

Potential loss and rehabilitation of stream longitudinal connectivity: fish populations in urban streams with culverts

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Abstract: Riverine connectivity is important to the persistence of fish communities, but culverts may impede fish movements to varying degrees and in both directions. Baffles can be installed in culverts to mitigate upstream connectivity loss; however, evaluation of their effectiveness is limited. To examine the potential impacts of culverts and their potential rehabilitation with baffles, we sampled fish populations in 26 streams that contained either (i) nonbaffled culverts or (ii) baffled culverts or (iii) lacked culverts (reference streams) in Metro Vancouver, British Columbia, Canada. Using mixed effects models, we compared fish responses across these three stream types to infer effects at the whole-stream scale (i.e., over both upstream and downstream positions equally), the within-stream scale (i.e., upstream versus downstream of culverts), and the interaction of scales. Densities ($n \cdot m^{-2}$) of coastrange sculpin (*Cottus aleoticus*) and prickly sculpin (*Cottus asper*) were significantly lower in nonbaffled and baffled stream types than in reference stream types, while densities of cutthroat trout (*Oncorhynchus clarkii*) and rainbow trout (*Oncorhynchus mykiss*) were significantly lower in reference stream types, indicating whole-stream differences. Using multivariate statistics, we similarly found that fish community compositions were significantly different across stream types. For our various fish responses, we found no interaction between stream type and upstream or downstream position. Further, we found reaches directly downstream of baffled culverts had greater fish biomass and that overall species richness increased with age of baffles. These data suggest that culverts may drive changes in fish populations at whole-stream scales, and restoration of these effects with baffles may take decades.

Résumé : Si la connectivité fluviale est importante pour la persistance des communautés de poissons, les ponceaux peuvent entraver les déplacements des poissons à différents degrés et dans les deux directions. Des déflecteurs peuvent être installés dans les ponceaux afin d'atténuer la perte de connectivité vers l'amont, mais l'évaluation de leur efficacité est limitée. Afin d'examiner les impacts éventuels des ponceaux et leur possible réhabilitation à l'aide de déflecteurs, nous avons échantillonné des populations de poissons dans 26 cours d'eau présentant (i) des ponceaux sans déflecteur, (ii) des ponceaux avec déflecteurs ou (iii) une absence de ponceau (cours d'eau témoins) dans la région métropolitaine de Vancouver (Colombie-Britannique, Canada). À l'aide de modèles d'effets mixtes, nous avons comparé les réactions des poissons dans ces trois types de cours d'eau afin d'inférer les effets aux échelles de l'ensemble du cours d'eau (c.-à-d. sur des positions amont et aval) et du tronçon (c.-à-d. comparaison de la situation en amont et en aval de ponceaux) et l'interaction de ces échelles. Les densités ($n \cdot m^{-2}$) des chabots côtiers (*Cottus aleoticus*) et des chabots piquants (*Cottus asper*) étaient significativement plus faibles dans les cours d'eau avec ponceau sans déflecteur et avec déflecteurs que dans les cours d'eau témoins, alors que les densités des truites fardées (*Oncorhynchus clarkii*) et des truites arc-en-ciel (*Oncorhynchus mykiss*) étaient significativement plus faibles dans les cours d'eau témoins, ce qui indique des différences à l'échelle de l'ensemble du cours d'eau. En utilisant l'analyse statistique multidimensionnelle, nous avons également relevé des différences significatives sur le plan de la composition des communautés de poissons selon le type de cours d'eau. Pour les différents types de réaction des poissons, nous n'avons relevé aucune interaction entre le type de cours d'eau et la position amont ou aval. En outre, nous avons constaté que les tronçons situés directement en aval de ponceaux avec déflecteurs présentaient une plus grande biomasse de poissons et que la richesse spécifique globale augmentait avec l'âge des déflecteurs. Ces données donnent à penser que les ponceaux peuvent entraîner des modifications des populations de poissons à l'échelle de l'ensemble du cours d'eau et que le rétablissement des conditions antérieures à de tels effets peut prendre des décennies. [Traduit par la Rédaction]

Introduction

Fragmentation of habitats is a major anthropogenic impact in riverine ecosystems. For example, structures such as large dams can fragment river systems by restricting sediment transport (Ligon et al. 1995) and filtering out native species (Mims and Olden 2013). However, there is growing appreciation that small structures such as culverts may also act as impediments to dispersal (Warren and Pardew 1998). For example, fish passage can be impeded by conditions in culverts that create high flows (Mahlum et al. 2014), high hanging height (Burford et al. 2009), or the phys-

ical blockage of culverts due to clogging with wood and fine sediments (Wellman et al. 2000; Wheeler et al. 2005). Because culverts are used to convey water under roads, they have potentially wide-ranging impacts on connectivity in urban streams, where road density is high (Elmore and Kaushal 2008; Cooney and Kwak 2013; Januchowski-Hartley et al. 2013). For example, on average only 36% of road crossings are fully passable to fish throughout the densely populated Great Lakes Basin of Canada and the USA (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

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species (Moore and Richardson 2003); therefore, maintaining their connection to the rest of the watershed is essential.

The effects of culverts on fish in small streams can manifest at multiple scales. At the broadest scale, culverts can reduce fish densities and diversity across entire streams (i.e., at the whole-stream scale). For example, a culvert that severs connectivity between different habitats can impede migrations needed for fish life cycles, and populations can subsequently decline throughout the stream network (Cote et al. 2009; Perkin and Gido 2012). In the case of diadromous fish, a culvert placed low in a watershed can reduce populations by isolating spawning areas from rearing habitats (Cote et al. 2009). At the within-stream scale, culverts can impact fish populations on either side of the culvert. For example, by impeding fish dispersal to upstream habitats, culverts can lead to decreases or extirpation of fish in those areas (Warren and Pardew 1998). Finally, at the local scale, the effects of culverts can be expressed in reaches and microhabitats. Deep pools with low to medium velocity can be created downstream of culverts by scouring, introducing a new microhabitat (Wellman et al. 2000). Alternatively, fine sediments may be deposited inside and downstream of the culvert (Wellman et al. 2000; Wheeler et al. 2005), reducing the quality of benthic habitat for fishes and invertebrates immediately downstream (Hawkins et al. 1983; Heggenes et al. 1991; Harper and Quigley 2000). In addition to impacts at a variety of spatial scales, culverts can also have varying effects on different species. Variability in fish population abundances between upstream and downstream sections can be driven by differences in swimming and leaping abilities for upstream passage (Nislow et al. 2011) or aversion to sections of high flows for downstream passage (Davis and Davis 2011).

A variety of measures can be 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 flows that help fish swim through them. The costs of baffles depend on culvert size, slope, and length, but they are typically US\$1000–8000 per culvert or on average 12.5% of the cost of culvert (Hansen et al. 2009). These costs are considerably lower than the median US\$30 000 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). Spoiler baffles are one type of design, composed of blocks arranged on the culvert bottom, which have been found to improve passage success for *Galaxias* spp. in Australia and New Zealand (Macdonald and Davies 2007; Feurich et al. 2012; Franklin and Bartels 2012). Weir baffles, another type of design, work by dividing culverts into cells. Weir baffles and their associated variants are simpler to design than other alternatives and are 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, the efficacy of rehabilitating fish passage through culverts with baffles, including weir baffles, remains unclear (Bernhardt et al. 2005; Moore and Moore 2013). Thus, there is a need to understand the array of consequences of altered connectivity by culverts for fish populations, as well as options for mitigation (Cooney and Kwak 2013).

The goal of our study was to investigate how culverts alter urban stream fish populations at the whole-stream scale, within-stream scale, and at local scales. We used a comparative study to infer effects of connectivity alteration by culverts because historical data are lacking on fish populations before and after culvert construction or their modification for fish passage rehabilitation. Specifically, we compared fish populations in three stream types:

those with (i) culverts without baffles or (ii) culverts with baffles and (iii) reference streams without culverts. We also considered time scales of change by including sites with baffles of various ages. We measured impacts in the following responses, hereafter referred to as “fish metrics”: fish density, fish biomass, and species richness. We had four principal hypotheses within our analytical framework. (1) Each of our selected response metrics would be significantly lower in stream types with culverts when compared with both streams with baffles in culverts and reference streams. This would provide evidence of whole-stream-scale impacts of culverts, perhaps because of habitat fragmentation driving stream-wide extirpation (Hanski et al. 1995). (2) Upstream habitats within culverted streams (and not reference streams) would have relatively lower fish densities, providing evidence of impeded dispersal acting on the within-stream scale. (3) Fish metrics at the local scale would show fine-scale spatial variation, providing evidence of microhabitat alteration due to culverts. (4) Whole-stream and within-stream fish metrics in stream types with baffled culverts would more closely resemble metrics in reference stream types, with time since rehabilitation indicating recovery of fish communities, as long-term processes such as recolonization or geomorphological changes take place. By considering both spatial and temporal patterns, important factors for the evaluation of rehabilitation (Roni et al. 2002; Suding 2011), we examine the impacts of culverts on fish distributions and, for the first time, their potential rehabilitation with weir baffles.

Materials and methods

Study sites

In British Columbia, Canada, there are an estimated 370 000 culverts (pipe or box structures that convey streams under roads), 76 000 of which are on fish-bearing streams (Forest Practices Board 2009). We carried out our study in the Lower Fraser River region of the greater Vancouver urban area, British Columbia, a region with a population of 2.3 million people (Metro Vancouver 2013). We sampled 26 streams (see online Supplementary material, Table S1¹) in the summer low flow season, between the dates of 6 July and 20 August 2012. We selected accessible, fish-bearing streams of similar size located in urban parks, residential areas, or commercial areas. Our selections were based on local knowledge of culvert locations and fish-bearing streams suggested by government employees and local stream stewards. In many cases, baffle installations occurred because of monitoring and efforts of stream stewardship groups; therefore, we relied on their local knowledge to select sites that had baffles installed and those without baffles that were potential candidates for future upgrades. All streams were in urban or suburban areas, with relatively high water velocities and no macrophyte presence and mean wetted width of 3.04 ± 1.49 m standard deviation (SD). Large wood was limited in study streams, which is typical in urban areas because of inhibited natural wood recruitment and direct wood removal by humans (Booth et al. 1997). All culverts were closed-bottom pipe or box structures and were predominantly free of natural substrates on the inside. We incorporated a mix of pipe and box structures in this study because both structures are widely used in the study area. Our study sites spanned multiple cities in a broad geographic area to correspond to our broad objectives of examining the effectiveness of baffles, and therefore different culvert types were unavoidable.

We used a spatial comparison with replication of stream types and sampling locations within streams to examine patterns among fish populations, culverts, and baffles, with a design similar to Mueller et al. (2011). At the stream level, we evaluated different stream types: streams with nonbaffled culverts ($n = 7$ streams),

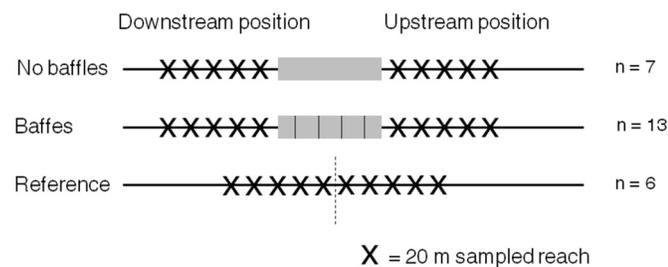
¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0199>.

Table 1. Culvert characteristics on nonbaffled and baffled stream types.

Stream	Shape	Length (m)	Slope (%)	Perch height (m)	Culvert material	Culverts DS	Constriction ratio	Baffles				
								Present	Spacing (m)	Pattern	Material	Year added
Dunlop	Box	18.4	0.5	0	C	1	0.64	–				
Eagle	Pipe	18.7	1.0	0	C	4	0.64	–				
Elgin	Pipe	27.3	2.0	0	CS	0	0.36	–				
Jacobson	Pipe	33.5	2.0	0.18	C	1	0.42	–				
Scott	Box	24.0	0.5	0	C	5	0.73	–				
Siegel	Pipe	38.9	4.0	0	CS	1	0.71	–				
Maple	Box	19.5	0.0	0	C	0	1.24	–				
Mossom	Pipe	39.0	2.5	0.20	CS	0	0.47	+	2.44	Wr	W	1976
Suter Brook	Box	50.6	1.0	0	C	0	0.88	+	3.37	OW	C	1995
Brothers	Box	31.2	4.5	0	C	0	0.60	+	2.08	OW	W	1997
Hadden	Box	109.0	3.0	0.18	C	0	0.78	+	2.42	OW	C	1997
Nelson	Box	76.7	2.5	0	C	0	1.32	+	2.74	OW	C	1999
Chantrell	Box	22.8	4.0	0	C	0	0.62	+	2.28	OW	C	2003
Stoney (b)	Pipe	57.4	2.0	0	C	1	0.42	+	4.78	Wr	W	2004
Yorkson	Pipe	92.0	3.0	0.27	CS	4	0.98	+	5.75	Wr	W	2004
Beecher	Pipe	30.5	3.0	0	C	2	0.35	+	1.79	Wr	W	2005
McLennan	Pipe	58.0	1.5	0.37	C	2	0.74	+	6.44	Wr	M	2007
Serpentine	Box	10.8	2.0	0	C	4	1.33	+	2.16	Wr	C	2007
Fergus	Pipe	76.0	4.0	0.62	CS	3	0.45	+	5.85	Wr	W	2010
Stoney (a)	Box	39.7	4.0	0.27	C	4	1.30	+	3.61	OW	C	2010

Note: W = wood, C = concrete, CS = corrugated steel, M = metal, DS = downstream, OW = offset weir, Wr = weir and Alberta fish weir. Two different study creeks were named “Stoney Creek” distinguished by “b” and “a”, in Burnaby and Abbotsford, respectively (see online Supplementary material, Table S1¹).

Fig. 1. Overview of study design. The dotted line crossing the reference site does not indicate the presence of any barrier; it refers to the grouping of variables for statistical analyses.



streams with baffled culverts ($n = 13$ streams), and reference (unculverted) streams ($n = 6$; Fig. 1). Within each stream, we sampled five consecutive 20 m reaches directly upstream and five consecutive 20 m reaches directly downstream of culverts (Fig. 1). We used 10 consecutive 20 m reaches in reference stream types as a comparison of potential natural gradients in fish assemblages (Wortley et al. 2013). The variable describing upstream and downstream location is referred to as “stream position”, and the specific 20 m reach of stream length is referred to as “stream reach”. Thus, there were five stream reaches within each stream position and two positions per stream. Reference stream types did not have culverts within or downstream of the study site, except Watkins and Partington creeks, which each had a three-barrel culvert downstream of sampling. However, the downstream three-barrel culvert of these two creeks apparently do not pose a fish passage impediment (Michalak 2004), because the three parallel open arch structures are large (~3 m diameter) and maintain channel width and contain natural substrates (unlike our study culverts). We collected various habitat and culvert measurements in each stream to examine physical variation among our study sites. 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 densiometer (Table S1¹). We measured elevation change (%) within the 20 m directly upstream and downstream of culverts with an Abney hand level, whereas for reference streams we measured this

elevation change in the two central reaches. We estimated the median sediment size (mm) in upstream and downstream positions across all reaches with haphazardly selected rocks ($n = 100$; Wolman 1954) measured across the axis perpendicular to the longest rock axis. When sites had culverts we noted shape, construction materials, and physical dimensions related to fish passage: width (or diameter), culvert length, culvert gradient, and perch height as measured by distance from the water surface at the culvert outflow to stream water surface (Table 1).¹ We calculated a stream width:culvert width ratio by dividing the mean stream width of reaches upstream of the culvert by width of the culvert at widest point, as described in Forest Practices Board (2009). We used Google Earth to count the number of road crossings downstream of the sample site assuming there was a culvert at each crossing. During early exploratory data analysis, we ruled out the above-mentioned culvert factors we measured from the remainder of the analysis, as they did not appear to have a clear effect on fish responses (not shown). To analyze time scales of rehabilitation, we researched the year that baffles were installed from municipalities (range: 1976–2010; Table 1).

Fish sampling

We used single-pass electrofishing to determine relative abundances and community measures of fish populations (Reid et al. 2009). We sampled a total of 100 m (5 m × 20 m; Fig. 1) of stream lengths in both stream positions, which was equivalent to the 30–40 stream widths recommended to capture diversity by single-pass electrofishing (Sály et al. 2009). We used a Smith Root LR24 Electrofisher assisted by one dip-netter with a 4.7 mm mesh dip net moving in an upstream direction. We did not use block nets because fish catchability tends to be high in small, shallow streams (Bohlin et al. 1989), and fish could not escape in an upstream direction, as they would soon become trapped in small pools or against large sediments. We recorded electrofishing effort in seconds per 20 m reach (Table S1¹). Upon capture, we lightly anaesthetized fish, identified the species, and collected measurements of length to the nearest 1 mm (fork length: *Oncorhynchus* spp.; total length: all other species) and mass to the nearest 0.01 g following Simon Fraser University approved animal care protocol. We recorded rainbow trout (*Oncorhynchus mykiss*) and cutthroat trout (*Oncorhynchus clarkii*) less than 70 mm long as generic “trout”

Table 2. Model terms included in mixed models that test whether physical conditions and fish responses vary by stream type and position.

Term	Fixed or random effect	Number and description of levels	Description	Interpretation
Stream type	Fixed	3 (nonbaffled, baffled, reference)	Tests the stream level effect of nonbaffled and baffled culverts and reference (unculverted) sites	A significant term would suggest impacts of culverts on the whole-stream scale. This could be due to severed connections between habitats needed for different life stages or a metapopulation effect, in which smaller habitat fragments increase risk of stream-wide extirpation.
Position	Fixed	2 (upstream and downstream)	Tests the effect of location relative to culvert or reference location	A significant term would suggest differences between upstream and downstream locations, perhaps owing to gradients in fish distributions.
Stream type × position	Fixed	6 (two positions each in three stream types)	Interaction to test whether responses in streams of each type vary between positions	A significant interaction term would suggest potential impacts of culverts or baffles at the within-stream scale. This pattern could be driven by impeded dispersal.
Individual stream	Random	26 streams	Accounts for random stream to stream variation at random intercept	—
Sediment size ^a	Fixed	Continuous	Accounts for negative relationship between fish abundance and sediment size	—

Note: Results of physical habitat models are shown in Table 3, and results of fish response models are shown in Table 5.

^aIncluded in fish response models only.

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.

For each of the 20 m reaches sampled, we computed relative densities ($n \cdot m^{-2}$) of the most abundant species: juvenile coho salmon (*Oncorhynchus kisutch*), cutthroat trout, rainbow trout, prickly sculpin (*Cottus asper*), and coastrange sculpin (*Cottus aleoticus*). We grouped together “trout” (cutthroat trout and rainbow trout) and “sculpin” (prickly sculpin and coastrange sculpin) because of their broadly similar life histories and because they gave qualitatively similar results separately (not shown). We also computed total fish density ($n \cdot m^{-2}$), total fish biomass ($g \cdot m^{-2}$), and species richness.

Statistical analysis

We used mixed-effects models to analyze the nested structure of our data. In our analysis, we identified factors for stream type and stream position with replication by reaches, which are nested within each stream position (Table 2). We analyzed the potential impacts of culverts at whole-stream and within-stream scales on physical variables and fish metrics by examining two main effects and their interaction. The first main effect was stream type (non-baffled culvert versus baffled culvert versus reference). Significant differences among stream types in response variables would indicate an effect of culverts and (or) baffled culverts at a given stream type (i.e., whole-stream scale). The second main effect we tested was position (upstream versus downstream). A significant stream position effect would suggest differences in a response upstream compared with downstream. Finally, we tested the interaction between stream type and position, which would provide evidence of potential impacts of culverts at the within-stream scale. We included a random intercept term for each individual stream to account for stream-specific variation (Table 2).

We visually examined residual plots for all our models to confirm the assumption of homoscedasticity in variance was not violated. We retained the fixed effects tested in our models, regardless of statistical significance. As such, we consider model parameter estimates 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 Development Core Team 2013) with the packages glmmADMB (Skaug et al. 2013) and nlme (Pinheiro et al 2013).

Physical variables

Prior to testing the effects of stream type and position on fish metrics, we conducted a two-part analysis to assess potential differences in physical characteristics of our study sites. First, we tested for differences in physical habitat conditions using linear mixed effects models (LMEs) with factors accounting for stream type, position, and the interaction between stream type and position, while accounting for individual stream differences by including a random intercept term for stream (Table 3). The random intercept term allowed us to account for random variation in other environmental variables between each stream. LMEs were used because data were normally distributed. Depth data were log-transformed to satisfy the assumption of normal residuals. Second, we used generalized linear mixed models (GLMMs) among stream types to test if fish responses were affected by physical variables commonly associated with fish distributions (Table 4). Specifically, we tested if fish densities were affected by 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). These analyses allowed us to determine whether we would need to formally account for the habitat differences in subsequent models. We specified Poisson error structure for species 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 for LME models with a normal error structure. To account for different areas sampled in each reach and to present count data as densities, models for each fish response included an offset term for reach area ($\log m^2$; except species richness model; O’Hara and Kotze 2010). Additionally, to account for variation among streams, we included a random intercept term for stream-specific effects.

Fish metrics at the whole-stream and within-stream scale

We assessed fish species densities, biomass, and species richness at the whole-stream and within-stream scale to test effects of

Table 3. Parameter estimates for linear mixed effect models (LMEs) examining habitat variation across stream types, positions, and the interaction between stream types and positions.

Response	Variable	Coefficient	SE	df	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 × upstream	-2.04	2.96	228	-0.69	0.491
Log depth	Reference × upstream	-1.93	3.50	228	-0.55	0.582
	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
Wetted width	Baffles × upstream	0.07	0.15	228	0.47	0.638
	Reference × upstream	0.28	0.18	228	1.52	0.130
	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
Sediment size	Upstream	-0.79	0.26	228	-3.10	0.002
	Baffles × upstream	0.85	0.32	228	2.69	0.008
	Reference × upstream	0.65	0.37	228	1.73	0.085
	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 × upstream	-9.17	2.35	228	-3.90	<0.001
	Reference × upstream	-16.20	2.78	228	-5.82	<0.001

Note: SE = Standard error, df = degrees of freedom. Responses examined were canopy cover (%), depth (cm), wetted width (m), and median sediment size (mm). Models included a random intercept term for stream. Coefficients represent relationship to the intercept, which represent conditions at nonbaffled culverts.

Table 4. Coefficient estimates for generalized linear mixed effects models (GLMMs) (fish densities ($n \cdot m^{-2}$), richness) and linear mixed effects models (LMEs) (log biomass ($g \cdot m^{-2}$)) examining fish responses to habitat variables.

Response	Variable	Coefficient	SE	z value	P
Coho salmon	Intercept	-2.741	0.522	-5.25	<0.001
	Sediment size	-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	Intercept	-2.367	0.507	-4.66	<0.001
	Sediment size	-0.006	0.003	-1.83	0.068
	Canopy cover	-0.006	0.006	-1.10	0.271
Sculpin	Depth	0.013	0.007	1.72	0.085
	Intercept	-9.173	1.811	-5.07	<0.001
	Sediment size	0.037	0.014	2.53	0.011
Total fish	Canopy cover	-0.005	0.007	-0.71	0.476
	Depth	0.011	0.012	0.89	0.371
	Intercept	-1.316	0.296	-4.45	<0.001
Total biomass	Sediment size	-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
Richness	Intercept	3.583	0.425	8.43	<0.001
	Sediment size	0.002	0.002	1.23	0.221
	Canopy cover	0.002	0.005	0.48	0.632
	Depth	0.013	0.007	1.74	0.082
	Intercept	-3.059	0.305	-10.03	<0.001
	Sediment size	-0.004	0.001	-3.54	<0.001
	Canopy cover	0.000	0.003	0.06	0.951
	Depth	0.009	0.005	1.81	0.071

Note: SE = standard error. All models include a random intercept for stream-level effects and an offset (log m^2 , except richness) to account for different areas in each reach.

culverts and baffles. For individual species counts (coho, trout, and sculpin) we used GLMM; for aggregate fish responses we used a combination of GLMM (total fish counts, species richness) and LME (biomass; Table 5). We modelled each fish response as a function of stream type, stream position, an interaction of stream type and position, a random intercept for stream-level effects, reach area (log m^2) offset, and median sediment size (because sediments

were found to influence fish; Table 4; Table 5). We fitted a simpler model for sculpin data without specifying the interaction between stream type and position because of high prevalence of zero values and lack of model convergence.

In addition, because the prior analyses considered species densities separately and did not examine assemblages, we used multivariate statistics to depict changes at the community level. We

Table 5. Coefficient estimates for generalized linear mixed effects models (GLMMs) (fish densities ($n \cdot m^{-2}$), richness) and linear mixed effects models LME (log biomass ($g \cdot m^{-2}$)) examining fish metrics across stream types and positions.

Response	Variable	Coefficient	SE	z value	P
Coho salmon	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
	Sediment size	-0.02	4.35×10^{-3}	-3.5	<0.001
	Baffles \times upstream	-0.12	0.19	-0.6	0.546
	Reference \times upstream	-0.39	0.25	-1.58	0.115
Trout	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
	Sediment size	-3.94×10^{-3}	2.87×10^{-3}	-1.37	0.170
	Baffles \times upstream	0.08	0.22	0.35	0.725
	Reference \times upstream	0.27	0.32	0.86	0.390
Sculpin	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
	Sediment size	0.02	0.01	1.78	0.076
	Baffles \times upstream	-0.15	0.15	-1.01	0.310
	Reference \times upstream	-0.04	0.18	-0.21	0.830
Total fish	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
	Sediment size	-3.15×10^{-3}	2.06×10^{-3}	-1.52	0.130
	Baffles \times upstream	-0.15	0.15	-1.01	0.310
	Reference \times upstream	-0.04	0.18	-0.21	0.830
Total biomass	Intercept	-6.96×10^{-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
	Sediment size	-7.17×10^{-4}	2.19×10^{-3}	-0.33	0.740
	Baffles \times upstream	-0.14	0.25	-0.57	0.570
	Reference \times upstream	-0.02	0.29	-0.08	0.940
Richness	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
	Sediment size	1.25×10^{-4}	1.10×10^{-3}	0.11	0.910
	Baffles \times upstream	-0.04	0.18	-0.2	0.840
	Reference \times upstream	0.21	0.22	0.98	0.330

Note: SE = standard error. Models include an offset for reach area ($\log m^2$, except richness) and a random intercept for stream-level effects. The intercept represents default values of fish counts for the downstream, nonbaffled stream type. Sediment size was included as a fixed effect to account for the association between stream type and sediment size (Table 3) and its influence on fish (Table 4). Because sculpin data were sparse, we fit a simpler model without specifying the interaction between stream type and position for sculpin data.

calculated Bray–Curtis dissimilarity indices based on mean fish abundances in each upstream and downstream position within each stream. We used permutational analysis of variance (PERMANOVA; Anderson 2001) to test for differences in fish assemblages between stream types and positions based on rank dissimilarities from the Bray–Curtis dissimilarity matrix with 9999 permutations. Using non-metric multidimensional scaling (nMDS) ordinations, we visualized how assemblages differed between stream types and positions. The assemblage analyses were performed using the vegan package (Oksanen et al. 2013) in R (R Development Core Team 2013).

Local-scale and baffle age effects

We tested if the distance from baffled culverts affected biomass and fish size at local scales near baffled culverts. We constructed GLMMs for each stream type by analyzing total biomass and fork length of trout as a function of reach distance from culvert (categorical: 10 bins of 20 m), an offset term for reach area, and a random intercept for stream-level effects. We performed the analyses on each stream type separately, rather than making one

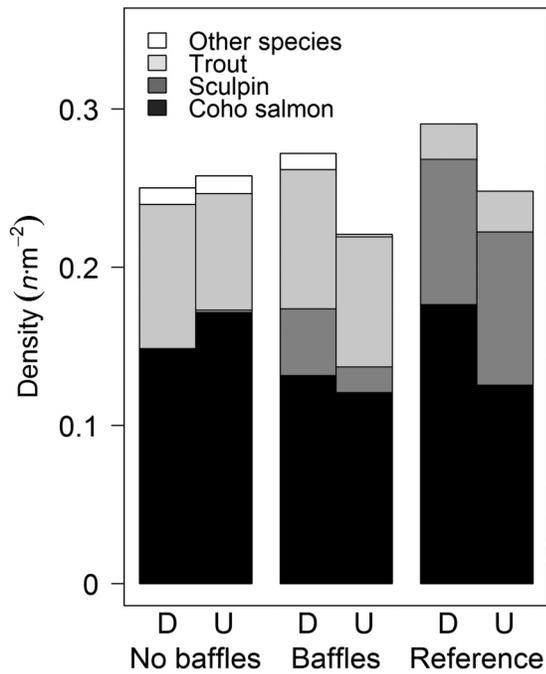
model that included a stream type factor, to simplify interpretation of the model output (Table S2¹). Although we performed this analysis on all our fish metrics, we present total biomass and trout size because we were primarily interested in whether areas near scoured outlet pools had more fish and larger fish (Wellman et al. 2000).

Finally, to consider the influence of time on potential rehabilitation with baffles, we explored how baffle age related to species richness. We used GLMM with species 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.

Results

We caught 3581 fish, comprising eight species in the 26 streams. We sampled $652 \pm 249 m^2$ SD per stream and caught 4.3 ± 1.2 SD species per stream on average. Juvenile coho salmon were the most abundant species, comprising 51% of fish captured, followed

Fig. 2. Mean species densities of species across stream types and positions. Grouped species are “trout” (cutthroat trout and rainbow trout), “sculpin” (prickly sculpin and coastrange sculpin), “other” (longnose dace, threespine stickleback, larval Pacific lamprey) as described in main text. U = upstream, D = downstream.



by trout at 29% (15% trout <70 mm, 10% cutthroat trout >70 mm, 4% rainbow trout >70 mm), coastrange sculpin (15%), and prickly sculpin (4%; Fig. 2). The remaining fish captured were composed of 16 longnose dace (*Rhinichthys cataractae*), 62 threespine stickleback (*Gasterosteus aculeatus*), and 15 larval lamprey (likely Pacific lamprey, *Entosphenus tridentatus*; McPhail and Carveth 1994).

Physical variables

We found that the physical characteristics among and within stream types differed among the factors we measured (Table 3). Reference stream types had on average 11.3% less canopy cover than culverted streams (LME: $\beta = -11.33$, standard error (SE) = 5.00, degrees of freedom (df) = 23, $t = -2.27$, $P = 0.033$). Mean depth was similar across positions and stream types. Wetted width upstream of culverts was 0.8 m narrower compared with downstream in nonbaffled stream types (LME: $\beta = -0.79$, SE = 0.26, df = 228, $t = -3.10$, $P = 0.002$). Also, upstream wetted width was 0.9 m wider compared with downstream when there were baffles (LME: $\beta = 0.85$, SE = 0.32, df = 228, $t = 2.69$, $P = 0.008$). Reference stream types had on average the largest sediments (LME: $\beta = 60.18$, SE = 25.24, df = 23, $t = 2.38$, $P = 0.026$). Sediment sizes also varied within stream types. Specifically, in nonbaffled stream types, median sediment size was on average 11.8 mm larger upstream relative to downstream positions (LME: $\beta = 11.78$, SE = 1.91, df = 228, $t = 6.18$, $P < 0.0001$). In contrast, in baffled stream types, median sediment size was on average 9.2 mm smaller upstream relative to downstream (LME: $\beta = -9.17$, SE = 2.35, df = 228, $t = -3.90$, $P < 0.0001$).

Median sediment size was the only variable that influenced our various fish responses (Table 4). Coho salmon density and species richness was negatively associated with increasing sediment size (coho salmon GLMM: $\beta = -0.014$, SE = 0.004, $z = -3.65$, $P = 0.0003$; richness GLMM: $\beta = -0.004$, SE = 0.001, $z = -3.54$, $P = 0.0004$). Conversely, sculpin densities were positively associated with sediment size (GLMM: $\beta = 0.036$, SE = 0.014, $z = 2.53$, $P = 0.011$).

Fish metrics at the whole-stream and within-stream scale

The effect of culverts was species-dependent after accounting for differences in sediment sizes. Coho salmon densities were highly variable and not significantly associated with stream type, position, or the stream type \times position interaction term (Fig. 3; Table 5), contrary to our predictions. Sediment size, the only significant predictor of coho salmon densities, had a negative association with coho salmon densities.

Trout densities were on average 68% lower in reference stream types than in nonbaffled culvert stream types (GLMM: $\beta = -1.14$, SE = 0.44, $z = -2.62$, $P = 0.009$; Fig. 3; Table 5), evidence of a whole-stream-scale positive association between trout and culverts. There was no difference in trout densities between stream types with baffled and nonbaffled culverts (GLMM: $\beta = 0.25$, SE = 0.33, $z = 0.75$, $P = 0.456$) and no significant effect of stream position on trout densities (GLMM: $\beta = -0.13$, SE = 0.18, $z = -0.69$, $P = 0.491$). A nonsignificant stream type \times position interaction indicated that while densities of trout differed across stream types, there was no evidence of within-stream-scale impacts of culverts.

Sculpin densities were strongly negatively associated with baffled and nonbaffled culvert stream types. There were on average 90 times more sculpin in reference streams compared with nonbaffled culvert sites (GLMM: $\beta = 4.50$, SE = 2.22, $z = 2.03$, $P = 0.043$; Fig. 3; Table 5) and no statistical difference between baffled and nonbaffled stream types (GLMM: $\beta = 1.56$, SE = 1.91, $z = 0.82$, $P = 0.415$). Upstream positions had on average 44% less sculpin, regardless of stream type (GLMM: $\beta = -0.57$, SE = 0.18, $z = -3.19$, $P = 0.001$). Thus, sculpin were much more abundant in reference stream types, and across all stream types their densities systematically decreased in upstream versus downstream positions, even after accounting for sediment size. The interaction between stream type and position could not be tested (only in the case of sculpin; see Materials and methods).

Although effects of culverted stream types were species-specific, stream type did not significantly influence total density ($n \cdot m^{-2}$), biomass ($g \cdot m^{-2}$), or species richness (Fig. 4; Table 5). There was no significant effect of stream position and no significant interaction between stream type and position on these response variables after controlling for sediment sizes. Analyses of fish community patterns using PERMANOVA indicated variability among stream types, but not between upstream and downstream positions or between the interaction of stream type and position (Fig. 5). Specifically, fish communities were significantly different across stream types ($F_2 = 3.21$, $P = 0.002$), but not significantly different as a function of stream position ($F_1 = 0.46$, $P = 0.82$) nor for the interaction between stream type and stream position ($F_2 = 0.18$, $P = 0.99$).

Local-scale and baffle age effects

We found evidence of local-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 ($g \cdot m^{-2}$) compared with the other reaches (GLMM: $\beta = 0.66$, SE = 0.33, $z = 2.04$, $P = 0.042$; Fig. 6; Table S2¹). This was likely 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 than in other reaches (LME: $\beta = 46.17$, SE = 13.20, $z = 3.50$, $P < 0.001$).

There was a significantly positive relationship between the age of baffles in streams and fish species richness (GLMM: $\beta = 0.021$, SE = 0.008, $z = 2.69$, $P = 0.007$; Fig. 7). Specifically, all reaches with only one species were found in streams with recent baffles (<10 years), while reaches with older baffles (>10 years) had two or more species. Stream position did not significantly affect the positive relationship between baffle age and species richness, suggesting that rehabilitation with baffles may have impacts that manifest at the whole-stream scale.

Fig. 3. Boxplots showing individual species densities across stream types and upstream and downstream positions. Note that y-axis scales differ among graphs. Abbreviations are as follows: -Baf = no baffles ($n = 7$), +Baf = baffles ($n = 13$), Ref = reference ($n = 6$). Significant across-stream type differences are marked above the bars with “a”, while significant within-stream (upstream versus downstream) differences are marked above the bars with “b”. Thick horizontal lines represent medians, and whiskers extend to 1.5 times the interquartile range. Points outside of this range (outliers) are shown with open circles.

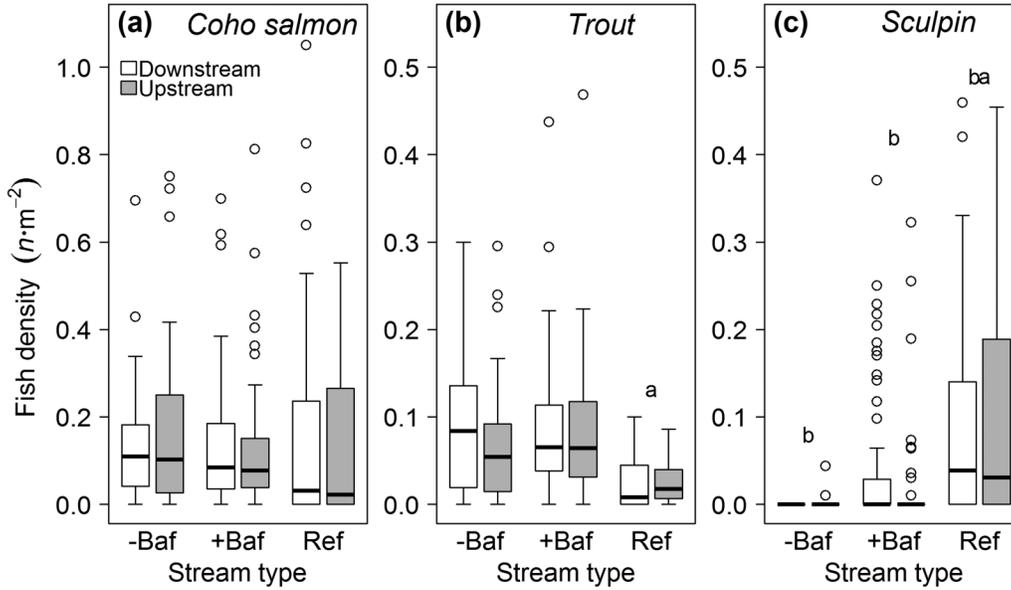
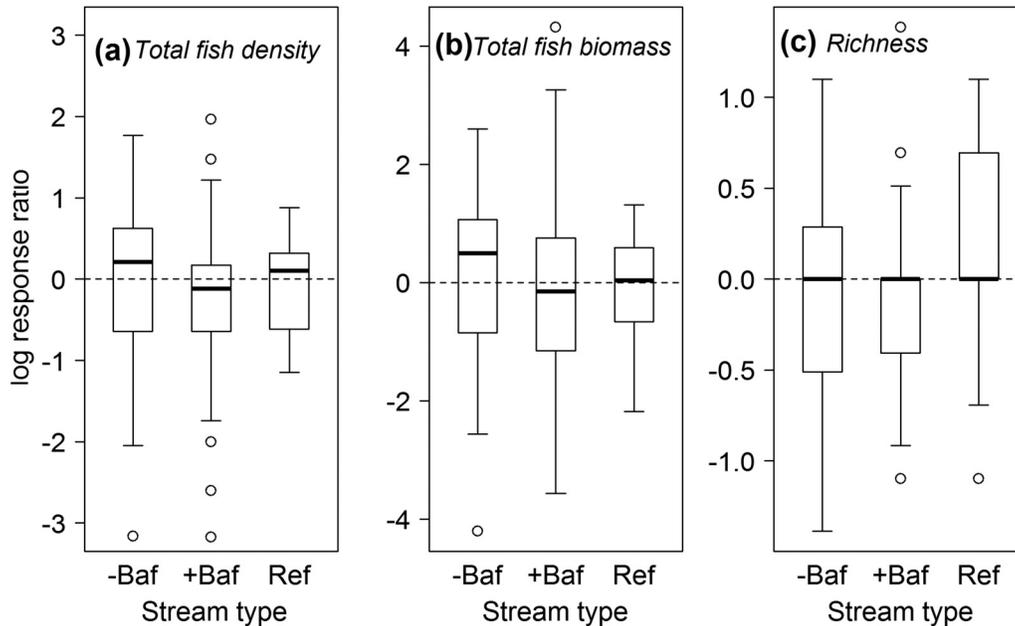


Fig. 4. Natural log response ratio by stream type for (a) total fish density ($n \cdot m^{-2}$), (b) total biomass ($g \cdot m^{-2}$), and (c) species richness per reach. Abbreviations are as follows: -Baf = no baffles ($n = 7$), +Baf = baffles ($n = 13$), Ref = reference ($n = 6$). Each bar represents the response between paired positions (upstream and downstream) in the same stream. Values greater than zero mean that there are more fish or higher biomass or richness upstream versus downstream. Thick horizontal lines represent medians, and whiskers extend to 1.5 times the interquartile range. Points outside of this range (outliers) are shown with open circles.



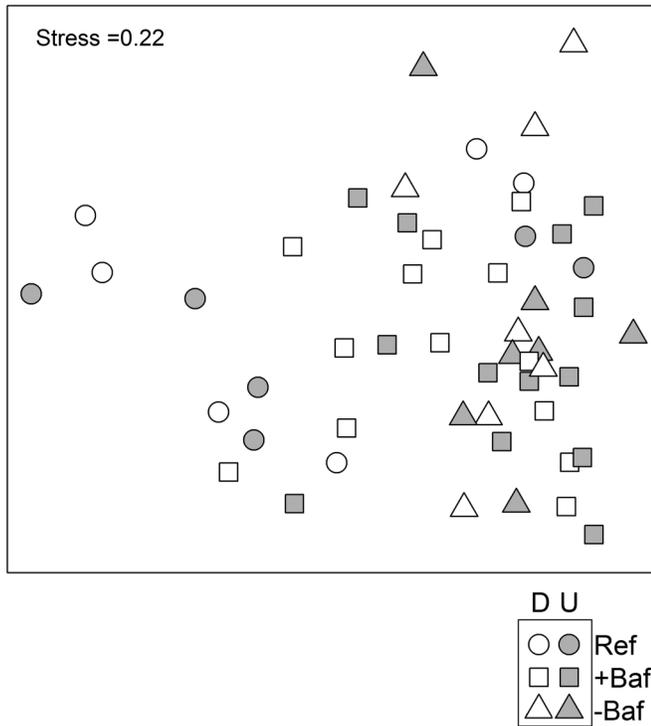
Discussion

We used a comparative approach to examine the impacts of culverts and their rehabilitation on stream fishes, quantitatively accounting for habitat differences among stream types. We found differences in physical habitat among reference and culverted stream types, most notably due to larger sediment sizes in reference streams. Larger sediment size was negatively associated with total fish densities, species richness, and coho salmon density and

positively associated with sculpin density. Previous research has also found that 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). After accounting for the effect of sediment size in our analysis, we found that culverts had species-specific effects at whole-stream scales. This result was corroborated by our fish assemblage analysis that found a significant effect of the stream type variable on fish com-

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Fig. 5. Nonmetric multidimensional scaling ordinations (nMDS) of fish assemblages for all study streams. The stress level represents the accuracy at which the ordination captures the multidimensional similarity matrix in two dimensions. Abbreviations for stream type are as follows: -Baf = no baffles, +Baf = baffles, Ref = reference; and abbreviations for stream position are as follows: U = upstream, D = downstream. Points closer to each other represent fish communities that are more similar in multidimensional space.



munities but not stream position or the interaction of the two terms.

Species densities varied in response to culverted stream types for cutthroat trout and rainbow trout and for prickly sculpin and coastrange sculpin, providing evidence of fragmentation effects acting on both sides of culverts (whole-stream scale). Trout density was on average 68% lower in reference stream types compared with baffled and nonbaffled culvert stream types. Whereas the positive association between culverts and trout density in our study occurred at the whole-stream scale, a previous study found within-stream-scale patterns of rainbow trout, where densities were higher upstream of culverts compared with downstream (MacPherson et al. 2012). The suggested mechanism for within-stream impacts was that culverts facilitated trout density increases by preventing upstream access to burbot (*Lota lota*), a weak-swimming but major competitor and predator (MacPherson et al. 2012). In our study, where culverted stream types (baffled and nonbaffled) both had lower overall densities of sculpin, it could be possible that trout are released from interspecific competition and predation (of eggs and juvenile trout) because of sculpin (Hunter 1959). In our reference streams, coastrange sculpin and prickly sculpin species densities were on average 90 times higher than in baffled and nonbaffled culvert stream types. This result corroborates previous findings of sculpin being more prevalent in sites without culverts (MacPherson et al. 2012). MacPherson et al. (2012) found that 69% (22 out of 32) of reference sites had spoonhead sculpin (*Cottus ricei*), while only 12% (6 out of 51) of culvert sites had spoonhead sculpin. Because fish from the genus *Cottus* are weak swimmers (LeMoine and Bodensteiner 2014), it is likely that fragmentation effects, expressed as overall declines for cul-

verted stream types, may occur at lower thresholds of connectivity loss than for other species. Thus, sculpin may prove to be a particularly effective indicator taxon for stream connectivity. Overall, our results support the hypothesis that culverts can impact fish at the whole-stream scale.

We found that sculpin responded to the effect of stream position, evidence of within-stream effects. On average, sculpin densities declined by 43% upstream relative to downstream positions; however, this was true across all stream types. Because of the strong negative effect of culverts on sculpin, there were too few sculpin data to test the stream type × position interaction owing to lack of model convergence. However, none of the other fish metrics responded to the stream position effect, nor to the interaction between stream position and stream type. For example, trout densities had no statistical difference between upstream and downstream reaches, regardless of whether baffles had been installed. Previous studies have found strong decreases upstream of culverts for densities of brook trout (*Salvelinus fontinalis*) and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; (Burford et al. 2009; Pépino et al. 2012). These decreases only occurred with >3% culvert slope and >0.61 m culvert perch (Pépino et al. 2012) or >4.5% culvert slope and >0.2 m culvert perch (Burford et al. 2009), respectively. Many of our culvert study sites had combinations of lower values for slope (mean = 2.4% ± 1.3% SD) and culvert perch (mean = 0.1 ± 0.2 m SD); therefore, it remains possible our study culverts remained passable to trout.

We detected significant effects of baffles at the local scale (i.e., 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, but not in nonbaffled culverts. This pattern of higher biomass near a baffled culvert outflow was likely driven in part by large-bodied cutthroat trout and rainbow trout. Deep pools with low to medium velocity can be created downstream of culverts by 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 had been rehabilitated within the last 10 years, and sites that had been rehabilitated with baffles greater than 10 years all had at least two species. This pattern of higher species richness with increasing time since rehabilitation occurred at the whole-stream level (i.e., both upstream and downstream of culverts). This suggests that rehabilitation of culverts may lead to stream-wide increases in diversity over long time periods, 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.

Culverts are known to restrict distribution of migratory salmonids (Davis and Davis 2011), yet we found that coho salmon juveniles were distributed across all stream types and stream positions. Specifically, we did not detect an effect of stream type, position, or a stream type × position interaction on coho salmon juveniles in our analysis. 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). Further, coho salmon juveniles may congregate, particularly in reaches directly upstream of culverts in avoidance of downstream migration through culverts (Davis and Davis 2011), likely because of aversion of fast downstream flow conditions created at culvert inlets (Kemp et al. 2005, 2008). Patterns of coho salmon distribution should be interpreted cautiously, as they may also have been influenced by hatchery releases in study creeks. Releases of hatchery coho salmon took place upstream of some culverts, but it was difficult to gather rigorous data on releases. Programs to mark some hatchery

Fig. 6. Top panels: total biomass ($\text{g}\cdot\text{m}^{-2}$) by reach position: (a) streams with no baffles, (b) streams with baffles, (c) reference streams. Bottom panels: maximum fork length of rainbow or cutthroat trout in each stream reach: (d) streams with no baffles, (e) streams with baffles, (f) reference streams. The dotted midline signifies aggregate median for all reaches in the given stream type, and thin vertical line signifies the midpoint between positions (and location of culvert if applicable). Asterisks indicate significance at $P < 0.05$. Note the logged y axis on panels a-c.

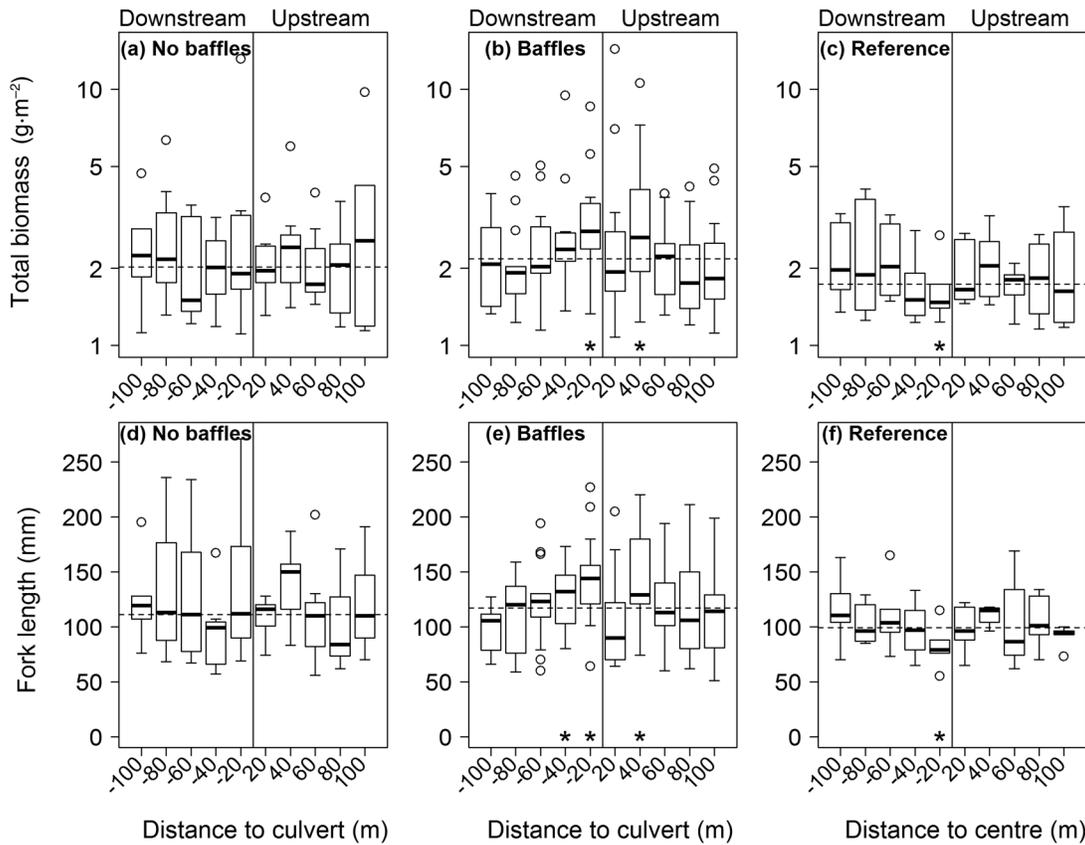
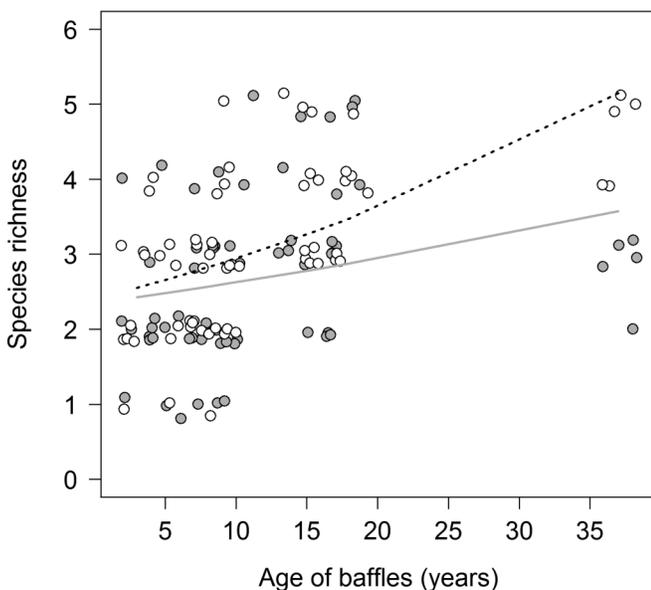


Fig. 7. Species richness versus age of baffles for reaches downstream (open circles, dotted line) and upstream (gray circles, solid line) of baffled culverts. Lines, which did not differ significantly, represent mean increase in species richness versus time as predicted by a generalized linear mixed effects model that accounts for random intercept effect of stream. A slight jitter was added to the points to avoid overlap.



salmon with adipose fin clips exist, but we did not encounter any marked coho salmon despite the apparent presence of hatchery inputs. Coho salmon passage through baffled and nonbaffled culverts in both directions in field conditions warrants further study with consideration of hatchery release locations.

Our study builds on understanding the potential impacts of culverts in streams, but it should be borne in mind that stream types (reference, baffled culvert, nonbaffled culvert) were not randomly assigned, as this was a large-scale and comparative study rather than an experiment. While models did account for differences in important habitat variables, namely sediment, and we tried to control for habitat differences in site selection, it is possible that other unmeasured habitat variables may be contributing to differences detected in fish populations across stream types. Furthermore, it was unavoidable that different streams had different sized and designed culverts, which may have contributed to variation within each stream type. In addition, we conducted this study in summer low flow seasons. Since passability of culverts may change in relation to flow (Bouska and Paukert 2010), it would be interesting to test their effects year-round. These types of challenges are common to large-scale studies such as ours that examine patterns rather than mechanisms.

The efficacy of baffles to rehabilitate fish passage in culverts depends on time and aspect of fish population or community of interest (e.g., fish density, species richness). While we found species richness increased through time since baffle construction, there were no other significant responses in our other fish metrics to baffles, nor were there significant stream type \times position interactions. Managers in British Columbia do not recommend baffles for new culvert installations because of the complex biological

and engineering input for designs and high maintenance costs to prevent debris clogs (BC Ministry of Forests, Lands and Natural Resource Operations et al. 2012). Yet, because baffles can be retrofitted into existing culverts, they remain an attractive rehabilitation option. Some success in spoiler baffles has been measured in field conditions for *Galaxias* spp. (Macdonald and Davies 2007). To date, ours is the first published field study that examines the effectiveness of weir baffles as a rehabilitation measure in North American culverts. As such, managers and restoration practitioners are left with inadequate information to decide if retrofitting culverts with baffles warrants further consideration as a rehabilitation 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.

Relative to reference streams, culverts were associated with higher trout densities and lower sculpin densities across both upstream and downstream positions. These findings suggest that fragmentation of habitats and populations acted on a whole-stream scale rather than being restricted to within-stream differences that related to position. The use of baffles did not influence the patterns associated with culverts. However, proximity to baffled culvert outlets was associated with higher biomass and larger trout, likely because of habitat alteration by culverts acting on a local scale. Together, these results indicate that assessment of stream impacts and rehabilitation should consider responses at various scales. Additionally, it is advantageous to include comparisons to reference sites for clearer understanding of impact and recovery trajectories. While our data suggest that culverts drive whole-stream shifts in fish populations, rehabilitation efforts with baffles may restore species richness at whole-stream scales as well, over decade-long time periods.

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