These fish were from a reach upstream of Lougheed Highway, just east of Production skytrain station.

Considering their urban locations, my study streams had surprisingly high fish densities and diversity (Figure 4-1). There was only one creek out of twenty seven that I excluded from analysis, due to a near lack of fish. This creek, Byrne Creek, Burnaby, was intriguing for two reasons. First, I only captured two cutthroat trout in the sample section of Byrne Creek, which were coincidentally the largest of the 2012 field season. Due to their large size, light belly, and silver coloration it is likely that these two individuals were “sea-run”, and had migrated in from the estuary or marine environment (W. Atlas and C. Phillis, pers. comm; Figure 4-2). Second, I found a non-native species, a single goldfish (*Carassius auratus*), in Byrne Creek (Figure 4-3). Due to its bright colours, large size and overall healthy appearance I suspect it was freshly deposited in the stream. I did not encounter any other non-native or invasive species that are known to invade small streams, such as non-indigenous crayfish (*Orconectes rusticus;* Foster and Keller 2011) or New Zealand mud snails (*Potamopyrgus antipodarum;* Twardochleb et al. 2012). While fish communities were composed of native species, invasive riparian plant species were rampant (e.g. blackberry (*Rubus armeniacus)*, policeman's helmet (*Impatiens glandulifera),* English ivy (*Hedera helix)*). Additionally, some streams sites had garbage, channelization, and narrow riparian vegetation zones. I focused sampling on streams in suburban residential areas, often in parks, but streams in more heavily densified areas may be even more degraded.

Figure 4-2. Cutthroat trout captured in Byrne Creek, Burnaby. This trout had likely migrated from the Fraser River estuary or near shore.

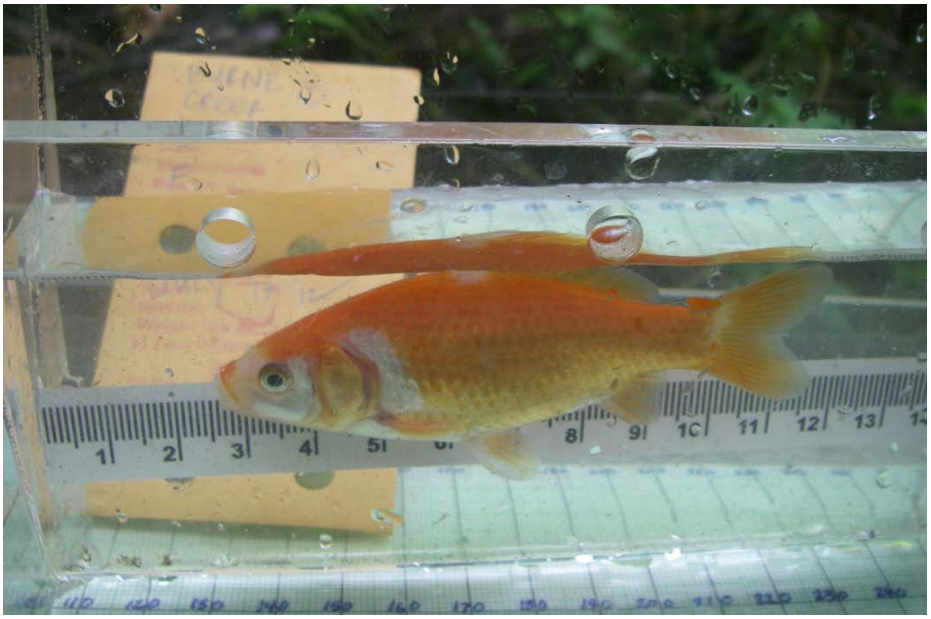

Figure 4-3. Goldfish caught in Byrne Creek, Burnaby.

4.2. Restoration of urban streams

Undertaking restoration requires setting clear objectives (Kondolf 1995), however, a common problem in restorative projects is that objectives are vague and results are unmonitored (Kondolf 1995, Palmer et al. 2005). I encountered these issues when I pursued examination of baffles, a type of culvert restoration. Restoration objectives for my chosen sites were not available, which made it difficult to determine whether they were performing as intended. However, local stream stewards informed me that baffles are primarily installed to facilitate adult salmon spawner passage. Additionally, I found no available data on pre-baffle fish communities and also no recorded data on fish communities after baffle construction. The lack of baselines precluded potential for temporal analyses, and caused me to undertake a spatial comparison. Because stream stewards suggested baffles were targeted at adult salmon, coho salmon fry provided an interesting perspective, as fry distributions may reflect spawning extents. I did not see differences in coho fry abundances between upstream vs. downstream reaches with baffled culverts, suggesting that adult coho spawners are not impeded by baffled culverts. However, I also did not see a difference in upstream vs downstream abundances in coho between non-baffled culverts, which could indicate some non-baffled culverts were potentially previously passable to adult spawners. Clear objectives and baseline data will make examination of effectiveness more streamlined in future instances.

To disentangle effects of one restoration treatment it is important to use appropriate control groups (Downes 2010, Wortley et al. 2013). Control streams should be similar in characteristics such as size, vegetation and geographic area, differing by only one isolated treatment (e.g. baffles). In restoration studies, researchers should also use reference sites, or a target, indicate whether the trajectory of a community subsequently shifts toward conditions in a reference site. I used both control (non-baffled) and reference (unculverted) streams in my Chapter 2. A recent review of 301 papers showed that only 74% of papers examining rehabilitative outcomes included reference sites or controls, while the remainder simply tracked changes through time (Wortley et al. 2013). Of those that did use controls and references, only 22% used both, and 40% used a control only (Wortley et al. 2013). In Chapter 2, I used all three types: reference, control and temporal analyses. I found indication that older baffles were associated with higher species richness. This suggests that baffles may have long term effects that act on decadal scales, an interesting potential future research direction. It is important to use both controls and references when examining or monitoring rehabilitative outcomes, to provide both a gauge of progress and direction of change, otherwise results may be incomplete.

New advances in river restoration science show support for holistic approaches (Stanford et al. 1996, Beechie et al. 2010). Under holistic approaches, managers create conditions where rivers interact with landscape components to restore functional processes (Ward et al. 2002). Restoration on a single species, or issue, may provide narrow benefits that are overwhelmed by larger scale processes. For example, addition of riparian buffering is reach-scale restorative action to dampen storm flows, mitigate impacts of particulate and chemical pollutants, increase inputs of nutrients and wood into the stream, and maintain stream temperature (Fullerton et al. 2006). However, recent literature has emerged demonstrating that degradation at the catchment scale through urbanization and agricultural land use overrides the benefits of riparian zones (Wahl et al. 2013, Imberger et al. 2013). Thus, a more holistic approach would include riparian buffers in addition to maintenance of vegetation patches throughout the catchment, and reduction of permeable surfaces. In terms of restoration of connectivity, baffles would not constitute solution holistic solution, but rather a reach-scale approach. A holistic approach would entail the longitudinal connection of flow and the daylighting of streams, removal of barrier and restoration of natural, open flows and riparian zones (Wild et al. 2011). Kemp and O’Hanley (2010) suggest that barriers for restoration be prioritized based on cost-effectiveness and optimized based on their spatial connectedness (location in watershed). Thus, planning restoration for streams requires clear goals that consider of processes that act at watershed scales.

4.3. Future directions

With modern pressures, the role of ecologists is expanding to include dissemination of science (Cooke et al. 2013). It has become expected that scientists undertake outreach in conjunction with their research programs to help their science influence change (Cooke et al. 2013). There are various methods for scientists to reach out, such as press releases, meetings with policy makers, or organizing social media campaigns. The method I used, and suggest other urban stream ecologists to undertake, is the direct engagement with community members, e.g. stream stewards, and local residents. The community members I met were keenly interested in issues directly relevant to their watersheds, such as development and pollution, and oftentimes had acted as advocates for stream sustainability. I met with several stream keepers both one-on-one and in group meetings, and I invited them to come out and lend a hand or observe fieldwork. During these field work outings, they were able to learn about species from their local creek. In turn, they shared local knowledge on topics such as spawning habitat extent, run timings, invasive species, and urban disturbances such as pollution spills and poaching. I give several reasons why engaging with community members was valuable to both myself as a researcher and the community member. 1) They hold valuable knowledge specific to streams in their neighbourhood, and much of this information is not available to researchers through any other means. 2) They are eager to volunteer physically in urban field work. 3) By interacting with researchers they may increase their knowledge of stream ecology and restoration methods. 4) Educated community members can provide a voice in the face of potential threats (such as pollution spill reporting or advocating for protection during development). I note that many people I engaged with were senior citizens, a demographic that might sometimes be ignored for outreach. However, many were able-bodied and eager to learn about their watersheds, and were surprised that small shallow streams could be teeming with native fish species. Contacting community members and recruiting volunteers through a simple mail-out was easy. People in the community were excited and demonstrated a hunger for this sort of activity, and we as ecologists are uniquely positioned to provide it.

The results in this thesis and points from the discussion lead to three recommendations for future researchers to pursue in the field of urban stream ecology. First, I recommend that urban streams be considered at multiple spatial scales. Rather than focusing on specific habitats, or sections of streams, sampling should reflect knowledge that watersheds integrate processes from the catchment scale, to reach scale, and microhabitat scale. Second, I recommend that stream ecologists engage with community members who may offer a wealth of local knowledge and support to field studies. Third, I recommend that urban streams be protected or restored with solutions that consider watershed-scale solutions. Solutions such as baffles for fish passage are in essence band-aid solutions and do not recognize the continuity and scales of processes at which a river functions.

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Appendix A.

Supporting material for Chapter 2

Table A-1. Study sites and physical characteristics (mean and standard deviation given). Position: A = Upstream, B = downstream; stream type: B= baffles, N = no baffles, R = reference.

Type	Stream	City, Access road	Position	Wet width (m)		Depth (cm)		Canopy cover (%)		Fishing effort (s reach^{-1})		Gradient (%)
				$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	
B	Beecher	Burnaby, Lougheed Hwy	A	3.3	0.9	8.6	2.3	77.7	23.6	127.6	13.3	3.0
			B	3.1	0.2	14.4	6.8	93.2	4.3	148.8	20.4	3.5
B	Brothers	W. Vancouver, Taylor Way	A	5.4	2.3	10.1	5.4	84.3	2.0	283.2	37.0	8.0
			B	5.2	2.2	12.2	5.1	81.8	7.4	323.0	47.7	4.0
B	Chantrell	Surrey, Crescent Rd	A	2.9	0.4	15.5	11.5	91.3	5.5	133.4	30.0	3.8
			B	2.6	0.8	12.1	8.5	80.1	6.6	161.4	57.0	2.0
B	Fergus	Surrey, Hwy 99	A	2.8	1.1	7.6	4.7	79.6	11	171.2	54.0	3.0
			B	2.3	0.5	14.1	7.7	85.6	7.0	183.8	32.3	3.5
B	Hadden	W. Vancouver, Hwy 1	A	2.4	0.7	9.1	2.8	85.3	9.3	154	18.3	5.0
			B	2.5	0.3	7.5	2.9	84.6	3.5	197.2	14.9	5.0
B	McLennan	Abbotsford, Downes Rd	A	2.3	0.5	14.2	3.2	74.1	9.8	126.8	43.8	0.5
			B	3.1	0.2	19.7	7.8	90.1	2.7	245.8	55.8	1.0
B	Mossom	Port Moody, Ioco Rd	A	6.1	2.3	15.6	7.1	87.0	3.4	361.2	96.6	1.5
			B	5.3	0.7	12.7	7.3	87.8	3.4	375.6	54.9	2.0
B	Nelson	W. Vancouver, Marine Dr	A	4.9	0.6	14.6	5.2	84.7	3.8	224.4	60.8	4.0
			B	3.6	1.5	20.2	9.8	77.0	9.6	209.6	71.8	4.5
B	Serpentine	Surrey, 155 St	A	2.8	1.7	8.5	4.2	86.4	6.3	123.2	29.0	1.5
			B	2.2	0.3	11.1	2.6	88.1	4.2	167.0	35.8	2.5
B	Stoney (i)	Burnaby, Lougheed Hwy	A	4.3	1.0	15.1	6.6	83.4	4.6	173.8	34.8	2.5
			B	5.3	1.7	12.6	5.8	87.2	3.0	251.2	17.5	3.0
B	Stoney (ii)	Abbotsford, Laburnum Ave	A	3.1	0.9	7.0	2.4	84.3	8.6	145.8	34.8	3.0
			B	3.0	1.0	7.0	2.4	86.2	5.1	148.8	25.2	2.0
B	Suter Brook	Port Moody, Rocky Point	A	2.0	0.3	16.4	3.2	83.3	5.3	207.9	42.5	2.0
			B	2.3	0.7	15.3	8.3	72.0	21.3	245.1	60.0	4.0
N	Yorkson	Langley, Hwy 1	A	2.0	0.4	4.2	1.8	90.2	1.4	116.4	27.0	2.0
			B	2.9	1.1	7.6	3.8	83.0	2.3	145.2	39.6	1.5
N	Dunlop	Maple Ridge, 112 Ave	A	2.4	0.6	6.4	2.9	83.6	6.9	131.0	18.2	2.0
			B	3.6	1.1	9.3	9.9	76.6	5.2	180.0	27.3	0.5
N	Eagle	Burnaby, Kraft Pl	A	3.4	0.6	8.5	2.4	89.2	3.3	219.6	75.2	1.5
			B	4.1	1.0	9.2	2.7	82.6	8.1	303.6	113.9	4.0

Type	Stream	City, Access road	Position	Wet width (m)		Depth (cm)		Canopy cover (%)		Fishing effort (s reach^{-1})		Gradient (%)
				$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	
N	Elgin	Surrey, Crescent Rd	A	2.6	1.0	8.8	4.2	80.5	5.6	199.6	50.4	1.5
			B	3.1	0.8	17.2	2.6	86.3	4.0	213.6	18.6	2.0
N	Jacobson	Surrey, 8 Ave	A	2.1	0.7	6.5	3.6	86.4	5.1	131.2	24.0	2.0
			B	2.6	0.5	8.0	4.6	92.7	2.1	156.2	64.5	5.0
N	Maple	Coquitlam, Chine Dr	A	1.7	0.5	12.9	5.5	85.0	5.7	157.8	23.0	0.0
			B	2.0	0.6	22.2	5.1	74.6	21.1	202.8	31.5	0.0
N	Scott	Coquitlam, Lansdowne Dr	A	4.4	1.1	23.5	8.8	87.6	4.8	178.0	36.4	7.0
			B	6.0	1.9	10.7	4.0	88.7	1.6	235.0	12.2	3.0
N	Siegel	Maple Ridge, 112 Ave	A	1.5	0.3	4.7	2.9	87.1	6.1	124.8	41.9	1.0
			B	2.1	0.8	7.9	4.3	85.9	7.0	121.4	29.8	1.5
R	Anderson	Langley, Colebrook Rd	A	4.5	1.0	24.0	9.6	33.2	15.4	201.6	41.1	0.0
			B	4.5	1.0	19.9	14.6	51.0	13.2	220.6	29.0	0.5
R	Cypress	W. Vancouver, Marine Dr	A	6.7	1.6	20	6.3	82.3	5.6	242.8	41.8	4.0
			B	5.2	0.8	14.5	2.8	76.8	20.1	228.6	50.0	3.0
R	Nathan	Abbotsford, Nathan Ave	A	2.4	0.5	6.7	2.2	78.7	2.9	225.2	25.2	4.0
			B	2.7	1.6	6.0	4.5	83.7	5.1	217.6	48.2	3.0
R	Noon's	Port Moody, Ioco Rd	A	2.5	0.7	13.5	2.8	70.1	23.6	191.0	54.4	5.0
			B	4.4	1.5	15.5	9.2	55.6	12.5	178.2	19.4	3.0
R	Partington	Coquitlam, Quarry Rd	A	3.6	0.9	15.1	3.8	86.4	3.5	229.4	81.8	3.8
			B	3.8	0.8	16.7	5.2	88.3	7.5	225.6	51.8	4.5
R	Watkins	Coquitlam, Windsor Ave	A	2.4	0.3	6.9	4.8	82.9	7.9	139.4	15.7	0.5
			B	2.4	0.4	16	24.6	80.9	13.6	157	31.7	0.5

Appendix A-2. Physical variables in relation to stream types and position: methods and results

We used linear mixed effects models (LME) to assess if intrinsic habitat differences were a function of stream type and position, the interaction between stream type and position, and a random intercept term for stream (Appendix A-3). Depth data were log transformed to satisfy the assumption of normal residuals. To account for random effects of each individual stream, each model included a random intercept term for stream.

Study stream types had some important differences in physical habitat, most notably in sediment sizes. Reference stream types had on average largest sediments (LME: β = 60.18, standard error (SE) = 25.24, degrees of freedom (DF) = 23, t = 2.38, P = 0.026; Appendix A-3). Sediment sizes also varied within non-baffled and baffled stream types. Specifically, in non-baffled stream types, median sediment size was on average 11.78 mm larger upstream relative to downstream positions (LME: β= 11.78, SE = 1.91, DF = 228, t = 6.18, $P < 0.0001$; Appendix A-3). In contrast, in baffled stream types, median sediment size was on average 9.17 mm smaller upstream relative to downstream (LME: β = -9.17, SE = 2.35, DF = 228, t = -3.90, $P < 0.0001$; Appendix A-3). Additionally, reference stream types had on average 11.33 % less canopy cover than culverted streams (LME: β = -11.33, SE = 5.00, degrees of freedom, (DF) = 23, t = -2.27, P = 0.033; Appendix A-3). Stream type and stream position influenced wetted width. Specifically, wetted width upstream of culverts was 0.79 m narrower compared to downstream in non-baffled stream types (LME: β = -0.79, SE = 0.26, DF = 228, t = -3.10, P = 0.002; Appendix A-3). Also, upstream wetted width was 0.85 m wider when there were baffles (LME: β = 0.85, SE = 0.32, DF = 228, t = 2.69, P = 0.008; Appendix A-3). Mean depth was similar across positions and stream types.

Table A-3. **Parameter estimates for linear mixed effect models (LMEs) examining habitat variation across stream types, upstream-downstream positions, and the interaction between stream types and positions. Models included a random intercept term for stream. Coefficients represent relationship to the intercept, which represent conditions at non-baffled culverts.**

Habitat response	Variable	Coefficient	Standard error	Degrees of freedom	t-value	*P*
Canopy cover (%)	Intercept	84.05	3.40	228	24.70	<0.001
	Baffles	0.49	4.22	23	0.12	0.909
	Reference	-11.33	5.00	23	-2.27	0.033
	Upstream	1.47	2.40	228	0.61	0.541
	Baffles x Upstream	-2.04	2.96	228	-0.69	0.491
	Reference x Upstream	-1.93	3.50	228	-0.55	0.582
Depth (log cm)	Intercept	2.30	0.17	228	13.67	<0.001
	Baffles	0.10	0.21	23	0.49	0.629
	Reference	0.12	0.25	23	0.48	0.633
	Upstream	-0.21	0.13	228	-1.66	0.098
	Baffles x Upstream	0.07	0.15	228	0.47	0.638
	Reference x Upstream	0.28	0.18	228	1.52	0.130
Wetted width (m)	Intercept	3.37	0.49	228	6.91	<0.001
	Baffles	-0.02	0.60	23	-0.03	0.979
	Reference	0.47	0.72	23	0.65	0.523
	Upstream	-0.79	0.26	228	-3.10	0.002
	Baffles x Upstream	0.85	0.32	228	2.69	0.008
	Reference x Upstream	0.65	0.37	228	1.73	0.085
Median sediment size (mm)	Intercept	21.65	17.15	228	1.26	0.208
	Baffles	25.59	21.27	23	1.20	0.241
	Reference	60.18	25.24	23	2.38	0.026
	Upstream	11.78	1.91	228	6.18	<0.001
	Baffles x Upstream	-9.17	2.35	228	-3.90	<0.001
	Reference x Upstream	-16.20	2.78	228	-5.82	<0.001

Table A-4. **Coefficient estimates for generalized linear mixed effects models GLMMs (fish densities, richness) and linear mixed effects models LME (log biomass) examining fish responses to habitat variables. All models include a random intercept for stream and an offset (log m^2, except richness) to account for different areas in each reach.**

Level	Response	Variable	Coefficient	Standard error	z-value	P
Species	Coho (number•m^{-2})	Intercept	-2.741	0.522	-5.25	<0.001
		Median sediment	-0.014	0.004	-3.65	<0.001
		Canopy cover	0.008	0.005	1.57	0.117
		Depth	0.004	0.006	0.66	0.510
	Trout (number•m^{-2})	Intercept	-2.367	0.507	-4.66	<0.001
		Median sediment	-0.006	0.003	-1.83	0.068
		Canopy cover	-0.006	0.006	-1.10	0.271
		Depth	0.013	0.007	1.72	0.085
	Sculpin (number•m^{-2})	Intercept	-9.173	1.811	-5.07	<0.001
		Median sediment	0.037	0.014	2.53	0.011
		Canopy cover	-0.005	0.007	-0.71	0.476
		Depth	0.011	0.012	0.89	0.371
Community	Total fish (number•m^{-2})	Intercept	-1.316	0.296	-4.45	<0.001
		Median sediment	-0.004	0.002	-1.93	0.054
		Canopy cover	-0.001	0.003	-0.33	0.741
		Depth	0.008	0.004	1.68	0.092
	Total biomass (g•m^{-2})	Intercept	3.583	0.425	8.43	<0.001
		Median sediment	0.002	0.002	1.23	0.2214
		Canopy cover	0.002	0.005	0.48	0.6323
		Depth	0.013	0.007	1.74	0.0826
	Species richness•reach^{-1}	Intercept	-3.059	0.305	-10.03	<0.001
		Median sediment	-0.004	0.001	-3.54	0.0004
		Canopy cover	0.000	0.003	0.06	0.9505
		Depth	0.009	0.005	1.81	0.0708

Table A-5. **Coefficient estimates for generalized linear mixed effects models GLMMs (fish densities and species richness) and linear mixed effects models LME (biomass) examining fish metrics across stream types and positions. Models include an offset for reach area (log m^2, except richness) and a random intercept for stream. The intercept represents default values of fish counts for the downstream, non-baffled stream type.**

Level	Response	Variable	Coefficient	Standard error	z-value	*P*
Species	Coho (number•m^{-2})	Intercept	-2.09	0.57	-3.64	<0.001
		Baffles	0.14	0.71	0.19	0.846
		Reference	-0.04	0.87	-0.05	0.962
		Upstream	0.15	0.16	0.93	0.352
		Median sediment size	-0.02	4.35 x 10^{-3}	-3.5	0.000
		Baffles x Upstream	-0.12	0.19	-0.6	0.546
		Reference x Upstream	-0.39	0.25	-1.58	0.115
	Trout (number•m^{-2})	Intercept	-2.64	0.28	-9.57	<0.001
		Baffles	0.25	0.33	0.75	0.456
		Reference	-1.14	0.44	-2.62	0.009
		Upstream	-0.13	0.18	-0.69	0.491
		Median sediment size	-3.94 x 10^{-3}	2.87 x 10^{-3}	-1.37	0.170
		Baffles x Upstream	0.08	0.22	0.35	0.725
		Reference x Upstream	0.27	0.32	0.86	0.390
	Sculpin (number•m^{-2})	Intercept	-10.02	1.85	-5.42	<0.001
		Baffles	1.56	1.91	0.82	0.415
		Reference	4.50	2.22	2.03	0.043
		Upstream	-0.57	0.18	-3.19	0.001
		Median sediment size	0.02	0.01	1.78	0.076
Community	Total fish (number•m^{-2})	Intercept	-1.32	0.21	-6.32	<0.001
		Baffles	0.07	0.26	0.28	0.780
		Reference	0.05	0.33	0.15	0.880
		Upstream	-0.05	0.12	-0.41	0.680
		Median sediment size	-3.15 x 10^{-3}	2.06 x 10^{-3}	-1.52	0.130
		Baffles x Upstream	-0.15	0.15	-1.01	0.310
		Reference x Upstream	-0.04	0.18	-0.21	0.830
	Total biomass (log g•m^{-2})	Intercept	-6.96 x 10^{-4}	0.22	0	1.000
		Baffles	0.20	0.27	0.73	0.470
		Reference	-0.19	0.34	-0.57	0.570
		Upstream	-0.03	0.20	-0.17	0.860

	Median sediment size	-7.17×10^{-4}	2.19×10^{-3}	-0.33	0.740
	Baffles x Upstream	-0.14	0.25	-0.57	0.570
	Reference x Upstream	-0.02	0.29	-0.08	0.940
Species richness• reach^{-1}	Intercept	1.04	0.12	8.89	<0.001
	Baffles	0.08	0.14	0.57	0.570
	Reference	-0.17	0.18	-0.94	0.350
	Upstream	-0.11	0.15	-0.74	0.460
	Median sediment size	1.25×10^{-4}	1.10×10^{-3}	0.11	0.910
	Baffles x Upstream	-0.04	0.18	-0.2	0.840
	Reference x Upstream	0.21	0.22	0.98	0.330

Notes: Sediment size was included as a fixed effect because we found an association between stream type and sediments (Appendices A-3, A-4). Because sculpin data was sparse, we fit a simpler model without specifying the interaction between stream type and position for sculpin data.

Table A-6. Coefficient estimates for linear mixed effects models (LMEs) examining biomass (log $g \bullet m^{-2}$) across each 20-m reach in relation to reach location for each of our three stream types. Reaches 1- 10 represent 20 m long reaches sampled from downstream to upstream, the culvert (if applicable) is located between reaches 5 and 6.

Stream type	Variable	Coefficient	Standard error	z-value	*P*
Reference	Intercept	-0.014	0.291	-0.05	0.962
	Reach 2	-0.084	0.300	-0.28	0.779
	Reach 3	0.053	0.300	0.18	0.859
	Reach 4	-0.570	0.300	-1.9	0.057
	Reach 5	-0.594	0.300	-1.98	0.047
	Reach 6	-0.203	0.300	-0.68	0.497
	Reach 7	-0.011	0.300	-0.04	0.971
	Reach 8	-0.416	0.300	-1.39	0.165
	Reach 9	-0.388	0.300	-1.29	0.196
	Reach 10	-0.450	0.300	-1.5	0.133
Baffled	Intercept	-0.099	0.261	-0.38	0.706
	Reach 2	-0.039	0.326	-0.12	0.906
	Reach 3	0.214	0.326	0.66	0.511
	Reach 4	0.437	0.326	1.34	0.180
	Reach 5	0.664	0.326	2.04	0.042
	Reach 6	0.104	0.326	0.32	0.750
	Reach 7	0.572	0.326	1.76	0.079
	Reach 8	0.094	0.326	0.29	0.772
	Reach 9	-0.152	0.326	-0.47	0.642
	Reach 10	-0.206	0.326	-0.63	0.527
Non-baffled	Intercept	0.014	0.408	0.04	0.97
	Reach 2	0.206	0.508	0.4	0.69
	Reach 3	-0.294	0.508	-0.58	0.56
	Reach 4	-0.183	0.508	-0.36	0.72
	Reach 5	0.121	0.508	0.24	0.81
	Reach 6	-0.027	0.508	-0.05	0.96
	Reach 7	0.197	0.508	0.39	0.70
	Reach 8	-0.082	0.508	-0.16	0.87
	Reach 9	-0.318	0.508	-0.63	0.53
	Reach 10	-0.148	0.526	-0.28	0.78

Note: Coefficients show relation reach 1 (furthest downstream of culvert).

Table A-7. Coefficient estimates for linear mixed effects models (LMEs) examining maximum fork length of cutthroat trout reach^{-1} in relation to reach location for each stream types. Reaches 1- 10 represent 20 m long reaches sampled from downstream to upstream, the culvert (if applicable) is located between reaches 5 and 6.

Stream type	Variable	Coefficient	Standard error	z-value	*P*
Reference	Intercept	114.7	9.3	12.39	<0.0001
	Reach 2	-12.5	13.1	-0.96	0.339
	Reach 3	-5.3	13.1	-0.41	0.684
	Reach 4	-17.0	13.1	-1.3	0.194
	Reach 5	-32.7	13.1	-2.5	0.013
	Reach 6	-17.2	13.1	-1.31	0.190
	Reach 7	-3.8	13.1	-0.29	0.770
	Reach 8	-12.7	13.1	-0.97	0.333
	Reach 9	-10.2	13.1	-0.78	0.437
	Reach 10	-23.3	13.7	-1.7	0.090
Baffled	Intercept	99.1	10.8	9.22	< 0.0001
	Reach 2	12.2	13.2	0.92	0.356
	Reach 3	22.4	13.2	1.7	0.090
	Reach 4	28.2	13.2	2.14	0.032
	Reach 5	46.2	13.2	3.5	0.000
	Reach 6	7.5	13.2	0.57	0.571
	Reach 7	42.8	13.2	3.24	0.001
	Reach 8	19.6	13.2	1.48	0.138
	Reach 9	18.6	13.2	1.41	0.158
	Reach 10	15.3	13.2	1.16	0.249
Non-baffled	Intercept	119.2	18.1	6.61	<0.0001
	Reach 2	15.8	20.0	0.79	0.43
	Reach 3	9.8	20.0	0.49	0.63
	Reach 4	-24.4	20.0	-1.22	0.22
	Reach 5	20.5	20.0	1.02	0.31
	Reach 6	-10.8	20.0	-0.54	0.59
	Reach 7	18.8	20.0	0.94	0.35
	Reach 8	-8.4	20.0	-0.42	0.68
	Reach 9	-16.6	20.0	-0.83	0.41
	Reach 10	-4.5	20.7	-0.22	0.83

Notes: Coefficients show relation to reach 1 (furthest reach downstream of culvert).

Appendix B.

Supporting material for Chapter 3

Table B-1. Description of culverts in the Suter Brook, measured in 2012.

Stream distance (~ m)	Shape	Material	Width (m)	Length (m)	Slope (%)	Water depth (cm)	Perch (cm)	Baffles
160	box	concrete	1.8	50.6	1	13	0	yes
390	round	corrogated steel	0.9	29.5	2	18	0	no
800 (West trib)	round	corrogated steel	0.7	19.4	0.5	4	15	no
830 (East trib)	round	corrugated steel	0.81	12	?	16	0	no

Note. Stream distance represents distance along watercourse to most downstream reach

Table B-2. Top ranked models for the set of models within 4 delta AICc points for fish responses in 2012. Densities represent fish m^{-2}. Cul = cumulative number of culverts downstream of a given reach, Dist = distance along stream network to reach closest to ocean (m), G = gradient (%), CC = canopy cover (%), D = mean depth at reach (cm), S = median sediment size (mm). Effect sizes were standardized to a mean of 0. DF = degrees of freedom, LogLik = log likelihood.

Response	Rank	Model	DF	LogLik	AICc	**ΔAICc**	Weight
Total fish density	1	G	4	24.11	-39.33	0	0.23
	2	~1	3	22.47	-38.41	0.92	0.14
	3	CC + G	5	24.39	-37.42	1.91	0.09
	4	G + S	5	24.25	-37.15	2.19	0.08
	5	G + D	5	24.18	-36.99	2.34	0.07
	6	G + Dist	5	24.13	-36.89	2.45	0.07
	7	Cul + Dist	7	26.66	-36.64	2.69	0.06
	8	CC	4	22.66	-36.44	2.9	0.05
	9	Dist	4	22.49	-36.09	3.24	0.05
	10	S	4	22.48	-36.08	3.26	0.04

Response	Rank	Model	DF	LogLik	AICc	**ΔAICc**	Weight
	11	D	4	22.47	-36.06	3.27	0.04
	12	CC + Cul + Dist	8	27.72	-35.93	3.4	0.04
	13	Cul + G + Dist	8	27.54	-35.56	3.77	0.03
Simpson's diversity	1	Cul + Dist	7	29.11	-41.55	0	0.3
	2	Cul	6	27.27	-40.58	0.96	0.19
	3	Cul + S + Dist	8	29.17	-38.82	2.73	0.08
	4	CC + Cul + Dist	8	29.14	-38.77	2.78	0.08
	5	Cul + G + Dist	8	29.11	-38.71	2.84	0.07
	6	Cul + D + Dist	8	29.11	-38.71	2.84	0.07
	7	CC + Cul	7	27.43	-38.19	3.35	0.06
	8	Cul + G	7	27.37	-38.07	3.47	0.05
	9	Cul + D	7	27.35	-38.04	3.51	0.05
	10	Cul + S	7	27.34	-38.01	3.53	0.05
Coho salmon density	1	G	4	50.43	-91.98	0	0.12
	2	Cul + G + Dist	8	55.36	-91.2	0.77	0.08
	3	Cul + G	7	53.92	-91.18	0.8	0.08
	4	G + D	5	51.08	-90.8	1.17	0.07
	5	G + Dist	5	51.06	-90.75	1.23	0.07
	6	G + S	5	50.83	-90.29	1.68	0.05
	7	Cul + Dist	7	53.46	-90.26	1.72	0.05
	8	CC + G	5	50.8	-90.24	1.74	0.05
	9	Cul + G + D + Dist	9	56.05	-89.6	2.37	0.04
	10	Cul + G + S	8	54.53	-89.55	2.43	0.04
	11	CC + Cul + G + Dist	9	56.01	-89.51	2.46	0.04
	12	G + D + S	6	51.69	-89.44	2.54	0.03
	13	G + S + Dist	6	51.56	-89.16	2.82	0.03
	14	G + D + Dist	6	51.47	-88.99	2.98	0.03
	15	CC + Cul + G	8	54.23	-88.95	3.03	0.03

Response	Rank	Model	DF	LogLik	AICc	**ΔAICc**	Weight
	16	Cul + G + S + Dist	9	55.71	-88.91	3.07	0.03
	17	CC + G + Dist	6	51.38	-88.81	3.17	0.03
	18	Cul + G + D	8	54.13	-88.75	3.23	0.02
	19	CC + G + D	6	51.3	-88.64	3.34	0.02
	20	CC + G + S	6	51.18	-88.4	3.57	0.02
	21	Cul	6	51.17	-88.38	3.6	0.02
	22	Cul + D + Dist	8	53.91	-88.3	3.68	0.02
	23	CC + Cul + Dist	8	53.83	-88.14	3.84	0.02
Cutthroat trout density	1	Cul + S	7	63.93	-111.2	0	0.14
	2	Cul	6	62.51	-111.08	0.12	0.13
	3	Cul + G	7	63.55	-110.43	0.77	0.09
	4	Cul + G + S	8	64.74	-109.96	1.24	0.07
	5	Cul + S + Dist	8	64.60	-109.68	1.51	0.06
	6	Cul + Dist	7	63.07	-109.48	1.72	0.06
	7	CC + Cul	7	63.02	-109.37	1.83	0.06
	8	CC + Cul + S	8	64.34	-109.17	2.02	0.05
	9	CC + Cul + G	8	64.25	-108.99	2.21	0.05
	10	Cul + G + Dist	8	64.03	-108.54	2.65	0.04
	11	Cul + D	7	62.59	-108.52	2.68	0.04
	12	Cul + D + S	8	63.95	-108.39	2.81	0.03
	13	Cul + G + S + Dist	9	65.33	-108.17	3.03	0.03
	14	CC + Cul + G + S	9	65.32	-108.14	3.05	0.03
	15	Dist	4	58.47	-108.05	3.15	0.03
	16	Cul + G + D	8	63.69	-107.87	3.33	0.03
	17	CC + Cul + Dist	8	63.65	-107.8	3.4	0.03
	18	CC + Cul + S + Dist	9	65.09	-107.67	3.52	0.02
	19	S + Dist	5	59.38	-107.4	3.8	0.02
Prickly sculpin	1	Dist	4	103.44	-198	0	0.31

Response	Rank	Model	DF	LogLik	AICc	**ΔAICc**	Weight
density	2	G + Dist	5	103.91	-196.45	1.55	0.14
	3	Cul + Dist	7	106.52	-196.37	1.63	0.14
	4	D + Dist	5	103.6	-195.85	2.15	0.11
	5	CC + Dist	5	103.45	-195.54	2.46	0.09
	6	S + Dist	5	103.44	-195.53	2.47	0.09
	7	Cul + G + Dist	8	107.34	-195.17	2.83	0.08
	8	G + D + Dist	6	104.13	-194.3	3.7	0.05
Coastrange sculpin density	1	Dist	4	91.5	-174.11	0	0.29
	2	~1	3	89.49	-172.45	1.65	0.13
	3	S + Dist	5	91.76	-172.16	1.94	0.11
	4	CC + Dist	5	91.52	-171.67	2.44	0.09
	5	G + Dist	5	91.51	-171.65	2.45	0.09
	6	D + Dist	5	91.5	-171.63	2.47	0.08
	7	S	4	89.85	-170.8	3.3	0.06
	8	Cul	6	92.11	-170.27	3.83	0.04
	9	G	4	89.55	-170.21	3.9	0.04
	10	D	4	89.51	-170.14	3.97	0.04
	11	CC	4	89.51	-170.12	3.98	0.04

Table B-3. **Top ranked models for the set of models within 4 delta AICc points for fish responses in 2013. Densities represent fish m^{-2}. Cul = cumulative number of culverts downstream of a given reach, Dist = distance along stream network to reach closest to ocean (m), G = gradient (%), CC = canopy cover (%), D = mean depth at reach (cm), S = median sediment size (mm). Effect sizes were standardized to a mean of 0. DF = degrees of freedom, LogLik = log likelihood.**

Response	Rank	Model	DF	LogLik	AICc	**ΔAICc**	Weight
Total fish density	1	D	4	24.22	-39.56	0	0.29
	2	~1	3	22.12	-37.71	1.85	0.12
	3	G + D	5	24.43	-37.5	2.06	0.1
	4	D + Dist	5	24.36	-37.36	2.2	0.1
	5	CC + D	5	24.32	-37.28	2.28	0.09
	6	D + S	5	24.24	-37.12	2.44	0.09
	7	CC	4	22.81	-36.74	2.82	0.07
	8	Dist	4	22.62	-36.35	3.21	0.06
	9	G	4	22.33	-35.76	3.8	0.04
	10	Cul + D	7	26.12	-35.57	3.98	0.04
Simpson's Diversity	1	Dist	4	8.03	-7.16	0	0.45
	2	D + Dist	5	8.16	-4.95	2.21	0.15
	3	G + Dist	5	8.04	-4.72	2.45	0.13
	4	CC +Dist	5	8.03	-4.7	2.46	0.13
	5	S + Dist	5	8.03	-4.69	2.47	0.13
Coho density	1	~1	3	126.96	-247.4	0	0.22
	2	G	4	128.07	-247.26	0.14	0.21
	3	D	4	127.21	-245.53	1.87	0.09
	4	Dist	4	127.18	-245.46	1.94	0.08
	5	G + D	5	128.31	-245.25	2.16	0.08
	6	S	4	127.07	-245.24	2.16	0.08
	7	CC	4	126.97	-245.04	2.36	0.07
	8	G + Dist	5	128.12	-244.87	2.53	0.06
	9	G + S	5	128.1	-244.84	2.56	0.06

Response	Rank	Model	DF	LogLik	AICc	**ΔAICc**	Weight
	10	CC + G	5	128.07	-244.78	2.62	0.06
Cutthroat trout density	1	D + Dist	5	27.47	-43.58	0	0.2
	2	Cul + D	7	29.93	-43.19	0.39	0.17
	3	Dist	4	25.38	-41.87	1.72	0.09
	4	CC + Cul + D	8	30.47	-41.42	2.16	0.07
	5	CC + D + Dist	6	27.58	-41.22	2.37	0.06
	6	G + D + Dist	6	27.52	-41.08	2.5	0.06
	7	D + S + Dist	6	27.52	-41.08	2.5	0.06
	8	CC + Cul	7	28.85	-41.03	2.55	0.06
	9	CC + Dist	5	26.08	-40.8	2.78	0.05
	10	Cul	6	27.21	-40.47	3.11	0.04
	11	Cul + G + D	8	29.96	-40.4	3.18	0.04
	12	Cul + D + S	8	29.95	-40.39	3.19	0.04
	13	Cul + D + Dist	8	29.94	-40.37	3.21	0.04
	14	D	4	24.37	-39.85	3.73	0.03
Prickly sculpin density	1	Cul	6	119.26	-224.58	0	0.36
	2	CC + Cul	7	119.7	-222.74	1.84	0.14
	3	Cul + D	7	119.55	-222.43	2.15	0.12
	4	Cul + Dist	7	119.43	-222.2	2.38	0.11
	5	Cul + S	7	119.29	-221.91	2.66	0.1
	6	Cul + G	7	119.27	-221.86	2.71	0.09
	7	CC + Cul + D	8	120.41	-221.31	3.26	0.07
Coast range sculpin density	1	G + S + Dist	6	116.5	-219.06	0	0.16
	2	CC + G + S + Dist	7	117.82	-218.98	0.08	0.15
	3	G + Dist	5	114.97	-218.58	0.48	0.12
	4	CC + G + Dist	6	116.21	-218.46	0.6	0.12
	5	S + Dist	5	114.57	-217.77	1.28	0.08
	6	CC + S + Dist	6	115.52	-217.08	1.97	0.06

Response	Rank	Model	DF	LogLik	AICc	**ΔAICc**	Weight
	7	G + D + S + Dist	7	116.76	-216.86	2.2	0.05
	8	CC + G + D + S + Dist	8	117.82	-216.14	2.92	0.04
	9	G + D + Dist	6	115.04	-216.13	2.92	0.04
	10	S	4	112.5	-216.12	2.94	0.04
	11	Dist	4	112.38	-215.87	3.18	0.03
	12	CC + G + D + Dist	7	116.24	-215.82	3.23	0.03
	13	G + S	5	113.55	-215.73	3.33	0.03
	14	D + S + Dist	6	114.77	-215.59	3.47	0.03
	15	CC + Cul + G + S	9	118.82	-215.15	3.91	0.02